Behavioural Ecology of New Zealand Invasive Rodents (*Rattus norvegicus* and *Mus musculus*): Implications for Rodent Control

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FRONTISPIECE

Walter: And let's also not forget… let's not forget, Dude… that keeping wildlife, an amphibious rodent, for uh, domestic, you know, within the city… that isn't legal either.

Dude: What're you, a fucking park ranger now?

(Ethan and Joel Coen, “The Big Lebowski”)

ABSTRACT

Biological invasions are natural phenomena that have occurred throughout the natural history of earth. The highly negative context of the term biological invasion is associated with the fact that many modern invasive processes are anthropogenically driven. Indeed, human affiliated invasions are among the primary drivers of the current biodiversity crises. Murid rodents (Rodentia: Muridea) of the genus *Rattus* and *Mus* have become among the worst vertebrate invasive species and apart from man are the most widespread mammals on earth. Invasive rodents have severe and negative effects on human health, agricultural systems, and natural environments. The practice of rodent control is extensive and substantial attempts are made to decrease rodents' severe impacts on the environment. However, although these attempts are largely successful, there are still issues in the control of invasive rodents and new methodologies, whether at a macro or micro scale are actively pursued.

Behavioural conservation attempts to understand and improve conservation processes and practices through the study of animal behaviour. Indeed, it is becoming increasingly apparent that the behaviour of animals can be a strong tool for conservation. The control of invasive species has the goal of reducing predatory or competition pressure on species of conservation concern and advocates for behavioural conservation acknowledge the importance of behavioural studies of invasive species that can directly benefit or inform control measures. In this thesis, I explore several aspects of behavioural ecology in the Norway rat *R. norvegicus* and the house mouse, *M. musculus*, with the overarching aim of informing and improving rodent control.

I conducted a series of laboratory and field experiments focused on rodent behaviour and pest control. 1) I tested whether laboratory rats can act as effective lures for wild Norway rats and hence overcome the problem of rats avoiding food baits. This field experiment was based on the highly social behaviour exhibited by this species. I found that live traps containing live lures were significantly more effective than those with food baits at capturing wild Norway rats. In a second series of tests, I found that live lures were more efficient than food baits at attracting rats to kill traps. A study of radio-collared rats released onto a rat-free island produced inconclusive but promising results on the potential of live lures to be used to control incursions. I suggest that the use of laboratory rats as lures should be considered as an additional tool for use in future pest control management plans for invasive Norway rats. 2) I used Y-maze laboratory experiments to examine the attractiveness of urine from mice fed high and low protein diets to male and female wild mice, whether the protein content of the diet of mice affected their response and the strength of attraction of wild mice towards wild and laboratory live lure conspecifics of the opposite sex. I found that mice preferred to spend more time close to urine from donors that had eaten a high protein diet, that mouse strain did not affected conspecific attraction and that males were more active than females toward the urine of the opposite sex. These results may have implications for improving mouse capture and control. 3) I assessed the impacts of mammalian odours (specific direct cues of predation or competition) and illumination intensity (a general indirect cue of predation) on the foraging of free-ranging mice that are naïve to mammalian predators, using feeding trials in the field. Here I found that phases of the moon, but not odour, had significant effects on mouse foraging behaviour. I suggest that repeating the study over multiple lunar cycles is required to confirm this influence and, if confirmed, recommend coordinating management

efforts according to the phases of the moon to improve mouse bait take and reduce bait wastage. 4) I tested for the responces of rat-naïve mice to scent cues from rats, which are competitors and potential predators in laboratory experiments, in a Y-maze apparatus. Mice behaviours revealed unexpected differences in male and female responces to rat scent. Male mice showed preference to control over rat scented food trays, while females were indiference in their preferation or even prefered rat scented food trays over control ones. These sex-based differences can suggest that males and females might be under different evolutionary pressures in regard to novel scents. 5) I looked at macronutrient selection in wild caught mice, under controlled laboratory conditions. I found that mice consumed more of diets with a high carbohydrate/protein ratio, but were highly generalist and opportunistic feeders, in general prioritising energy over macronutrients. These results demonstrate that the pattern of macronutrient selection is sensitive to ecological circumstances, and associates an opportunistic strategy with successful invasion by a small mammal in a temperate environment.

The understanding and improvement of conservation practices directly through the study of animal behavioural processes is an emerging and rapidly growing science, but relatively little attention is given to the benefits that we can draw from incorporating and understanding of invasive species behaviour into their control. To maintain an effective and continuous control of invasive species, managers need comprehensive knowledge of the behaviour of the species they target. This can be achieved only through targeted behavioural research of invasive species that is directed at improving pest control. In this thesis I have attempted to do just this.

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"One of the symptoms of an approaching nervous breakdown is the belief that one's work is terribly important".

(Bertrand Russell)

I had my semi nervous breakdown at the end of the first year of my PhD. Luckily, my children Omer and Alma, who were born during this PhD have knocked me back to my senses. This thesis is dedicated to them with love.

First and foremost I would like to thank my supervisors. To Dianne Brunton, the principle supervisor, who told me to come over from Israel after one email correspondence, and always made sure I had everything I needed. Hopefully she doesn't regret placing my desk just next to her office, an act that resulted in countless knocks upon her door... Nonetheless, all my visits were met with a smile! To the one and only Uri Shanas, who after supervising my MSc in Israel, (understandably) had to send me to the most far away place possible, but still provided professional and emotional support. And to David Raubenheimer, who was last to jump aboard but nevertheless delivered significant scientific perspectives and new research directions. Not to mention the mutual respect we share for the Dude… I have learned much from you all!

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I would like to further dedicate this PhD to my grandmother Zehava Teper (passed away 2013), my aunt Chava Dovrovni (passed away 2011) and my friend Einav Brill (passed away 2011). My they rest in peace.

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CHAPTER 1: INTRODUCTION

1.1. Biological invasions

"Invasion: invading or being invaded. Invasive: making invasion, *aggressive*" (Hornby et al. 1963). Aggressiveness is probably the most common action associated with invasion and to cite Davis (2009), "[the field of invasion biology] would have been much better off had it [the term invasion] never been adopted, along with its accompanying military metaphors". However, we cannot overlook the fact that many invasions do have devastating consequences for local species, populations, communities and even ecosystems; a fact demonstrated by anthropogenic invasions alone (Crosby 1986). Biological invasions are regarded as one of the most important drivers in the loss of native biological diversity and of species homogenization (Meffe & Ronald 1997; Lockwood et al. 2007; Davis 2009; Primack 2010).

Biological invasions are a natural phenomenon. Based on discussions of scientific terminology, Reise et al. (2006) defined biological invasion as "any process of [species] colonisation and establishment beyond a former range, particularly in which a species plays a conspicuous role in the recipient ecosystems". Indeed, biological invasions have occurred (and still do) as a natural process throughout the history of life, for as long as there have been suitable places to inhabit (Lockwood et al. 2007; Davis 2009). The highly negative connotation associated with the term biological invasion has likely arisen because many modern invasive processes are anthropogenically driven (Elton 1958; Meffe & Ronald 1997; Primack 2010). These events can be referred to as introductions and defined as "a deliberate or accidental transfer or release of organisms into the open environment by human activities

across natural barriers of dispersal" (Reise et al. 2006). It should be emphasized that these introduced organisms are new species to these environments.

For the purpose of this thesis and the species it studies, the terms *invasive* and *introduced* are applied in relation to the unintentional spread of organisms with the aid of human agents. Invasive species have significant, well documented and, by definition, negative effects on natural ecosystems, agricultural systems and/or human health and economics (Elton 1958; Meffe & Ronald 1997; Perrings et al. 2000; Long 2003; Simberloff 2003; Olson 2006; Crowl et al. 2008; Davis 2009; Pejchar & Mooney 2009; Primack 2010). As a result, attempts to control invasive species occur across all fronts. However, as control of invasive species involves their destruction, debates are ongoing over our rights to actively do so (see review by Simberloff 2003). In my view the debate surrounding the use of control measures against invasive species is a *moral* not a *scientific* decision, and as such, cannot be rationalized. If we *decide* to *value* our native biota, then control actions must be made. We should not forget however, that by far the worst invasive species (and the one from which all other "unnatural" invasions are driven) is *Homo sapiens*.

1.2. Invasive rodents

Few rodent species have become invasive worldwide (Long 2003), but four murid rodents (Rodentia: Muridea) of the genera *Rattus* and *Mus* have become among the worst vertebrate invasive species, and apart from man are the most widespread mammals on earth (Long 2003). With the exception of the Kiore or Pacific rat *Rattus exulans* (Peale, 1848), carried as a food source with Polynesian voyages and thus intentionally spread across the South Pacific

(Wodzicki & Taylor 1984), the other three invasive murid species are mostly self or accidental introductions.

The black or ship rat *R. rattus* (Linnaeus, 1758) and the house mouse *Mus musculus* (Linnaeus, 1758), likely originated in the Indian subcontinent (Innes 2005a; Ruscoe & Murphy 2005). The brown or Norway rat *R. norvegicus* (Berkenhout, 1769) likely originated in the temperate regions of Asia (Lindsey & Baker 2006). All three species were either associated with the spread of human settlements throughout Euro-Asia or dispersed later as stowaways on European ships across the world. Rats and mice are generalists and thus highly adaptable. They exhibit a short reproductive cycle and high dispersal capacity (Berry 1970; Nowak 1999; Long 2003; Atkinson & Towns 2005; Innes 2005b, a; Ruscoe & Murphy 2005), are omnivorous with extremely broad diets (Berry 1970; Nowak 1999; Long 2003; Ruscoe & Murphy 2005; MacKay 2010) and, when they have access to sufficient shelter and food resources, can survive in both hot and cold environments (Long 2003). Rodents are active learners (Berry 1970; Aisner & Terkel 1992; Galef & Allen 1995; Galef 2005), and highly commensal with humans. All of the above contribute to their remarkable potential for invasiveness and indeed between them, the four species have now established populations in all but the most extreme habitats (Long 2003).

Invasive rodents have severe and negative effects on human health (Epstein 1995; Mills & Childs 1998; Meerburg et al. 2009a), agricultural systems (Meyer 1999; Stenseth et al. 2003; Meerburg et al. 2009b) and natural environments (Atkinson 1978; Campbell 1978; Ramsay 1978; Cuthbert & Hilton 2004; Gibbs 2009; Simberloff 2009; St Clair 2011). Being so widespread means that invasive rodents are of global concern as is the efforts for their control (Meehan 1984; Parkash 1988; Long 2003).

1.3. Invasive rodents in New Zealand

For approximately 80 million years Zealandia/New Zealand has been mostly free of terrestrial mammalian species, with the few species existing having minor effects on the environment (Atkinson 2006; Gibbs 2009). This attribute together with geographic isolation resulted in a unique reptile- and avian-based fauna (Worthy & Holdaway 2002; Tennyson 2010). The arrival of Polynesians to New Zealand some 800 years ago (Wilmshurst et al. 2008) with their Kiore and Kuri (dogs, *Canis familiaris*) put an end to that era (Atkinson 2006). This first wave of mammalian invasion resulted in the extinction of all of the archipelago's mega-avifauna, together with many smaller bird, reptile and invertebrate species (Holdaway 1989; Tennyson 2010). Since the arrival of Europeans during the 18th and 19th centuries, a further 28 mammalian species have been introduced; all but three species of rodents, intentionally (Atkinson 2006).

Soon after their introduction as ship stowaways, *R. norvegicus, R. rattus* and *M. musculus* became widespread throughout mainland New Zealand, as well as on many of the smaller offshore islands (Atkinson 2006). The severe (if not catastrophic) effects these rodents pose on the native flora and fauna of New Zealand are well documented (Atkinson 1978; Bell 1978; Campbell 1978; Ramsay 1978; Bremner et al. 1984; Moors 1985; Holdaway 1989; Innes 2001; Towns & Broome 2003; Atkinson 2006; Le Corre 2008; Gibbs 2009; Innes et al. 2010; Tennyson 2010).

New Zealand invasive rodent communities have been subject to various shifts in species dominance and their distributions have fluctuated significantly since their arrivals (Taylor 1975, 1978; Yom-Tov et al. 1999; King et al. 2011a). Currently however, *R. rattus*

and *M. musculus* are arguably the most widespread species, especially on the mainland (Innes 2005a; Ruscoe & Murphy 2005). *R. norvegicus* is generally more scarce on the mainland and until recently was widespread on offshore islands (Innes 2005b). The Kiore, once the only rodent present across the archipelago, is now confined to a few small populations (Atkinson & Towns 2005), probably due to competitive exclusion from the larger and more aggressive European rats (Taylor 1975; Yom-Tov et al. 1999; Atkinson & Towns 2005). Nonetheless, at least one of these species is present within almost all suitable habitats in the New Zealand archipelago.

1.4. Ecology of the Norway rat *Rattus norvegicus* with emphases to New Zealand

The Norway rat likely originated in central Asia, from which it dispersed and colonised Europe, where it is mostly associated with human settlements (Nowak 1999). Since then, the species has spread as a stowaway on European ships and successfully colonised and established populations worldwide (Long 2003). Upon their arrival in New Zealand, Norway rats essentially replaced the Kiore as the dominant rodent species (Innes 2005b), only to be later supplanted in many areas by the ship rat *R. rattus* (Innes 2005a), which is presumably a stronger competitor in bush habitats (King et al. 2011a). It did stay relatively common near settlements and before eradication on many offshore island (Innes 2005b).

Norway rats are omnivorous and opportunistic feeders (Long 2003; Innes 2005b). In natural habitat they will eat anything from plant material, through to terrestrial and aquatic invertebrates, and vertebrates. The latter include reptiles, bird eggs, chicks and also adult birds (Innes 2005b). Feeding habits are culturally learned from mothers and other adult rats

and include learning to avoid harmful foods (Galef 2005). Breeding in New Zealand may occur year round, depending on the climate. Number of embryos in pregnant females is between 6 and 8 but up to 32. Pups wean at about 28 days of age and are sexual maturity in the same season of birth (for early born) or the next (late born). Annual production can be very high and reach 33.5 young per female (Innes 2005b). Population densities vary greatly between seasons, spring typically being the lowest (representing higher death rates during winter) and autumn the highest (representing high numbers of juveniles). Precise population densities are hard to assess, but they can reach high levels (13 rats/ha; 123.5 rats captured per 100 trap nights) when food and shelter are abundant (e.g. rubbish dumps), or when predators are absent (Innes 2005b).

Norway rats are mainly nocturnal (Innes 2005b) and highly social (Barnett 1958). They tend to become familiarised with their environment and spend considerable amounts of time foraging and exploring (Calhoun 1963). These movements can vary between tens to several hundreds of metres per night (Innes 2005b). When colonising new environments, Norway rats tend to be cautious and exhibit neophobic behaviour (Innes 2005b; Russell et al. 2005; Russell et al. 2008b). These attributes can lead to failures in the detection and capture of invading individuals (Russell et al. 2005; Masuda & Jamieson 2013; Shapira et al. 2013) Russell et al. (2009) found that a newly established Norway rat colony exhibits a clear bottleneck signal from the founding population resulting from mating dominance by a few individuals and hence high levels of inbreeding. Despite these findings, invading Norway rats achieved population structure similar to established island populations very rapidly. These findings are consistent with the ability of Norway rats to establish new and large populations from a small number of invaders.

1.5. Ecology of the house mouse *Mus musculus* with emphases to New Zealand

Like *R. norvegicus*, the house mouse dispersed as stowaways on European vessels and successfully invaded most suitable habitats (i.e. excluding extreme dry hot and cold environments) worldwide (Long 2003). In New Zealand, there is a complex genetic mix of three subspecies (primary *M. m. domesticus* and to a lesser extent *M. m. musculus* and *M. m. castanaeus*), inferring multiple invasions from different parts of the world (Ruscoe & Murphy 2005). The species is widespread across the main islands (up to heights of > 1300m) as well as on many offshore islands (Ruscoe & Murphy 2005).

The house mouse can live and thrive on an extremely wide variety of foods, both human associated and natural. In New Zealand natural ecosystems, mice eat mainly plant material and invertebrates. On offshore islands (especially when they are the only predator species) they are probably responsible for the extinction or critical reduction of many invertebrate species (Ruscoe 2001) and are also capable of seabirds predation (Cuthbert & Hilton 2004). Mice in New Zealand do not usually breed in winter, but a short gestation period and rapid sexual maturation (as short as 10-12 weeks in total) mean that females can produce multiple litters per season and that offspring from early litters may reproduce the season they were born. Large litter size (up to nine) mean that mouse populations can grow rapidly over short periods and population densities can be very high when conditions are favourable. The highest capture rates in New Zealand were 77 captures per 100 trap nights (i.e, 77 mice per 100 trapping attempts) after a beech seed fall event (Ruscoe & Murphy 2005), a common phenomenon causing mice population irruptions in New Zealand (Murphy 1992; Choquenot & Ruscoe 2000; Ruscoe 2001; Fitzgerald et al. 2004; Ruscoe & Murphy

2005). In the wild, mice can exhibit territorial, non-territorial (but with home-range hierarchy), nomadic, and clan-structure behaviours, depending on the availability of resources and population density. In New Zealand, both individual and group territories can be found (Ruscoe & Murphy 2005)

Of all the common invasive rodent species, mice are the hardest to eradicate (Howald et al. 2007). The commonest wide-scale eradication method is based on aerial poison drops (Towns & Broome 2003; Howald et al. 2007) and unless bait is densely and evenly distributed, the relatively small home ranges of mice (Berry 1970; Berry 1981), especially when densities are high (Ruscoe & Murphy 2005), might result in some mice not encountering poison bait populations persistence. In addition, it is worth noting that predator-proof fences struggle to keep mice out and mouse populations rapidly establishing after eradications in predator-proof fenced areas (Goldwater 2007).

1.6. Rodent control for conservation

The practice of rodent control is extensive, and substantial attempts are made to decrease rodent impacts on human health, agriculture products and natural ecosystems (Long 2003). For the purpose of this study though, I will primarily discuss the aspects of rodent control within a conservation context. At the beginning of the 20th century, invasive rodents were already found throughout New Zealand and with the establishment of several governmental wildlife and scientific agencies during the 1940s to 1960s, the effect of rodents on the native ecosystems started to be better understood (Thomas & Taylor 2002). Ground based poisoning operations for the control of rodents were initiated on numerous New Zealand

offshore islands. As many of these islands were recognised as the last or most important refuge for native biota (Daugherty et al. 1990), control operations increased (Thomas & Taylor 2002; Towns & Broome 2003) and as a consequence of their success have been implemented in other parts of the world (Howald et al. 2007; Witmer et al. 2011) as well as in mainland New Zealand (Hooker & Innes 1995; Innes et al. 1995; King et al. 1996; Innes et al. 2001; Thomas & Taylor 2002; Speedy et al. 2007).

The traits of invasive rodents, discussed above (1.2), pose inherent difficulties to their control (Steiniger 1950; Dilks & Towns 2002; Towns & Broome 2003; Russell & Clout 2005; Atkinson 2006; Clapperton 2006; Russell et al. 2008b; Russell et al. 2010). Nonetheless, as control techniques have improved (Thomas & Taylor 2002; Towns & Broome 2003; Russell et al. 2008b) and especially with the introduction of aerial poisoning (Towns & Broome 2003; Howald et al. 2007), complete eradications have been highly successful on offshore islands, with a 95% success rate in eradication of *R. norvegicus*, 92% for *R. rattus*, 90% for *R. exulans* and 81% for *M. musculus* (Howald et al. 2007). The smallest of these species, *M. musculus*, has proven the most difficult species to eradicate (Clapperton 2006; MacKay et al. 2007). Mainland sites are more difficult to manage and eradications are at present possible only inside predator-proof fences (Speedy et al. 2007). Both these and other mainland sites usually require continuous/regular control to keep population densities low and new incursions to a minimum (Hooker & Innes 1995; Innes et al. 1995; King et al. 2011b).

Most control measures against rodents in New Zealand, either ground based or aerial, use poisonous substances (primarily 1080 and Brodifacoum) within a food bait (Myers et al. 2000; Simberloff 2001; Towns & Broome 2003; Clapperton 2006; Howald et al. 2007).

Ground based kill traps are also baited with food (King et al. 1996; Clapperton 2006). Although largely successful, and despite ongoing research on improvements to pest control (O'Connor & Eason 2000; Spurr et al. 2007; Nugent et al. 2011), there are still issues in the control of invasive rodents that mean that methodology could be optimised. First, the effectiveness of the control operation (i.e. the ability to target all or most of the individuals): some eradication campaigns have not achieved complete rodent eradication despite substantial efforts (Towns & Broome 2003; Howald et al. 2007). Second, the long-term effectiveness of the eradication, which reflects the ability to maintain the treated sites free from reinvasions or prevent an eruption of a remnant untreated population as demonstrated by the ability of rodents to reinvade into rodent free sites via carriers or neighbouring land masses (Towns & Broome 2003; Abdelkarim et al. 2005; Russell et al. 2005; Atkinson 2006; Goldwater 2007; Russell et al. 2009; King et al. 2011b). A third issue is the negative effects on non-target and native species (Eason & Spurr 1995; Eason et al. 2002; Howald et al. 2007; Eason et al. 2013). Finally, despite the lack of solid evidence for large scale harmful effects of rodenticides on the environment, there is insufficient knowledge about the selectivity and pathways of the poisons through food webs and their long-term effects on the environment (Simberloff 2001; Dilks & Towns 2002; Towns & Broome 2003) .The use of poison is still, in the eye of the general public, controversial (Myers et al. 2000; Simberloff 2001).

1.7. Animal behaviour and the control of invasive species

Although now obvious, it was less than 20 years ago that the connection between animal behaviour and conservation biology gained attention (Ulfstrand 1996; Clemmons &

Buchholz 1997). Despite this late recognition, much of the research in conservation biology already integrated behaviour of focal species with their conservation status and management strategies (Reed & Dobson 1993; Clemmons & Buchholz 1997; Sutherland 1998). Behavioural conservation attempts to understand and improve conservation processes and practices through the study of animal behaviour (Clemmons & Buchholz 1997; Caro 1999). Indeed, it is becoming increasingly apparent that the behaviour of animals can be a strong tool for conservation (Sutherland 1998; Buchholz 2007; Berger-Tal et al. 2011).

The control of invasive species has the goal of reducing predatory or competition pressure from species of conservation concern. Advocates for behavioural conservation acknowledge the importance of behavioural studies of invasive species in that they can directly benefit or inform control measures (Sutherland 1998; Holway & Suarez 1999; Moore et al. 2008). Although the behaviour of many invasive species is well studied, research directly addressing behavioural implications for their control is relatively scarce. For example, *Rattus* and *Mus* spp. are among the most studied vertebrates and a huge body of work has been conducted on their ecological behaviour (see table 1.5.1 for a selected reference list). Studies directly connecting rodent behaviour and control are less common in comparison (see table 1.5.1 for reference list) and many researchers emphasize the importance and the lack of knowledge of the behaviour of invasive rodents in relation to their short and long term control (Wace 1986; McClelland 2002; Sowls & Byrd 2002; Amori & Clout 2003; Courchamp et al. 2003; Towns & Broome 2003; Clapperton 2006; Moore et al. 2008).

Table 1.5.1. Reference list for comparison between general works on behavioural ecology of rodents and works relating rodent behaviour to their control.

Examples of general studies on rodents' behavioural ecology (selection only)	Examples of studies on rodents' control related behaviours
(a very partial list include: Barnett 1958; Calhoun 1963; Berry 1970; Ewer 1971; Boreman & Price 1972; Alberts & Galef 1973; Robitaille & Bovet 1976; Berry 1981; Takahashi & Blanchard 1982; Aisner & Terkel 1992; Dickman 1992; Galef & Allen 1995; Galef & Buckley 1996; King et al. 1996; Rich & Hurst 1998; Gray et al. 2002; Jensen et al. 2003; Thom & Hurst 2004; Arthur et al. 2005; Jensen et al. 2005; Major & Jones 2005; Harper 2006; Cheetham et al. 2007; Major et al. 2007; Grant-Hoffman & Barboza 2010; Hughes & Banks 2010)	(Rowe 1973; Inglis et al. 1996; Ji et al. 1999; Shumake & Hakim 2000; Moro 2002; Russell et al. 2005; Moore et al. 2008; Russell et al. 2008b; Russell et al. 2008a; Russell et al. 2010; MacKay et al. 2011; Volfova et al. 2011; Price & Banks In Press)

1.8. Objectives

In this thesis, I explore several aspects of the behavioural ecology of the Norway rat *R. norvegicus* and the house mouse *M. musculus* with the aim of informing and improving rodent control. Although behavioural conservation is the common theme of this thesis, each of Chapters II to VII has been written as a scientific paper and can therefore be viewed as an independent study. Therefore, some repetition between chapters is inevitable. Being written as scientific papers, the chapters are presented in (my) singular voice. However, they do represent the efforts of several co-authors and these are credited in the order of significance after the objectives presented below, chapter-by-chapter.

1.8.1. Chapter II: Laboratory rats as trap lures for invasive Norway rats: field trial and recommendations

1.8.1.1. Objectives

In this chapter I tested whether laboratory rats can act as effective lures for wild Norway rats in order to overcome the problem of rats avoiding food baits. The reasoning behind this was based on the highly social behaviour exhibited by this species. My objectives were to (1) detect possible differences in the attractiveness of cages containing lure rats (males and females) vs. control cages (which contained everything as in the lure animal cages apart from the lure animals themselves), (2) detect possible differences in the attractiveness of male vs. female lure rats, and (3) compare the attractiveness of lure rats vs. food bait for wild Norway rats.

1.8.1.2. Credits

A version of this chapter has been published in *New Zealand Journal of Ecology* (Appendix 1), co-authored with Dianne Brunton, Uri Shanas and David Raubenheimer.

1.8.2. Chapter III: Laboratory rats as conspecific bio-control agents for invasive Norway rats Rattus norvegicus

1.8.2.1. Objectives

Following the findings in Chapter I, I performed direct, spatial and temporal comparisons between live lures and control food baits to test whether conspecific attraction can be more efficient than food bait for the detection and capture of invasive Norway rats in three

different scenarios: low rat population densities, abundance of available food in the environment, and manipulated island rat incursions. My objectives were to (1) assess the efficacy of conspecific live luring compared to food bait, in all three scenarios, and (2) assess possible differences of wild rat attraction to male vs. female lures.

1.8.2.2. Credits

A version of this chapter has been published in *Biological Control* (Appendix 2), co-authored with Dianne Brunton, Uri Shanas, Craig Knapp, Susan Alberts and David Raubenheimer.

1.8.3. Chapter IV: Conspecific attraction in wild house mice: effects of strain, sex and diet

1.8.3.1. Objectives

In this chapter I tested the attraction of urine from mice fed high and low protein diets on male and female wild mice, and whether the protein content of the diet of mice affected their response. I further compared the strength of attraction of wild mice towards wild and laboratory live lure conspecifics of the opposite sex. My objectives were to (1) assess the general effect of diet on conspecific attraction through scent, and (2) determine whether mouse strain has an effect on mouse attraction to live conspecifics.

1.8.3.2. Credits

A version of this chapter has been published in *Applied Animal Behaviour Science* (Appendix 3), co-authored with David Raubenheimer, Dianne Brunton and Uri Shanas.

1.8.4. Chapter V: Responses to direct versus indirect cues of predation and competition in naïve invasive mice: implications for management

1.8.4.1. Objectives

In this chapter I tested the impacts of mammalian odours (a specific direct cue of predation or competition) and illumination intensity (a general indirect cue of predation) on foraging of free-ranging mice that are naïve to mammalian predators, in the field. My objectives were to (1) measure the behavioural responses of these mice to predatory and competitive cues, (2) assess the relative importance of these two factors to mouse foraging, and (3) draw implications for mice control management.

1.8.4.2. Credits

A version of this chapter has been published in *New Zealand Journal of Ecology* (Appendix 4), co-authored with Elizabeth Walker, David Raubenheimer and Dianne Brunton.

1.8.5.Chapter VI: First encounters of wild house mice with novel rat scent: risk-taking females and cautious males?

1.8.5.1. Objectives

In this chapter I tested the response of rat naïve wild mice to rat scent in a laboratory apparatus. My objectives were to (1) observe behavioural responses of wild mice (males and females) in the present of novel rat scent and control (water), (2) assess the effect of time of exposure to novel rat scent on mice behavioural responses .

1.8.6. Chapter VII: Prioritizing energy over macronutrient balance in wild Mus musculus: implications for mouse domestication and invasiveness

1.8.6.1. Objectives

In this chapter I tested macronutrient selection in wild caught mice, under controlled conditions. My objectives were to (1) assess whether wild mice have gone through different evolutionary routes than have laboratory mice, which have resulted in different nutritional requirements, and (2) determine whether macronutrient regulation in wild mice can potentially explain their invasiveness success.

1.8.7. Chapter VIII: Discussion

1.8.7.1 Objectives

The understanding and improvement of conservation practices through the study of animal behavioural processes is a rapidly growing, emerging science. An increasing number of

researchers are directly exploring control implications and conservation benefits based on the behaviour of invasive species. Nonetheless, despite many researchers emphasizing the significance of this approach, the study of the behaviour of invasive species in direct relation to their control is very limited. In the last chapter of this thesis, I discuss the importance of behavioural conservation, the main results from my research, potential implications of these results for rodent control, and suggest some directions for further research.

1.7. References

Abdelkarim J, Pascal M, Calmet C, Samad S 2005. Importance of assessing population genetic structure before eradication of invasive species: examples from insular Norway rat populations. Conservation Biology 19: 1509-1518.

Aisner R, Terkel J 1992. Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus*. Animal Behaviour 44: 372-336.

Alberts JR, Galef BG 1973. Olfactory cues and movement: stimuli mediating intraspecific aggression in wild Norway rat. Journal of Comparative and Physiological Psychology 85(2): 233-242.

Amori G, Clout MN 2003. Rodents on islands: a conservation challenge. In: Singleton GR, Hinds IA, Krebs CJ, Spratt DM eds. Rats, Mice and People: Rodent Biology and Management. Canbara, Australian Centre for International Agricultural Research. Pp. 63-67.

Arthur AD, Pech RP, Dickman CR 2005. Effects of predation and habitat structure on the population dynamics of house mice in large outdoor enclosures. Oikos 108(3): 562-572.

Atkinson IAE 1978. Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands. In: Dingwell PR, Atkinson IAE, Hay C eds. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Department of Lands and Survey Information. Pp. 7-30.

Atkinson IAE 2006. Introduced mammals in a new environment. In: Allen RB, Lee WG ed. Biological Invasions in New Zealand. Berlin, Springer-Verlag. Pp. 49-66.

Atkinson IAE, Towns DR 2005. Kiore. In: King CM ed. The Handbook of New Zealand Mammals. Second ed. New York, Oxford University Press. Pp. 159-174.

Barnett SA 1958. An analysis of social behaviour in wild rats. Proceedings of the Zoological Society of London 130: 107-152.

Bell BD 1978. The Big South Cape Islands rat irruption. In: Dingwall PR, Atkinson IAE, Hay C eds. The Ecology and Control of Rodents in New Zeland Nature Reserves. Wellington, Department of Lands and Survey Information. Pp. 33-40.

Berger-Tal O, Polak T, Oron A, Lubin Y, Kotler BP, Saltz D 2011. Integrating animal behavior and conservation biology: a conceptual framework. Behavioural Ecology 22: 236-239.

Berry RJ 1970. The natural history of the house mouse. Field Studies 3: 219-262.

Berry RJE 1981. Biology of the house mouse. London, Academic Press. 715 p.

Boreman J, Price E 1972. Social dominance in wild and domestic Norway rats (*Rattus norvegicus*). Animal Behaviour 20(3): 534-542.

Bremner AG, Butcher CF, Patterson GB 1984. The density of indigenous invertebrates on 3 islands in Breaksea Sound, Fiordland, in relation to the distribution of introduced mammals. Journal of the Royal Society of New Zealand 14(4): 379-386.

Buchholz R 2007. Behavioural biology: an effective and relevant conservation tool. Trends in Ecology & Evolution 22(8): 401-407.

Calhoun JB 1963. The Ecology and Sociology of the Norway Rat. Bethesda, U.S. Dept. of Health, Education, and Welfare, Public health Service. 288 p.

Campbell DJ 1978. The effects of rats on vegetation. In: Dingwell PR, Atkinson IAE, Hay C eds. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Department of Lands and Survey Information. Pp. 99-119.

Caro T 1999. The behaviour–conservation interface. Trends in Ecology & Evolution 14: 366–369.

Cheetham SA, Thom MD, Jury F, Ollier WER, Beynon RJ, Hurst JL 2007. The genetic basis of individual-recognition signals in the mouse. Current Biology 17(20): 1771-1777.

Choquenot D, Ruscoe WA 2000. Mouse population eruptions in New Zealand forests: the role of population density and seedfall. Journal of Animal Ecology 69(6): 1058-1070.

Clapperton BK 2006. A review of the current knowledge of rodent behaviour in relation to control devices. Science for Conservation 263. Wellington, Department of Conservation. 55 p.

Clemmons JR, Buchholz R 1997. Linking conservation and behavior. In: Clemmons JR, Buchholz R eds. Behavioral Aporoaches to Conservation in the Wild. Cambridge, Cambridge University Press. Pp. 3-22.

Courchamp F, Chapuis JL, Pascal M 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78(3): 347-383.

Crosby AW 1986. Ecological Imperialism. Cambridge, Cambridge University Press. 368 p.

Crowl TA, Crist TO, Parmenter RR, Belovsky G, Lugo AE 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. Frontiers in Ecology and the Environment 6: 238-246.

Cuthbert R, Hilton G 2004. Introduced house mice *Mus musculus*: a significant predator of threatened and endemic birds on Gough Island, South Atlantic Ocean? Biological Conservation 117(5): 483-489.

Daugherty CH, Towns DR, Atkinson IAE, Gibbs GW 1990. The significance of the biological resources of New Zealand islands for ecological restoration. In: Towns DR, Daugherty CH, Atkinson IAE eds. Ecological Restoration of New Zealand Islands. Wellington, Department of Conservation. Pp. 9-21.

Davis MA 2009. Invasion Biology. Oxford, Oxford University Press. 288 p.

Dickman CR 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73(1): 313-322.

Dilks P, Towns DR 2002. Developing tools to detect and respond to rodent invasions of islands: workshop report and recommendations. DOC Science Internal Series 59. wellington, Department of conservation. Pp 5-18.

Eason CT, Spurr EB 1995. Review of the toxicity and impacts of brodifacoum on non target wildlife in New Zealand. New Zealand Journal of Zoology 22(4): 371-379.

Eason CT, Ross J, Miller A 2013. Secondary poisoning risks from 1080-poisoned carcasses and risk of trophic transfer—a review. New Zealand Journal of Zoology In Press.

Eason CT, Murphy EC, Wright GRG, Spurr EB 2002. Assessment of risks of brodifacoum to non target birds and mammals in New Zealand. Ecotoxicology 11(1): 35-48.

Elton CS 1958. The Ecology of Invasions by Animals and Plants. London, Methuen.

Epstein PR 1995. Emerging diseases and ecosystem instability: new threats to public health. American Journal of Public Health 85(2): 168-172.

Ewer RF 1971. The biology and behaviour of a free-living population of black rats (*Rattus rattus*). Animal Behaviour Monographs 24: 939-942.

Fitzgerald BM, Efford MG, Karl BJ 2004. Breeding of house mice and the mast seeding of southern beeches in the Orongorongo Valley, New Zealand. New Zealand Journal of Zoology 31(2): 167-184.

Galef BG 2005. Social learning. In: Whishaw IQ, Kolb B eds. The Behavior of the Laboratory Rat. New York, Oxford University Press. Pp. 363-370.

Galef BG, Allen C 1995. A new model system for studying behavioral traditions in animals. Animal Behaviour 50: 705-717.

Galef BG, Buckley LL 1996. Use of foraging trails by Norway rats. Animal Behaviour 51: 765-771.

Gibbs GW 2009. The end of an 80-million year experiment: a review of evidence describing the impact of introduced rodents on New Zealand's 'mammal-free' invertebrate fauna. Biological Invasions 11(7): 1587-1593.

Goldwater N 2007. Ecology of House Mice within the Tawharanui Open Sanctuary. Unpublished MSc thesis, University of Auckland, Auckland. 128 p.

Grant-Hoffman MN, Barboza PS 2010. Herbivory in invasive rats: criteria for food selection. Biological Invasions 12(4): 805-825.

Gray SJ, Jensen SP, Hurst JL 2002. Effects of resource distribution on activity and territory defence in house mice, *Mus domesticus*. Animal Behaviour 63: 531-539.

Harper GA 2006. Habitat use by three rat species (*Rattus spp*.) on an island without other mammalian predators. New Zealand Journal of Ecology 30(3): 321-333.

Holdaway RN 1989. New Zealands pre-human avifauna and its vulnerability. New Zealand Journal of Ecology 12: 11-25.

Holway DA, Suarez AV 1999. Animal behavior: an essential component of invasion biology. Trends in Ecology & Evolution 14(8): 328-330.

Hooker S, Innes J 1995. Ranging behavior of forest dwelling ship rats, *Rattus rattus*, and effects of poisoning with brodifacoum. New Zealand Journal of Zoology 22(3): 291-304.

Hornby AS, Gatenby EV, Wakefield H 1963. The advanced learner's Dictionary of Current English. 2nd ed. London, Oxford University Press. 1200 p.

Howald G, Donlan CJ, Galvan JP, Russell JC, Parkes J, Samaniego A, Wang YW, Veitch D, Genovesi P, Pascal M and others 2007. Invasive rodent eradication on islands. Conservation Biology 21(5): 1258-1268.

Hughes NK, Banks PB 2010. Interacting effects of predation risk and signal patchiness on activity and communication in house mice. Journal of Animal Ecology 79(1): 88-97.

Inglis IR, Shepherd DS, Smith P, Haynes PJ, Bull DS, Cowan DP, Whitehead D 1996. Foraging behaviour of wild rats (*Rattus norvegicus*) towards new foods and bait containers. Applied Animal Behaviour Science 47(3-4): 175-190.

Innes J 2001. Advances in New Zealand mammalogy 1990-2000: European rats. Journal of the Royal Society of New Zealand 31(1): 111-125.

Innes J, Kelly D, Overton JM, Gillies C 2010. Predation and other factors currently limiting New Zealand forest birds. New Zealand Journal of Ecology 34(1): 86-114.

Innes J, Warburton B, Williams D, Speed H, Bradfield P 1995. Large scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North island, New Zealand. New Zealand Journal of Ecology 19(1): 5-17.

Innes JG 2005a. Ship rat. In: King CM ed. The Handbook of New Zealand Mammals. Second ed. New York, Oxford University Press. Pp. 187-203.

Innes JG 2005b. Norway rat. In: King CM ed. The Handbook of New Zealand Mammals. Second ed. New York, Oxford University Press. Pp. 174-187.

Innes JG, King CM, Flux M, Kimberley MO 2001. Population biology of the ship rat and Norway rat in Pureora Forest Park, 1983-87. New Zealand Journal of Zoology 28(1): 57-78.

Jensen SP, Gray SJ, Hurst JL 2003. How does habitat structure affect activity and use of space among house mice? Animal Behaviour 66: 239-250.

Jensen SP, Gray SJ, Hurst JL 2005. Excluding neighbours from territories: effects of habitat structure and resource distribution. Animal Behaviour 69: 785-795.

Ji W, Veitch CR, Craig JL 1999. An evaluation of the efficiency of rodent trapping methods: the effect of trap arrangement, cover type, and bait. New Zealand Journal of Ecology 23(1): 45-51.

King CM, Foster S, Miller S 2011a. Invasive European rats in Britain and New Zealand: same species, different outcomes. Journal of Zoology 285(3): 172-179.

King CM, Innes JG, Flux M, Kimberley MO, Leathwick JR, Williams DS 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. New Zealand Journal of Ecology 20(2): 215-240.

King CM, Innes JG, Gleeson D, Fitzgerald N, Winstanley T, O'Brien B, Bridgman L, Cox N 2011b. Reinvasion by ship rats (*Rattus rattus*) of forest fragments after eradication. Biological Invasions 13(10): 2391-2408.

Le Corre M 2008. Cats, rats and seabirds. Nature 451(7175): 134-135.

Lindsey J, R., Baker HJ 2006. Historical foundations. In: Suckow MA, Weisbroth SH, Franklin CL eds. The Laboratory Rat. 2nd ed. San Diego, Elsevier Academic Press. Pp. 1-52.

Lockwood JL, Hoopes MF, Marchetti MP 2007. Invasion Ecology. Malden MA, Blackwell. 304 p.

Long JL 2003. Introduced Mammals of the World. Collingwood, CSIRO. 589 p.

MacKay JWB 2010. *Mus musculus*. Retrieved May 10th 2012, (updated September 17, 2010) from: http://www.issg.org/database/species/ecology.asp?si=97&fr=1&sts=&lang=EN

MacKay JWB, Russell JC, Murphy EC 2007. Eradicating house mice from islands: successes, failures and the way forward. In: Witmer GW, Pitt WC, Fagerstone KA eds. Managing Vertebrate Invasive Species. Pp. 294-304.

MacKay JWB, Murphy EC, Anderson SH, Russell JC, Hauber ME, Wilson DJ, Clout MN 2011. A successful mouse eradication explained by site-specific population data. In: Veitch CR, Clout MN, Towns DR eds. Island Invasives: Eradication and Management. Gland, IUCN.

Major HL, Jones IL 2005. Distribution, biology and prey selection of the introduced Norway rat *Rattus norvegicus* at Kiska Island, Aleutian Island, Alaska. Pacific Conservation Biology 11: 1-9.

Major HL, Jones IL, Charette MR, Diamond AW 2007. Variations in the diet of introduced Norway rats (*Rattus norvegicus*) inferred using stable isotope analysis. Journal of Zoology 271(4): 463-468.

Masuda BM, Jamieson IG 2013. Response of a reintroduced bird population to a rat reinvasion and eradication. New Zealand Journal of Ecology 37(2): 224-231.

McClelland PJ 2002. Island quarantine—prevention is better than cure. In: Veitch CR, Clout MN eds. Turning the Tide: The Eradication of Invasive Species. Gland and Cambridge, IUCN SSC Invasive Species Specialist Group. Pp. 173-181.

Meehan AP 1984. Rats and Mice: their Biology and Control. East Grinstead, Rentokill.

Meerburg BG, Singleton GR, Kijlstra A 2009a. Rodent-borne diseases and their risks for public health. Critical Reviews in Microbiology 35(3): 221-270.

Meerburg BG, Singleton GR, Leirs H 2009b. The year of the rat ends - time to fight hunger! Pest Management Science 65(4): 351-352.

Meffe GK, Ronald CC 1997. Principles of Conservation Biology. 2nd ed. Massachusetts, Sinauer Associates Inc.

Meyer AN 1999. Commensal rodent control: chalanges for the new millennium. In: Robinson WH, Rettich F, Rambo GW eds. 3rd International Conference on Urban Pests. Prague, Graficke Zavody. Pp. 99-103.

Mills JN, Childs JE 1998. Ecologic studies of rodent reservoirs: their relevance for human health. Emerging Infectious Diseases 4(4): 529-537.

Moore JA, Bell BD, Linklater WL 2008. The debate on behavior in conservation: New Zealand integrates theory with practice. BioScience 58: 454-459.

Moors PJ 1985. Norway rats (*Rattus norvegicus*) on the Noises and Motukawao Islands, Hauraki gulf, New Zealand. New Zealand Journal of Ecology 8: 37-54.

Moro D 2002. Comparison of baits and bait stations for the selective control of wild house mice on Thevenard Island, Western Australia. In: Veitch CR, Clout MN eds. Turning the Tide: The Eradication of Invasive Species. Gland and Cambridge, IUCN SSC Invasive Species Specialist Group. Pp. 213-218.

Murphy EC 1992. The effects of a natural increase in food supply on a wild population of house mice. New Zealand Journal of Ecology 16(1): 33-40.

Myers JH, Simberloff D, Kuris AM, Carey JR 2000. Eradication revisited: dealing with exotic species. Trends in Ecology & Evolution 15(8): 316-320.

Nowak RM 1999. Walker's mammals of the world. 6th ed. Baltimore and London, Johns Hopkins University Press.

Nugent G, Warburton B, Thomson C, Sweetapple P, Ruscoe WA 2011. Effect of prefeeding, sowing rate and sowing pattern on efficacy of aerial 1080 poisoning of small-mammal pests in New Zealand. Wildlife Research 38(3): 249-259.

O'Connor CE, Eason CT 2000. Rodent baits and delivery systems for island protection. DOC Science for Conservation 150. Wellington, Department of Conservation. 25 p.

Olson LJ 2006. The economics of terrestrial invasive species: a review of the literature. Agricultural and Resource Economics Review 35: 178-194.

Parkash IE 1988. Rodent pest management. Boca Raton, CRC Press.

Pejchar L, Mooney HA 2009. Invasive species, ecosystem services and human well-being. Trends in Ecology & Evolution 24: 497-504.

Perrings C, Williamson M, Dalmazzone S 2000. The Economics of Biological Invasions. Cheltenham, Edward Elgar Publishing.

Price CJ, Banks PB In Press. Exploiting olfactory learning in alien rats to protect birds' eggs. Proceedings of the National Academy of Sciences.

Primack RB 2010. Essentials of Conservation Biology. 5th ed. Sunderland, Sinauer. 601 p.

Ramsay GW 1978. A review of the effects of rodents on the New Zealand invertebrate fauna. In: Dingwell PR, Atkinson IAE, Hay C eds. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Dept. of Lands and Survey Informations. Pp. 89-95.

Reed JM, Dobson AP 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. Trends in Ecology & Evolution 8: 253-256.

Reise K, Olenin S, Thieltges DW 2006. Are aliens threatening European aquatic coastal ecosystems? Helgoland Marine Research 60: 77-83.

Rich TJ, Hurst JL 1998. Scent marks as reliable signals of the competitive ability of mates. Animal Behaviour 56: 727-735.

Robitaille JA, Bovet J 1976. Field observations on social behavior of Norway rat, *Rattus norvegicus* (Berkenhout). Biology of Behaviour 1(4): 289-308.

Rowe FP 1973. Aspects of mouse behaviour related to control. Mammal Review 3: 58-63.

Ruscoe WA 2001. Advances in New Zealand mammalogy 1990-2000: house mouse. Journal of the Royal Society of New Zealand 31(1): 127-134.

Ruscoe WA, Murphy EC 2005. House mouse. In: King CM ed. The Handbook of New Zealand Mammals. Second ed. New York, Oxford University Press. Pp. 204-221.

Russell JC, Clout MN 2005. Rodent incursions on New Zealand Islands. In: Parks J, Statham M, Edwards G eds. Proceedings of the 13th Australian Vertebrate Pest Conference. Pp. 324-330.

Russell JC, Towns DR, Clout MN 2008a. Review of rat invasion biology: implications for islands biosecurity. Science for Conservation. Lincoln, Landcare Research. 53 p.

Russell JC, Abdelkrim J, Fewster RM 2009. Early colonisation population structure of a Norway rat island invasion. Biological Invasions 11(7): 1557-1567.

Russell JC, McMorland AJC, MacKay JWB 2010. Exploratory behaviour of colonizing rats in novel environments. Animal Behaviour 79(1): 159-164.

Russell JC, Towns DR, Anderson SH, Clout MN 2005. Intercepting the first rat ashore. Nature 437(7062): 1107-1107.

Russell JC, Beaven BM, MacKay JWB, Towns DR, Clout MN 2008b. Testing island biosecurity systems for invasive rats. Wildlife Research 35(3): 215-221.

Shapira I, Shanas U, Raubenheimer D, Knapp C, Alberts S, Brunton D 2013. Laboratory rats as conspecific biocontrol agents for invasive Norway rats *Rattus norvegicus*. Biological Control 66: 83-91.

Shumake SA, Hakim AA 2000. Evaluating Norway rat response to attractant and repellant odors to improve rodenticide baiting effectiveness. In: Brittingham MC, Kays J, McPeake R eds. Wildlife Damage Management. State College PA, University of Nebraska. Pp. 103-110.

Simberloff D 2001. Eradication of island invasives: practical actions and results achieved. Trends in Ecology & Evolution 16(6): 273-274.

Simberloff D 2003. Confronting introduced species: a form of xenophobia? Biological Invasions 5: 179-192.

Simberloff D 2009. Rats are not the only introduced rodents producing ecosystem impacts on islands. Biological Invasions 11(7): 1735-1742.

Sowls AI, Byrd GV 2002. Preventing rat introductions to the Pribilof Islands, Alaska, USA. In: Veitch CR, Clout MN eds. Turning the Tide: the Eradication of Invasive Species. Gland and Cambridge, IUCN SSC Invasive Species Specialist Group. Pp. 413.

Speedy C, Day T, Innes J 2007. Pest eradication technology - the critical partner to pest exclusion technology: the Maungatautari experiance. In: Witmer GW, Pitt WC, Fagerstone KA eds. Managing Vertebrate Invasive Species. Fort Colins, University of Nebraska. Pp. 115-126.

Spurr EB, Morriss GA, Turner J, O'Connor CE, Fisher P 2007. Bait station preferences of ship rats. Doc Research & Development Series 271. Wellington, Department of Conservation. 21 p.

St Clair JJH 2011. The impacts of invasive rodents on island invertebrates. Biological Conservation 144(1): 68-81.

Steiniger F 1950. Beiträge zur soziologie und sonstigen biologie der wanderratte. Zeitschrift für Tierpsychologie 7: 356-379.

Stenseth NC, Leirs H, Skonhoft A, Davis SA, Pech RP, Andreassen HP, Singleton GR, Lima M, Machang'u RS, Makundi RH and others 2003. Mice, rats, and people: the bio-

economics of agricultural rodent pests. Frontiers in Ecology and the Environment 1(7): 367-375.

Sutherland WJ 1998. The importance of behavioural studies in conservation biology. Animal Behaviour 56: 801-809.

Takahashi LK, Blanchard RJ 1982. Attack and defense in laboratory and wild Norway and black rats. Behavioural Processes 7(1): 49-62.

Taylor RH 1975. What limits kiore (*Rattus exulans*) distribution in New Zealand. New Zealand Journal of Zoology 2(4): 473-477.

Taylor RH 1978. Dstribution and interactions of rodet species in New Zealand. In: Dingwell PR, Atkinson IAE, Hay C ed. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Department of Lands and Survey Information. Pp. 135-141.

Tennyson AJD 2010. The origin and history of New Zealand's terrestrial vertebrates. New Zealand Journal of Ecology 34(1): 6-27.

Thom MD, Hurst JL 2004. Individual recognition by scent. Annales Zoologici Fennici 41(6): 765-787.

Thomas BW, Taylor RH 2002. A history of ground-based rodent eradication techniques developed in New Zealand, 1959-1993. In: Veitch CR, Clout MN eds. Turning the Tide: The Eradication of Invasive Species. Gland and Cambridge, IUCN SSC Invasive Species Specialist Group. Pp. 301-310.

Towns DR, Broome KG 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. New Zealand Journal of Zoology 30(4): 377-398.

Ulfstrand S 1996. Behavioural ecology and conservation biology. Oikos 77: 183.

Volfova R, Stejskal V, Aulicky R, Frynta D 2011. Presence of conspecific odours enhances responses of commensal house mice (*Mus musculus*) to bait stations. International Journal of Pest Management 57(1): 35-40.

Wace NM 1986. The rat problem on oceanic islands - research is needed. Oryx 20: 79-86.

Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH 2008. Dating the late prehistoric dispersal of polynesians to New Zealand using the commensal Pacific rat. Proceedings of the National Academy of Sciences of the United States of America 105(22): 7676-7680.

Witmer GW, Pierce J, Pitt WC 2011. Eradication of invasive rodents on islands of the United States. In: Veitch CR, Clout MN, Towns DR ed. Island Invasives: Eradication and Management. Gland, IUCN.

Wodzicki KA, Taylor RH 1984. Distribution and status of the Polynesian rat *Rattus exulans*. Acta Zoologica Fennica 172: 99-101.

Worthy TH, Holdaway RN 2002. The Lost World of the Moa. Indiana, Indiana University Press.

Yom-Tov Y, Yom-Tov S, Moller H 1999. Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. Journal of Biogeography 26(5): 947-958.

CHAPTER 2: LABORATORY RATS AS TRAP LURES FOR INVASIVE NORWAY RATS: FIELD TRIAL AND RECOMMENDATION

2.1. Abstract

The Norway rat (*Rattus norvegicus*) is a highly destructive invasive species but while rat eradications on islands are effective, detection of survivors or reinvasions is challenging. I tested whether laboratory rats can act as lures for wild rats. I live-trapped rats first by using food baits, followed by live trapping using male and female lure rats vs controls (i.e. the same trapping device but without the lure animal). Norway rats were more frequently attracted to lure rats compared with controls. There was no sex bias in the trapped animals. Numbers of Norway rats caught with food baits compared with lure rats did not differ, but catch rates per trapping unit were higher when using lure rats. Rat activity was detected only around lure rats. Ship rats (*Rattus rattus*) were not caught with Norway lure rats. I demonstrate the potential for detecting invasive Norway rats using conspecific rats as lures. Further research looking at conspecific attraction in other situations and in direct comparison with food-baited traps is needed to determine the efficacy of this method as a control measure.

2.2. Introduction

The Norway rat (*Rattus norvegicus*) is a highly successful and destructive invasive species worldwide (Long 2003; Jones et al. 2008). Norway rats have been eradicated from many

offshore islands (Towns & Broome 2003; Howald et al. 2007) and from several predator-proof-fenced inland sites (Speedy et al. 2007). However, because of the species' remarkable swimming abilities (Harper 2005; Russell et al. 2005) and its capacity to survive on small vessels (Harper 2005), reinvasions to rat-free islands remain a threat. Thus, the detection and targeting of new invasions or remaining survivors is a high management priority.

The methods most commonly employed for the detection and control of invasive rats include kill traps, tracking tunnels, and poison stations, all of which are food baited (Dilks & Towns 2002; Howald et al. 2007; Russell et al. 2008a). In New Zealand, the Department of Conservation is also using rat-detecting dogs (Dilks & Towns 2002). However, when populations of pest rats are at low densities, such as during the early stages following reinvasions, these methods often prove ineffective, probably because competition is low and food is abundant (Thorsen et al. 2000; Dilks & Towns 2002; Russell et al. 2005, 2008b). In 2010, for example, the detection system on rat-free Ulva Island (off Stewart Island, New Zealand) failed to detect the presence of invading Norway rats, which subsequently resulted in the establishment of a new population (Masuda & Jamieson in press). In some other recent island incursions, it took 3–4 weeks to capture individual rats after an incursion was detected (F. Buchanan, S. O'Connor, DOC, pers. comm.).

Norway rats are highly sociable, and complex intraspecific interactions are key components in their behaviours. These reflects not only in the formation of hirarchal social groups that might include tens of animals, but also in between groups interactions and between new indivduals and established groups. In general, dominant males and females are more active within these interactions but all ranks exhibit interest. The investigation of new individuals by group members is intensive for both sexes, although males are in general more

active than females in this respect (Barnett 1958; Calhoun 1963; Boreman & Price 1972; Alberts & Galef 1973; Robitaille & Bovet 1976; Galef & Allen 1995; Agmo 2003; Galef 2005). Both olfactory communication (Cheal 1975) and vocalisation (Barfield et al. 1979) play crucial roles in Norway rat social behaviour.

Based on these attributes, I tested whether caged laboratory rats (*Rattus norvegicus*) could act as lures for wild Norway rats. In this case, a caged animal represent a new individual entered into an environment in which Norway rats presumably have established teritories. Previously, the feasibility of intraspecific attraction in an invasive rodent using live conspecifics under field conditions had only been superficially tested. Wace (1986) tried to lure Norway rats with laboratory rats, but in sites that retrospectively were found not to be inhabited by Norway rats. Gsell et al. (unpubl. data) tested the efficacy of lure rats with considerable success, but as they used only track counts, the species and sex of the attracted animals could not be determined. Conspecific odours as attractants are more common, and traps scented with conspecific odours enhanced trappability in the house mouse (*Mus musculus*) (Volfova et al. 2011), and voles (*Microtus townsendii*) (Boonstra & Krebs 1976), see also a review by Stoddart (1986) for more species. Other rodent species (*Peromyscus maniculatus, Dipodomys agilis* and *D. merriami*), however, when not in reproductive condition, were more attracted to neutral over scented traps, implying periodic avoidance of social interactions (Daly et al. 1980).

I used live animals because the relative importance of each sense in this species' social interactions is largely unknown, and confining the study to scent alone might limit the power of attraction. Live animals, such as goats (Taylor & Katahira 1988), mynas and crows (Tidemann 2005; Tsachalidis et al. 2006), have been used elsewhere as conspecific decoys,

thus providing encouraging examples of the importance of social behaviour in the detection and capture of invasive animals.

My objectives were to (1) detect possible differences in the attractiveness of cages containing lure rats (males and females) vs control cages (which contained the same food as in the lure animal cages), (2) detect possible differences in the attractiveness of male vs female lure rats, and (3) compare the attractiveness of lure rats vs food bait for wild Norway rats.

2.3. Methods

I conducted the study during May–June 2010 at Shakespear Regional Park (36°36′23.42″ S, 174°48′38.85″ E), Auckland, New Zealand. Mammalian pest control in the park consisted of trap lines (~ 50 traps baited with meat) and poison-bait stations (~ 10 stations baited with brodifacoum pellets). I conducted the experiments in bush and scrub in the western section of the park's wetland.

In order to assess population density and tag as many individual Norway rats as possible, I performed preliminary trapping at the site during 180 trap nights (TN) using double-door live traps (16 × 16 × 70 cm; Neal Blaymires, Te Puke, New Zealand) partly covered with corrugated plastic for weather protection and baited with carrots and peanut butter. Traps were spaced between 30 and 70 m apart, depending on the terrain (Fig. 2.3.1 B, C). Traps were visited early mornings and re-baited as required (where bait was missing) or every 3 days.

Trapped Norway rats were removed into an anaesthesia chamber (13 × 13 × 30 cm), anaesthetised with isoflurane gas, and had PIT tags (Allflex Australasia, Palmerston North, New Zealand) injected under the skin between the shoulders. Animals were placed in a cotton bag for weighing and recovery, after which they were released at the site of capture. I identified tagged animals with a reader (Allflex RS200-1, France). Ship rats (*Rattus rattus*) were not tagged.

I used four male and four female laboratory rats (cross breeds between albino and hooded races) as lures. The lure rats were housed individually in custom made wooden and metal wire mesh cages (25 × 25 × 50 cm). Each cage incorporated a nest box, an inner food compartment and a water bottle. Grain-based pellets (Rodent chow 86, Massey University, Palmerston North, New Zealand) and fresh water were provided *ad libitum* throughout the experiment. Control cages were set up identically but without the lure rats.

All cages (lure rats and controls) were placed individually inside rectangular enclosures made of white corrugated plastic and metal wire mesh (40 × 60 × 80 cm) on a wooden frame. The top and sides of the enclosures were covered by corrugated plastic and the front, rear and floor were covered with wire mesh. Inside the enclosure, the cage was placed on one side and a double door live trap (as above) was placed on the other side with doors open to the front and the rear of the enclosure (Fig. 2.3.1 A). This design enabled me to protect the lure animals from the weather while providing the wild rats with a corridor to access the inner cage through the trap. To provide trapped animals with food and at the same time minimise the effect of food bait, I placed inside the traps small sealed plastic bags containing two or three rodent pellets. I distributed the enclosures in four clusters, each with a lure male, a lure female and control, separated by 20 (±5) m. The clusters fall within the

minimum home ranges recorded for both male and female Norway rats in natural and farming habitats (85–90 m; Innes 2005b). Control enclosures were always placed between the lure rat enclosures. The orientation of the male and female enclosures was random. Distances between clusters were 100 and 500 m apart (Fig. 2.3.1 C).

I conducted the experiment over 17 consecutive nights (total of 68 trap nights for each type of treatment). Enclosures were visited early mornings (0600–0800 hours) and any trapped Norway rats were processed using the same handling and tagging procedure as in the preliminary trapping. To avoid rat habituation to an enclosure, which could prevent other individuals from entering the traps, any Norway rats that were caught three times in the same trap were euthanased with isoflurane and removed from the site. I also recorded signs of rat activity around the enclosure (i.e. faeces and digging) and sprung traps. I used two infrared cameras coupled with a portable digital video recorder (AVerMedia, EB1304 MOB, Taiwan) to verify that the observed signs of activity were due to wild Norway rats.

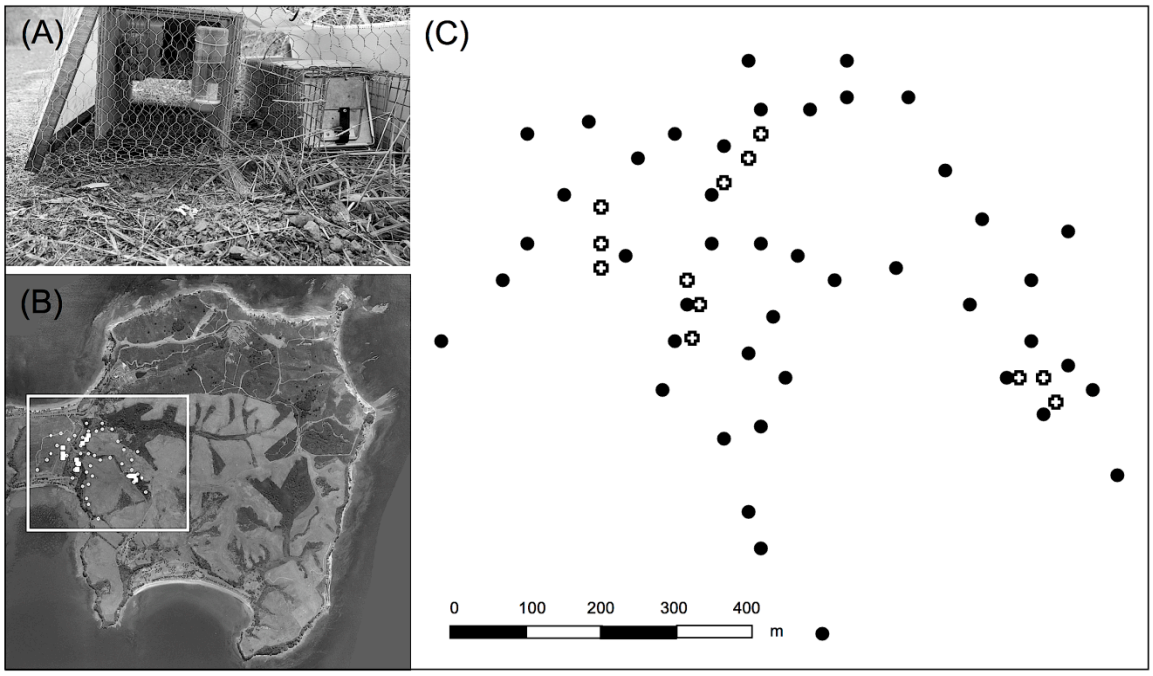

Figure 2.3.1. (A) Front view of a live lure enclosure showing the lure rat's cage (left) and the live trap (right). (B) Shakespear Regional Park with the study site and trap locations. (C) Enlarge scheme showing traps arrangement. Circles represent food bait traps and crosses represent lure rats and controls (each crosses cluster includes male and female lures and control). Aerial map courtesy of Land Information New Zealand. GIS layers by B. Kreigenhofer.

2.3.1 Data analysis

Conservative estimation of Norway rat densities was made by dividing the number of unique animals caught (during both bait and live-lure trappings) by the total area they were caught in. I considered 200 m beyond the clusters to be the area borders. I calculated corrected trap-night (CTN) values by subtracting half the number of trapping events and trap setoffs from the total number of trapping nights (Cunningham & Moors 1996). I compared trapping rates of Norway rats (not including recaptures) as a function of treatment (conspecifics vs controls), cluster (fixed factor), and CTN (variate), using ANOVA. I also used ANOVA to

compare trapping rates of Norway rats as a function of treatment (male vs female lures) and cluster. I used chi-square tests to compare gender distributions of trapped Norway rats for each treatment, as well as gender distributions of trapped Norway rats between lure males and lure females.

To evaluate trap efficiency, I compared the number of unique Norway rats caught per trap between food bait preliminary trapping and lure rat traps, using Chi-square contingency test. I also calculated rates of non-trapping activity made by Norway rats near the traps. Signs of activity (digging and scats) were marked as 1 for each night if present and 0 if not present. I then calculated the mean activity for near each.

2.4. Results

Total trappings of unique Norway rats (food-bait and live-lure trappings combined) yielded an estimation of five rats per hectare. Trapping rates of Norway rats were higher with lure rats than with control cages (ANOVA; $F_{1,25} = 248.18$, $P = 0.004$; Table 2.4.1). Cluster, but not CTN, had an effect on trapping rates (ANOVA; $F_{3,23} = 30.02$, $P = 0.032$; and $F_{1,25} = 0.062$, $P = 0.825$; respectively). There were no differences in trapping rates between male and female lures (ANOVA; $F_{1,25} = 0.333$, $P = 0.604$. Cluster did not have an effect on trapping rates (ANOVA; $F_{3,23} = 1.111$, $P = 0.466$).

Trapping efficiency (i.e. captures per trap laid) were higher using lure rats than food bats (Chi-square, $\chi^2 = 8.754$, df = 1, $P = 0.003$; Fig. 2.4.1). Signs of activity (in the form of digging and faeces) were recorded near six of the eight lure-rat enclosures (on up to 13 nights out of the total 17 per enclosure). Four of those had major digging under the enclosures and

they were re-excavated by the wild rats every night after I blocked the tunnels each morning. Rodent activity of this nature was never observed near control enclosures or near food-baited traps. Video footage verified that Norway rats were responsible for these signs of activity (no other species were recorded) and revealed that on eight occasions there were multiple wild rats at the enclosures simultaneously (six occasions of two rats and two occasions of three rats) and multiple cases of rats investigating the trap entrance but not entering the trap.

Ship rats were caught during the preliminary trapping and in the control cages (total of 17 animals) but never in the lure-rat cages. Video footage revealed that digging under enclosures was done by wild Norway rats, which otherwise exhibited non-aggressive behaviour. The infrared cameras detected ship rats near a lure-rat enclosure only after the lure animal was removed.

Table 2.4.1. Number of unique Norway rats caught with lure rats (males and females pooled) and controls (without lure rats) in four clusters (traps in a cluster were 20-25 m apart with the control always in the middle between the lures).

Cluster	Treatment	Trap nights (TN)	Corrected TN (CTN)	Total trappings	Trappings/CTN
A	Lures	34	30	7	7.93
A	Control	17	14.5	2	2.34
C	Lures	34	31.5	4	4.32
C	Control	17	17	0	0
E	Lures	34	31.5	5	5.4
E	Control	17	16	0	0
F	Lures	34	29	8	9.38
F	Control	17	15.5	3	3.29

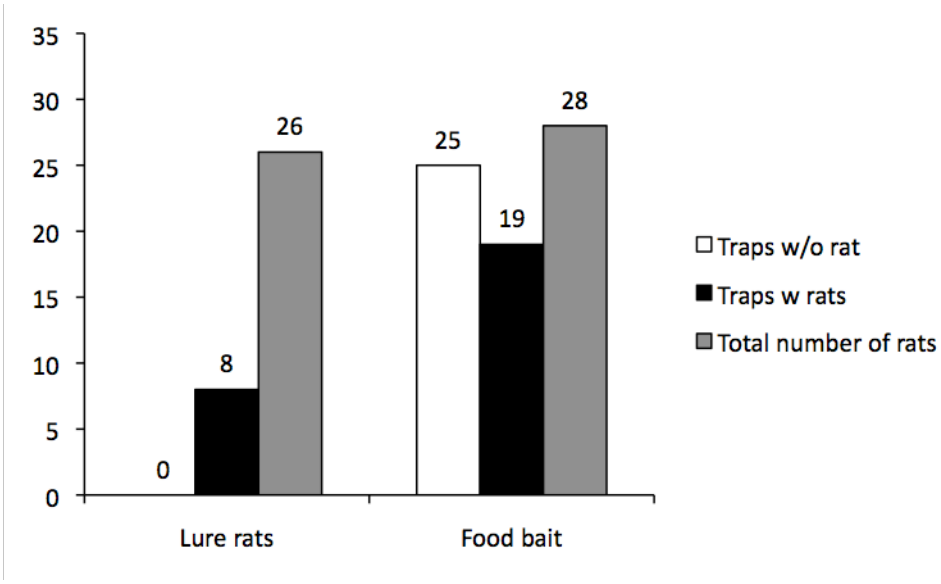

Figure 2.4.1. Trap efficacy showing traps that caught rats, traps that haven't caught rats and total numbers of rats caught (n values above columns). Lure rat traps were significantly more efficient ($P < 0.01$).

2.5. Discussion

All strains of laboratory rats are derived from wild Norway rats. Norway rats are highly social animals, exhibiting complex interactions including inter- and intra-sexual and within and between familiar and unfamiliar individuals (Barnett 1958; Calhoun 1963; Boreman & Price 1972; Alberts & Galef 1973; Robitaille & Bovet 1976; Galef & Allen 1995). I report here for the first time on the manipulation of the Norway rats' social traits, successfully using laboratory rats as lures for invasive wild Norway rats.

Norway rat density at the study site was estimated at five per hectare. This is probably an underestimate however, as trapping usually underestimates actual rat numbers (Innes 2005b). Moreover, at least half of the area used as the denominator for calculating density was formed of grazing paddocks (a very poor habitat) and therefore the realistic rat density in

the experimental area was probably higher. It is therefore safe to assume that rat density at the time of the study was relatively high (2.6–4.2 rats ha^{-1}, but up to 13 rats ha^{-1} in similar habitats; Innes 2005b).

Norway rats were more attracted to lure rats than to the control cages containing the same food and water as supplied to the lure animals. Norway rats are mobile foragers, but their home ranges can vary widely depending on population densities and food availability (Innes 2005b). Chance and Mead (1955) found that investigative behaviour in Norway rats was the dominant trait in an unfamiliar environment, but it did not conflict with other behaviours (i.e. feeding) once the animal was familiar with the environment. My results suggest, therefore, that the higher trapping rate with the lure-rat cages, and the rat activity observed near the lure rats' enclosures compared with the controls, were not random. Significant differences in trapping rates between the clusters were probably due to Norway rats' uneven spatial distribution, which is habitat dependent, as demonstrated by Innes et al. (2001).

There was no difference between the absolute numbers of rats caught with lure rats and by food baiting. However, trapping rates (average number of animals caught per trap laid) were higher when lure rats were used (i.e. the same number of unique trappings using many fewer traps). Moreover, detection of rat activity, in the form of faeces and digging, was observed only near lure rats. The observations from the video footage suggest that lure rats have the potential to attract more than one animal at a time, and that rats were visiting the lure rats without going into the traps. This suggests that the trapping rates with the lure rats are underestimating the true potential of this luring method.

I failed to detect significant differences in attractiveness based on the gender of the lure rats. Studies of social behaviour in the Norway rat have shown that when a new male (but not female) was introduced to a colony, it was attacked by the alpha male and to a lesser extent by the alpha female (Barnett 1958; Takahashi & Blanchard 1982). Calhoun (1963) found aggressive interactions within a colony to be inter- and intra-sexual, but male–male interactions were more common. The high trapping rates observed in this study suggest that it was not only dominant individuals that approached the cages. However, the apparently calm behaviour of the wild rats near the enclosure revealed by the video footage suggests that aggressiveness toward lure rats at these densities is probably not common and that attraction seems not to be based on aggression.

Our results also support findings by Shapira et al. (unpubl. data) suggesting that ship rats avoid laboratory rats when the latter are used as lures in the field. Findings by Wace (1986) suggesting some degree of trappability of invasive ship rats with lure laboratory rats might be the result of the former's naïveté to Norway rats at the study site. These rat species often share the same environment (Yom-Tov et al. 1999; Innes 2005a, b), where they compete for food and space. Dominance trends in the interactions of these species are apparently strongly influenced by habitat use (Harper et al. 2005; Harper 2006; King et al. 2011). However, the actual mechanisms of competition and competitive exclusion (i.e. direct or indirect) are poorly understood. My trapping results, together with the video footage (showing that ship rats were visiting the enclosure only after the lure animal was removed), suggest that this species avoids physical contact with Norway rats.

Species' behavioural traits are important considerations for understanding biological invasions (Holway & Suarez 1999), but despite their potential as a powerful tool for

conservation management (Buchholz 2007), the manipulation of invasive species' behaviour for pest control has been mostly limited to food baiting. Live animals are employed as lures for invasive heterospecifics, as in the case of the brown tree snake *Boiga irregularis* in Guam, which is attracted into traps by live mice (Vice et al. 2005), and invasive conspecifics such as radio-tagged wild goats are used to locate otherwise hidden aggregations of animals (Taylor & Katahira 1988). Examples of live luring, especially using conspecifics, are very limited however. My results demonstrate for the first time that conspecific attraction in an invasive rodent is feasible as a detection and capture tool.

Our lure system does not discriminate between the means of attraction and the relative importance of each sense. Both olfactory communication (Cheal 1975) and vocalisations are crucial aspects of Norway rat social behaviour (Barfield et al. 1979). The video footage hints that the presence of the actual animal can have considerable appeal, in which event a multi-modal form of signalling is probably the most effective method for luring conspecifics. Conspecific chemical attraction in the form of pheromones is regularly used to enhance pest-insect trapping rates (Burkholder & Ma 1985; Copping & Menn 2000) and attracting birds with conspecific playbacks is common as a conservation tool (Ward & Schlossberg 2004; Hahn & Silverman 2007). Rat beddings as well as playbacks will probably attract wild rats as well and I suggest that the effectiveness of rodent bedding and vocalisation should be tested as alternatives to live animals.

The live-lure-rat method discussed here is novel. My results demonstrate that there is a potential for its employment as an additional tool. Lawrence (1999) concluded that "live lures had no practical place in a stoat management operation and added considerably to the time it takes to check a trap line". Maintnance of caged live animals in the field can be

laborious and is definitely more complex than just food baiting. From my experience however, apart from the need to visit the traps daily, the maintanance of the lure animals was reasonable for a limited period of time and regarding the possible outcome of trappimg an invassive animal is probably worth the extra effort. Because maintenance of caged live animals in the field is probably impractical for long periods, I suggest that the potential to use this method as a part of a management strategy should be for specific events where food bait might fail (i.e. incursions, reinvasions) or for enforcement of existing control measures during sensitive periods (i.e. native birds' breeding seasons). In addition, by-products of signs of activity around lure traps (i.e. faeces, fur) might be useful for analysis of species present and individual recognition through DNA sampling. Further direct comparisons with other trapping methods are still required in these scenarios in order to determine this method's efficacy. Given the severe effects that invasive Norway rats pose on the environment, I believe this to be a promising line of research.

2.6. Acknowledgements

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2.7. References

Agmo A 2003. Unconditioned sexual incentive motivation in the male Norway rat (*Rattus norvegicus*). Journal of Comparative Psychology 117(1): 3-14.

Alberts JR, Galef BG 1973. Olfactory cues and movement: Stimuli mediating intraspecific aggression in the wild Norway rat. Journal of Comparative and Physiological Psychology 85: 233–242.

Barfield RJ, Auerbach P, Geyer LA, McIntosh TK 1979. Ultrasonic vocalizations in rat sexual behavior. American Zoologist 19: 469–480.

Barnett SA 1958. An analysis of social behaviour in wild rats. Proceedings of the Zoological Society of London 130: 107–152.

Boonstra R, Krebs CJ 1976. The effect of odour on trap response in *Microtus townsendii*. Journal of Zoology 180: 467-476.

Boreman J, Price E 1972. Social dominance in wild and domestic Norway rats (*Rattus norvegicus*). Animal Behaviour 20: 534–542.

Buchholz R 2007. Behavioural biology: an effective and relevant conservation tool. Trends in Ecology & Evolution 22: 401–407.

Burkholder WE, Ma M 1985. Pheromones for monitoring and control of stored-product insects. Annual Review of Entomology 30: 257–272.

Calhoun JB 1963. The ecology and sociology of the Norway rat. Bethesda, MD, U.S. Dept. of Health, Education, and Welfare, Public Health Service.

Chance MRA, Mead AP 1955. Competition between feeding and investigation in the rat. Behaviour 8: 174–182.

Cheal M 1975. Social olfaction: a review of the ontogeny of olfactory influences on vertebrate behavior. Behavioral Biology 15: 1–25.

Copping LG, Menn JJ 2000. Biopesticides: a review of their action, applications and efficacy. Pest Management Science 56: 651–676.

Cunningham DM, Moors PJ 1996. Guide to the identification and collection of New Zealand rodents. 3rd edn. Wellington, Department of Conservation. 24 p.

Daly M, Wilson MI, Behrends P 1980. Factors affecting rodents' responses to odours of strangers encountered in the field: experiments with odour-baited traps. Behavioral Ecology and Sociobiology 6: 323–329.

Dilks P, Towns D 2002. Developing tools to detect and respond to rodent invasions of islands: workshop report and recommendations. DOC Science Internal Series 59. Wellington, Department of Conservation. 19 p.

Galef BG 2005. Social Learning. In: Whishaw IQ, Kolb B ed. The Behavior of the Laboratory rat. New York, Oxford University Press. Pp. 363-370.

Galef BG Jr, Allen C 1995. A new model system for studying behavioural traditions in animals. Animal Behaviour 50: 705–717.

Hahn BA, Silverman ED 2007. Managing breeding forest songbirds with conspecific song playbacks. Animal Conservation 10: 436–441.

Harper GA 2005. Heavy rimu (*Dacrydium cupressinum*) mast seeding and rat (*Rattus* spp.) population eruptions on Stewart Island/Rakiura. New Zealand Journal of Zoology 32: 155–162.

Harper GA 2006. Habitat use by three rat species (*Rattus spp*.) on an island without other mammalian predators. New Zealand Journal of Ecology 30: 321–333.

Harper GA, Dickinson KJM, Seddon PJ 2005. Habitat use by three rat species (*Rattus spp*.) on Stewart Island/Rakiura, New Zealand. New Zealand Journal of Ecology 29: 251–260.

Holway DA, Suarez AV 1999. Animal behavior: an essential component of invasion biology. Trends in Ecology & Evolution 14: 328–330.

Howald G, Donlan CJ, Galván JP, Russell JC, Parkes J, Samaniego A, Wang Y, Veitch D, Genovesi P, Pascal M, Saunders A, Tershey B 2007. Invasive rodent eradication on islands. Conservation Biology 21: 1258–1268.

Innes JG 2005a. Ship rat. In: King CM ed. The handbook of New Zealand mammals. 2nd edn. Melbourne, Oxford University Press. Pp. 187–203.

Innes JG 2005b. Norway rat. In: King CM ed. The handbook of New Zealand mammals. 2nd edn. Melbourne, Oxford University Press. Pp. 174–187.

Innes JG, King CM, Flux M, Kimberley MO 2001. Population biology of the ship rat and Norway rat in Pureora Forest Park, 1983-87. New Zealand Journal of Zoology 28: 57–78.

Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22: 16–26.

King CM, Foster S, Miller S 2011. Invasive European rats in Britain and New Zealand: same species, different outcomes. Journal of Zoology 285: 172–179.

Lawrence B 1999. Live rats and mice as lures for stoats. Conservation Advisory Science Notes 234. Wellington, Department of Conservation. 2 p.

Long JL 2003. Introduced mammals of the world. Collingwood, CSIRO. 589 p.

Masuda BM, Jamieson IG 2013. Response of a reintroduced bird population to a rat reinvasion and eradication. New Zealand Journal of Ecology In Press.

Robitaille JA, Bovet J 1976. Field observations on social behaviour of the Norway rat, *Rattus norvegicus* (Berkenhout). Biology of Behaviour 1: 289–308.

Russell JC, Towns DR, Anderson SH, Clout MN 2005. Intercepting the first rat ashore. Nature 437(7062): 1107.

Russell JC, Towns DR, Clout MN 2008a. Review of rat invasion biology: implications for island biosecurity. Science for Conservation 286. Wellington, Department of Conservation. 53 p.

Russell JC, Beaven BM, MacKay JWB, Towns DR, Clout MN 2008b. Testing island biosecurity systems for invasive rats. Wildlife Research 35: 215–221.

Speedy C, Day T, Innes J 2007. Pest eradication technology – the critical partner to pest exclusion technology: the Maungatautari experience. In: Witmer GW, Pitt WC, Fagerstone KA ed. Managing Vertebrate Invasive Species. Fort Collins, Colorado, University of Nebraska. Pp. 115-126.

Takahashi LK, Blanchard RJ 1982. Attack and defense in laboratory and wild Norway and black rats. Behavioural Processes 7: 49–62.

Taylor D, Katahira L 1988. Radio telemetry as an aid in eradicating remnant feral goats. Wildlife Society Bulletin 16: 297–299.

Thorsen M, Shorten R, Lucking R, Lucking V 2000. Norway rats (*Rattus norvegicus*) on Frégate Island, Seychelles: the invasion; subsequent eradication attempts and implications for the island's fauna. Biological Conservation 96: 133–138.

Tidemann C 2005. Indian mynas – can the problems be controlled? In: Hayward M ed. Proceedings of the 15th National Urban Animal Management Conference, Canberra, 19–21 October 2005. Artamon, Australian Veterinary Association. Pp. 55–57.

Towns DR, Broome KG 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. New Zealand Journal of Zoology 30: 377–398.

Tsachalidis EP, Sokos CK, Birtsas PK, Patsikas NK 2006. The Australian crow trap and the Larsen trap: their capture success in Greece. In: Manolas EI ed. Proceedings of the 2006 Naxos International Conference on Sustainable Management and Development of Mountainous and Island Areas. Island of Naxos, Democritus University of Thrace. Pp. 325–329.

Stoddart DM 1986. The comparative responses of mice and voles to conspecific and heterospecific odors in the field - a lesson in social behavior. Chemical Signals in Vertebrates 4: 533-540.

Vice DS, Engeman RM, Vice DL 2005. A comparison of three trap designs for capturing brown treesnakes on Guam. Wildlife Research 32: 355–359.

Volfová R, Stejskal V, Aulicky R, Frynta D 2011. Presence of conspecific odours enhances responses of commensal house mice (*Mus musculus*) to bait stations. International Journal of Pest Management 57: 35–40.

Wace NM 1986. The rat problem on oceanic islands—research is needed. Oryx 20: 79–86.

Ward MP, Schlossberg S 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18: 519–525.

Yom-Tov Y, Yom-Tov S, Moller H 1999. Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. Journal of Biogeography 26: 947–958.

CHAPTER 3: LABORATORY RATS AS CONSPECIFIC BIOCONTROL AGENTS FOR INVASIVE NORWAY RATS *RATTUS NORVEGICUS*

3.1. Abstract

I tested whether conspecific attraction can be more efficient than food bait for the detection and capture of an invasive, social species, the Norway rat *Rattus norvegicus*. I compared trapping rates between male and female laboratory rats and food-baited controls at four mainland sites with low rat population densities, three recreational sites (zoos) with an abundance of food in the environment, and in manipulated island rat incursions. Live lures were more efficient than food baits at both the mainland and recreational sites. There were no differences between the attractiveness of lure animals based on gender either of the lure or of the captured animals. In the manipulated rat incursions, where three radio collared male rats were released on a rat free island, two animals were caught using female lures, and the third lost its collar and evaded detection. The current study attempts to promote the idea that animal behaviour can help inform and guide innovative tools for the control and management of invasive species. I show that laboratory rats can be more efficient as lures for their wild counterparts than food bait. Furthermore, these results emphasize the need for a flexible and varied rat control toolbox. I suggest that the use of laboratory rats as lures should be considered in future control management plans for invasive Norway rats.

3.2. Introduction

Biological invasions are recognized as one of the main drivers of biodiversity loss and the advancement of species homogenization (Clavero et al. 2009; Davis 2009; Primack 2010). Many vertebrate species have been intentionally or accidentally introduced worldwide and are now the target of intensive control measures (Long 2003). The Norway rat *Rattus norvegicus* (Rodentia: Muridae, Berkenhout 1769) is a highly invasive species worldwide (Long 2003), and as with other invasive rodents, it can pose major threats in terms of human health (Epstein 1995; Mills & Childs 1998; Meerburg et al. 2009b), agricultural crop damage (Meyer 1999; Stenseth et al. 2003; Meerburg et al. 2009a) and to natural ecosystems (Atkinson 1978; Campbell 1978; Ramsay 1978; Simberloff 2009; St Clair 2011). To eradicate or control invasive and pest rodents, considerable resources are invested annually by governmental and non-governmental agencies (Meyer 1999; Dilks & Towns 2002; Stenseth et al. 2003; Coomes et al. 2006; Meerburg et al. 2009a).

Eradication campaigns of *R. norvegicus* have gained much success on islands (Howald et al. 2007), but the detection of reinvasions and the eradication of remnant populations that have evaded control measures, remain a challenge (Russell et al. 2005; Russell et al. 2008a; Russell et al. 2008b). When rats invade new environments or when their populations are at low densities, natural food is usually abundant and animals tend to avoid food-baited trapping devices (Russell et al. 2005; Russell et al. 2008b; Masuda & Jamieson 2013). Moreover, exploratory and movement behaviour of invading *R. norvegicus* is thus far unpredictable (Russell et al. 2010), leading to difficulties in spatial placing of surveillance systems. Therefore, the detection and capture of rats usually requires broadly based surveillance systems, considerable effort in manpower, and may extend over long periods of time (Russell et al. 2005; Clapperton 2006; Russell et al. 2008b). The early detection and

capture of invasive species is critical to prevent establishment (Masuda & Jamieson 2013), and thus limiting the negative effects on vulnerable native species (Taylor & Hastings 2005).

The most widespread control method for invasive rodents is trapping and poisoning using food as bait (Clapperton et al. 1994b; Murphy et al. 1999; Donlan et al. 2003; Clapperton 2006; Howald et al. 2007; King et al. 2009). Baiting is probably the easiest way to target animals, as supplementary food will be attractive in most environments. However, when populations of the target animals are at low densities or when food is abundant, bait might be ignored (Russell & Clout 2005; MacKay et al. 2007; Russell et al. 2008b; King et al. 2009).

Exploiting conspecific attraction by means of live lures has been used, although in a limited way, to aid the control of invasive and pest vertebrate species. These include the so-called "Judas" goats, where GPS-collared animals help in the location of remnant invasive counterparts (Taylor & Katahira 1988), as well as in improving the luring of invasive crows and mynas into traps (Tidemann 2005; Tsachalidis et al. 2006). Conspecific odours were found to be efficient as attractants for some rodent species (Boonstra & Krebs 1976; Stoddart 1986; Volfova et al. 2011), but other studies show limited success (Daly et al. 1980). Here, I test the live lure hypothesis, which predicts that in a highly social species at low population densities, animals may prioritize intraspecific interactions over foraging for supplementary food. Vocalizations, as well as, olfactory cues, plays an important role in rodent communication (Barfield et al. 1979). I therefore chose to use live animals because the relative importance of each sense in rodent social interactions is largely unknown, and confining the study to scent alone might limit the power of attraction.

Rattus norvegicus is a highly sociable species, with complex inter- and intra-sexual interactions (Barnett 1958; Calhoun 1963; Boreman & Price 1972; Alberts & Galef 1973; Robitaille & Bovet 1976; Galef & Allen 1995; Agmo 2003; Galef 2005). A recent study demonstrated that social traits in laboratory rats may be the motivation for performing 'helping' actions towards captive conspecifics (Ben-Ami Bartal et al. 2011). However, despite the apparent relevance of species-specific traits for invasive species control measures (Clapperton 2006), current practices tend to ignore them and use general food items with no specific target. The highly social traits of *R. norvegicus* can potentially aid its control, but the efficacy of targeting animals using conspecifics as lures compared with food-baited devices has not been tested before.

Based on *R. norvegicus* incursion characteristics (e.g. the potential for avoiding surveillance systems) and their social behaviour characteristics, I tested the live lure hypothesis using live laboratory rats (the domesticated form of *R. norvegicus*) as lures for wild invasive conspecifics in three scenarios: low rat population densities, abundance of available food, and manipulated island incursion. In all three scenarios, the live lure hypothesis predicts that invasive *R. norvegicus* would be more attracted to conspecifics than to food bait. I further predicted that males, the more spatially active sex (Innes 2005), would be trapped more frequently than females, and that female lure rats would be more attractive than males, because of their sexual attractiveness to males and their less aggressive social attraction (Barnett 1958; Boreman & Price 1972) to other females compared with males. Based on the findings of this study, I aimed to provide an assessment of the feasibility of the live luring method as a supplementary and effective tool to aid *R. norvegicus* control management.

3.3. Methods

Sexually mature female and male laboratory rats (albino and hooded) were used as live lures for wild invasive *R. norvegicus*. Rats were obtained from the University of Auckland (New Zealand experiments) and the National Cancer Institute (Washington DC experiment). Rats were provided with *ad libitum* rodent pellets (diet 86, Massey University, Palmerston North, New Zealand, and Prolab RMH 3000, LabDiet, St. Louis, MO, USA) and water throughout the experiments in both the laboratory and in the field. This study was approved by, and carried out according to the requirements and restrictions of, The Massey University Animal Ethics Committee, Auckland Zoo Animal Ethics Committee and the Animal Ethics Committee of the Smithsonian National Zoological Park.

Shapira et al. (2013) demonstrated that live lures were significantly more attractive to invasive wild *R. norvegicus* than similar trapping devices without a rat, and also that the rat food (pellets) by itself did not affect rat trappability. Therefore, I did not used rat food control during the following experiments. The majority of the control trapping devices used as food-baited traps was wooden boxes (25 x 25 x 40 cm) containing a DOC 200 break-back trap (CMI Springs, Auckland, New Zealand) (Fig. 3.3.1A, D). The DOC 200 trap comprises a treadle plate and parallel strike bars on an arm powered by two coil springs (120 x 90 mm). When set, the strike bars are in a vertical position 90^{o} to the treadle. When an animal walks across the treadle, the trap is triggered and the strike bars rapidly close over the treadle and onto the animal's dorsal surface. I also used black plastic tunnels with Fenn kill traps (Philproof, Hamilton, New Zealand). Both these trapping devices are widely used in New Zealand for pest control.

Two types of live lure trapping devices were used across the experiments. The type 1 live lure trapping device was designed as an A-frame shaped enclosure (80H x 85W x 92L cm), made from a wooden frame, coreflute roofing and metal wire mesh sides and floor (Fig. 3.3.1B), enclosing a live lure animal housed in a wood/metal wire mesh cage (25H x 25W x 50L cm) with an elevated nest box. Each enclosure had four entrances (two in each meshed side), with a DOC 200 kill trap fitted to each entrance. To approach the caged live lure, a wild rat had to go through one of the kill traps. The entrances were either flat holes 9 cm in diameter or, when necessary, were fitted with a 10-cm long plastic pipe to prevent pets and the general public from reaching the traps. The type 2 live lure trapping devices were wooden freestanding cages (70 x 25 x 25 cm), with two compartments separated by wire mesh: a trap compartment (30 x 25 x 25 cm) with a single DOC 200 (in type 1, the set-off of one trap usually resulted in the triggering of the other three traps); and a cage compartment (40 x 25 x 25) housing the live lure (Fig. 3.3.1C, E). The latter had a wire mesh floor to prevent accumulation of debris, and an elevated nest box. The cages were covered with coreflute to protect the live lures from rain. For both cage types, straw was provided as bedding material in the nest boxes.

3.3.1. Experiment 1 (E1): Conspecific attraction at low rat population densities

The efficacy of live lures versus food-baited control was tested in situations where rats were found at low population densities. The experiment took place during the austral spring and summer of 2010-2011 at four sites near Auckland, New Zealand with ongoing rodent control. Low and high population densities are relative and as incomplete data were available

quantitative estimates were not possible. Hence, I define low density as rare trapping events within the managed sites (J. Staniland, T. Lawson, P. Stevenson, S. Burgess, *pers. comm.*). In each location, experimental work was approved by site authorities/owners. Site 1 (S1; 36º52'07.06" S-174º28'31.79 E), Matuku Reserve (Forest and Bird), was dominated by regenerating forest and borders the Bethells River wetlands. Extensive pest control at this site included kill traps and poison bait stations. No *R. norvegicus* have been caught inside the reserve within the last three years (J. Staniland, *pers. comm*.). Sites 2 and 3 (S2; 36º52'14.97" S-174º27'45.04 E and S3; 36º52'36.19" S-174º26'58.81 E) were privately owned properties, comprising livestock pastures and bordering the Bethells River wetlands. Moderate *ad hoc* pest control on both properties has occurred over the last few years, including kill traps and poison bait stations. Quantitative information on the rates of rat trapping was not available at these sites, but trappings prior to my trial were low (T. Lawson, P. Stevenson, *pers. comm.*). Site 4 (S4; 36º36'16.37" S-174º49'32.24 E), Shakespear Open Sanctuary (Auckland Council), is composed of regenerating bush, livestock pasture and wetlands. The trapping sessions were conducted at the boundary zone immediately outside the park's predator proof fence. The fence was constructed between 2010 and 2011 and an aerial poison drop was conducted within the Sanctuary. Extensive and ongoing pest control operations, including kill traps and poison bait stations, occur in the boundary zone. *Rattus norvegicus* had been caught regularly at the site prior to the construction of the predator proof fence, but in low numbers the years prior to the 2010 trial (S. Burgess, *pers. comm*.) and none was caught during the three months prior to the 2011 trial (M. Maitland, *pers. comm*.).

Control traps at S1 and S4 were based on existing trap lines plus additional traps placed as part of this study. At S2 and S3 I provided all of the control traps. Control traps

were baited with hen eggs and peanut butter (refreshed every 3-4 days). Existing traps were baited weekly with rabbit meat. Within a site, the distance between two neighbouring live lure traps was 25-100 m. The distance between live lure and control traps was generally 50 m, although two were approximately 10 m. This variation was due to the availability of suitable locations (i.e. levelled surface, relative shelter for the live lure cages and site access). All trapping devices were placed on the margins of wetlands (1-50 m from the waterline). Table 3.3.1 summarizes the numbers of traps, trapping effort and trapping device types at each site.

3.3.2. Experiment 2 (E2): Conspecific attraction in areas of high food abundance

The efficacy of live lures versus food-baited controls was tested in situations where food was abundant and pest control (especially the use of poison) was limited. Zoological parks are ideal environments for this as they meet both of the above criteria. I conducted all of these experiments during 2012. Sites included the Auckland Zoo (AZ, Auckland, New Zealand) where experiments were conducted during the austral summer (January-February) and winter (July), Hamilton Zoo (HZ, Hamilton, New Zealand) where experiments were conducted during the austral autumn (May), and the Smithsonian National Zoological Park (SNZP, Washington DC, USA) where experiments were conducted during the boreal summer (July). The seasonal timing of the experiments was dictated by each zoo's administration.

I used type 2 devices as live lure traps and boxed DOC 200s as food-baited control traps (see above) at all zoos, with the exception of one Fenn trap, which was used as a control at HZ. Each live lure trap was paired with a control trap, separated by 2-4 m. Other control

measures (i.e. kill traps and bait stations) deployed by site management in different locations on site were normally active during the experiments. Experimental design varied between sites in accordance with site regulations, size and management constraints. At AZ, traps were relocated after two weeks. At HZ, traps containing male and female lures were swapped between locations after two weeks. At SNZP, two traps were relocated, and all traps were deactivated during the weekends and during harsh weather conditions (e.g., an extreme heat wave of over 35° Celsius). Controls were baited with hen eggs and peanut butter. At SNZP, salami was added to control traps because peanut butter was eaten by ants. Table 3.3.1 summarizes the number of traps and trapping nights used at each site. All traps were visited daily and food and water for the lure rats was checked and added/replaced as necessary. Food bait was refreshed every three to four days.

Table 3.3.1. Type of trapping devices and trapping effort during experiments 1 (E1) and 2 (E2).

Trapping devices and effort at sites with low rat population densities (E1)						
Site	Year	LL devices	C devices	FL No./TN	ML No./TN	C No./TN
S1	2010	Type 1 [a]	DOC 200/Fenn	5/75	5/75	18/270
S2	2010	Type 1 [a]	DOC 200	3/45	3/45	3/45
S3	2010	Type 1 [a]	DOC 200	2/30	2/30	2/30
S4	2010	Type 1 [a]	DOC 200/Fenn	5/75	5/75	56/840
S4	2011	Type 2 [b]	DOC 200/Fenn	4/116	4/116	45/1305
Total				19/341	19/341	124/2490
Trapping devices and effort at sites with high food abundance (E2)						
Site	Season	LL devices	C devices	FL No./TN	ML No./TN	C No./TN
AZ	Summer	Type 2 [b]	DOC 200	5/115	5/115	10/230
AZ	Winter	Type 2 [b]	DOC 200	4/108	4/108	8/216
HZ	Winter	Type 2 [b]	DOC 200/Fenn	3/78	3/78	6/156
SNZP	Summer	Type 2 [b]	DOC 200	5/65	5/65	10/130
Total				17/366	17/366	34/732

LL = live lure, C = control, FL = female lure, ML = male lure, TN = trap nights.

AZ = Auckland Zoo, HZ = Hamilton Zoo, SNZP = Smithsonian National Zoological Park.

[a] A-frame shaped enclosure housing live lure cage (see Fig. 3.3.1 B).

[b] Two compartments (live lure/DOC-200) freestanding cage (see Fig. 3.3.1 C, E).

3.3.3. Experiment 3 (E3): Conspecific attraction in island rat incursions

The efficacy of live lures versus food-baited controls was tested in a scenario resembling a rat incursion of a rat free island. The experiment took place during the austral autumn-winter of 2012 on 60-ha Browns Island (Motukorea; 36º49'50.21" S-174º53'40.14 E), Hauraki Gulf, New Zealand. The experiment was approved by the New Zealand Department of Conservation (DOC), permit number AK-26759-RES. *R. norvegicus* and the house mouse *Mus musculus* (Linnaeus 1758) were eradicated from the island in 1995 (Veitch 2002). The island comprises a conical volcanic crater 60 m high on its northern side, two plateaus to the

south and west, and a valley and ridge to the east. Vegetation cover is almost exclusively rank grasses, dominated by kikuyu *Pennisetum clandestinum*. Small patches of regenerating bush and stand-alone mature trees are found mainly on cliffs and along the coastline. The island is a recreational reserve managed by the Department of Conservation.

I manipulated three single incursion scenarios by male *R. norvegicus*. The rats were live trapped in marshlands, west of Auckland, using double doors traps (16H x 16W x 70L cm, Neal Blaymires, Te Puke, New Zealand) baited with peanut butter. Trapping was conducted five to six days before the island releases occurred. Captured animals were housed in a large outdoor cage (3m L x 1m W x 2m H) and were provided with *ad libitum* water, rodent pellets, fruit and vegetables. The rats were anesthetized (using isoflurane via the respiratory system) and a single stage VHF radio transmitter (Sirtrack, Havelock, New Zealand) was attached using a neck collar (total weight <5% of the animal's body weight) within 48 hours of capture. To minimize the effect of conspecific scent, the first two animals were released at two different coastal points (c. 600 m apart) on the island and the third animal was released 10 days after the first animal was removed from the island.

The island has permanent traps and tracking tunnels along the coastline as a surveillance measure against pest incursions. On the days of release, all regular permanent traps were closed, but the tracking tunnels were kept baited with peanut butter. Each animal was released during the day and allowed to run free for three consecutive nights. Each day I monitored their positions using a VHF receiver (Model R1000, Communications Specialists Inc., CA, USA) fitted with a directional antenna and checked tracking tunnels for footprints (to minimize disturbance to the rats, I did not track them during the night). After three nights, I placed two type 2 (see above) live lure traps (one containing a male and one containing a

female) and four control (boxed DOC 200, see above) traps (baited with hen eggs and peanut butter) 5 to 10 m from the last confirmed position for each rat. Two of the control traps were paired with the live lure traps and the other two control traps were placed separately (Fig. 3.3.2). This trapping effort continued until the released rat was recaptured.

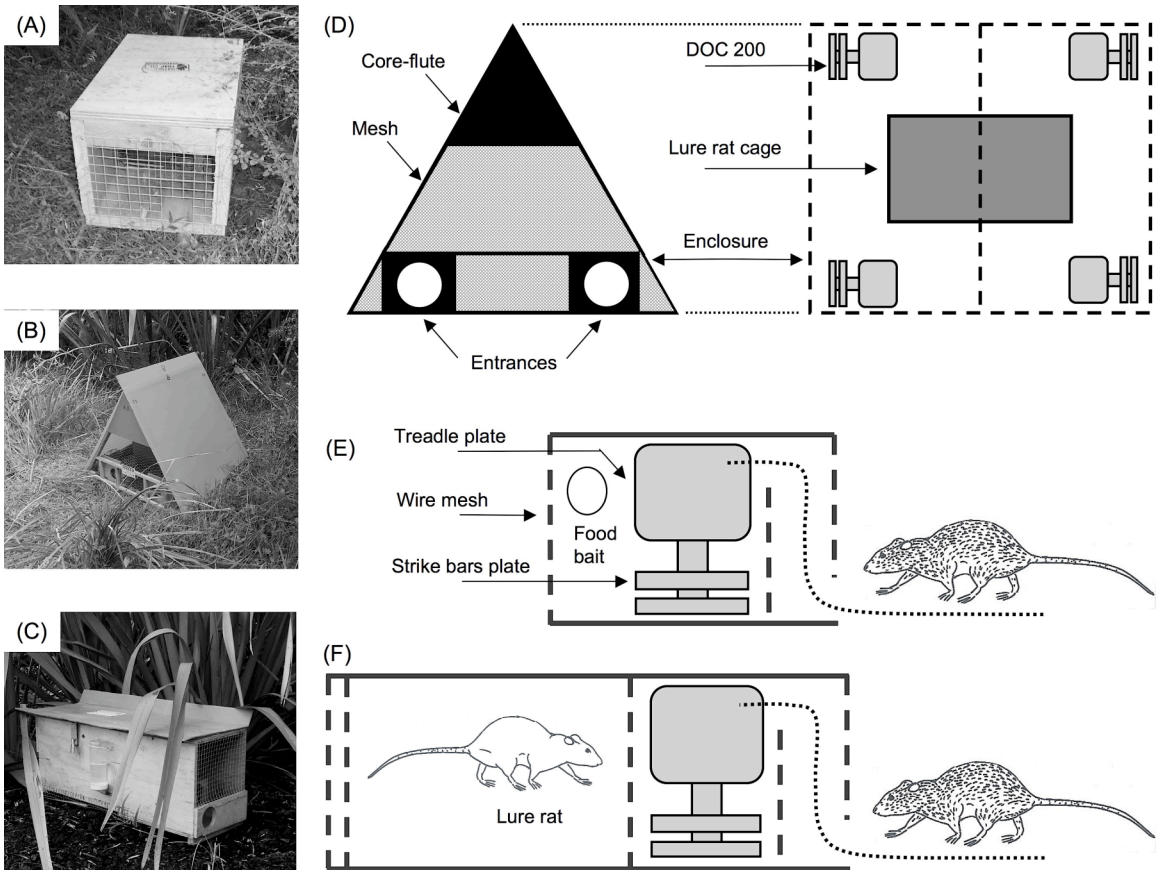

Figure 3.3.1. Three trapping devices used during the experiments. **(**A) The commonly used wooden box designated for DOC 200 trap and food bait. (B) An A-frame shaped enclosure housing the live lure rat's cage with four DOC 200 traps at the entrances (live lure device type 1). (C) Two compartments (live-lure/DOC-200) freestanding live lure cage (live lure device type 2). (D) Schematic side and upper views of live lure device type 1. (E) Schematic upper view of boxed DOC 200 (food baited). (F) Schematic upper view of live lure device type 2. A rat entering through the two opposite holes steps on the treadle plate and triggers the strike bars plate that close down from 90^{o} onto the treadle plate with the force of two coil springs and thus render the rat unconscious within 20 s maximum.

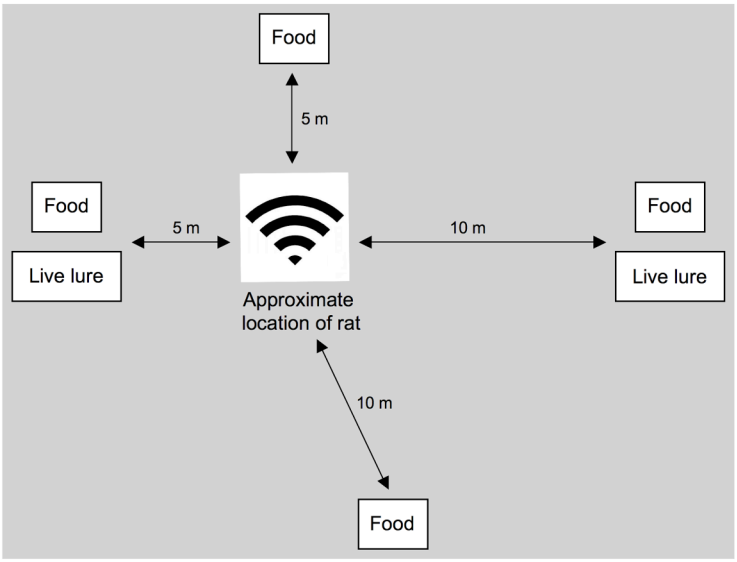

Figure 3.3.2. Arrangement of traps laid around a rat rest site (as indicated from the VHF signal) at Browns Island (E3). Indicated distances are approximate. Assignment of male and female lures was random.

3.3.4. Data analysis

In E1 I calculated the number of trap nights (TN) at each site (see Table 3.3.1) for male lures, female lures, and controls. I combined the TN across the sites and calculated the expected trapping frequencies and proportions of the total number of *R. norvegicus* trapped relative to the TN. A one-dimensional Goodness of Fit test was performed to calculate the value of Chi-square, comparing the actual frequencies of capture by male lures, female lures, and controls against expected frequencies. I also calculated the percentage deviation, standardized residuals and adjusted standardized residuals for each group to provide an estimation of each group's contribution to the deviation from the expected frequencies. I performed paired t-tests to compare trapping frequencies of male and female rats trapped with lures only and trapping frequencies between male and female lures (see table 3.3.2. for specific data).

Table 3.3.2 Trapping frequencies of *R. norvegicus* caught with female (F) and male (M) lures and of females and males caught.

Site	Caught in F lure	Caught in M lure	F caught	M caught
S1 (2010)	3	0	0	3
S2 (2010)	2	3	3	2
S3 (2010)	1	0	0	1
S4 (2010)	3	1	2	2
S4 (2011)	2	0	0	2

In E2 I compared the total number of captures throughout the experiments between lures (males and females combined) versus controls for each trap pair using multifactor ANOVA. I tested the effect of treatment (lure and control), site, and season (summer and winter) on capture rates. I performed Goodness of Fit Chi-square tests on lure captures only, to test for differences between 1) gender of the trapped animals and 2) gender of the lure animals.

In E3, having only two animals in the experiment, I was able to refer to the results only as qualitative but not quantitative.

3.4. Results

During E1 I caught 11 *R. norvegicus* in female lure traps, four in male lure traps, and two in control traps (Fig. 3.4.1A-C). At all of the sites except for S3, the first animals were always caught between days one and two of the start of the trappings and most of the animals were caught during the first half of the trapping sessions (table 3.4.1). Trapping frequencies were significantly higher with live lures compared with controls ($\chi^2_2 = 58.27$, $P < 0.0001$). Calculations of percentage deviation, standardized residuals and adjusted standardized

residuals revealed that all factors (female lures, male lures and controls) significantly contributed to the deviation from the expected values (see table 3.4.2 for summary). Trapping frequencies of male and female rats were not different (paired t-test; t = -1.414, df = 4, P = 0.23). Differences between numbers of rats caught with female versus male lures were not significant (paired sample t-test; t = 2.064, df = 4, P = 0.108; see table 3.4.3 for summary of captures as a function of gender).

During E2 I caught 11 *R. norvegicus* in female lure traps, 14 in male lure traps and seven in control traps (Fig. 3.4.2). Treatment had a significant effect on trapping, with more animals trapped in lure traps than in controls (ANOVA; $F_{1,62}$ = 8.8944, P = 0.004). There was no effect of either site or season (ANOVA; $F_{1,62}$ = 1.496, P = 0.225; $F_{1,62}$ = 0.347, P = 0.557; respectively). There were no differences between the numbers of female and male rats caught or the trapping frequencies by female and male lures (χ^2_1 = 1.44, P = 0.23; χ^2_1 = 0.00, P = 1.00; respectively; see table 3.4.3 for summary of captures as a function of gender).

During E3, two of the male *R. norvegicus* released on Browns Island were recaptured with female lures (see table 3.4.3 for summary of captures as a function of gender), one on the first night of trapping and one on the fifth night. Trapping frequencies significantly differed from the expected (Goodness of Fit; χ^2_2 = 9.76, P < 0.001). The first rat remained at the release point during the day but footprints in two tracking tunnels indicated that it travelled at least 500 m during the night. The second rat travelled (without going into tracking tunnels) at least 650 m from the release point to a rest point where it remained during the day and for the period prior to recapture (Fig. 3.4.3A-B). The third rat (a young animal) lost its VHF collar shortly after release and is not included in the analyses presented here, as its location is required to fulfil my methodology. I attempted to locate this missing

rat by setting eight lure rat traps and 10 baited traps around the island for a 10 day period, along with two extensive searches with a New Zealand Department of Conservation (DOC) certified rodent sniffing dog (Gsell et al. 2010; Shapira et al. 2011). A Norway rat was caught on the island five to six weeks later in the existing trap grid. This is likely to have been the rat I released but I cannot confirm this.

Table 3.4.1. First and last animals to be caught and total captures at each site during experiment 1 (E1).

Site	Year	First and last animal trapped with lures (night /total nights)	First and last animal trapped with controls (night /total nights)	Total trapped with lures	Total trapped with controls
S1	2010	1/15 – 6/15	0/15	3	0
S2	2010	2/15 – 15/15	15/15	5	1
S3	2010	10/15	0/15	1	0
S4	2010	2/15 – 4/15	2/15	4	1
S4	2011	5/28 – 15/28	0/28	2	0

Table 3.4.2. Calculations of adjusted standardized residuals to test category contribution to the observed deviation from the expected frequencies for trappings in experiment 1 (E1).

Trap lure	Observed frequency	Expected frequency	Expected proportion	Percentage deviation	Standardized residuals (SR)	Row total proportions	Column total proportions	Adjusted SR (ASR)	Test statistic for ASR= +/-2.0
Females	11	1.83	0.1075	501.9	6.78	1	0.61	8.67	$P < 0.05$
Males	4	1.83	0.1075	118.58	1.6	1	0.22	3.4	$P < 0.05$
Controls	2	13.35	0.785	-85.02	-3.11	1	0.11	-9.32	$P < 0.05$

Table 3.4.3. Capture frequencies of *R. norvegicus* as a function of the gender of both the trapped and the lure animals in the three experiments.

Experiment	M at lure M	M at lure F	F at lure M	F at lure F
E1	3	9	1	2
E2	8	8	4	5
E3	0	2	0	0

M = males, F = females

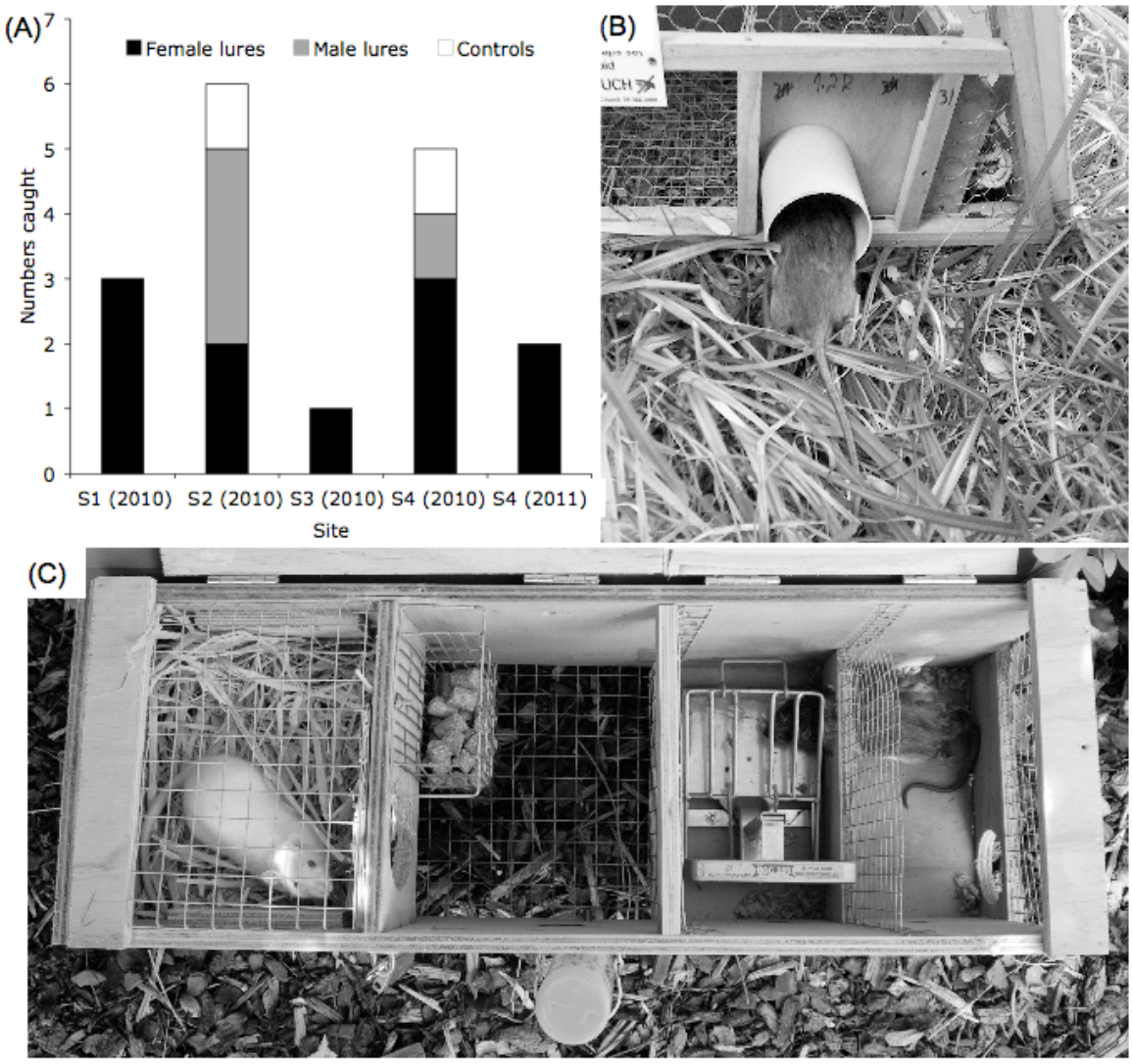

Figure 3.4.1. Wild invasive Norway rats caught at the four mainland sites (S1-4, E1) with low rat population densities. (A) Rats trapped with female and male live lures and food-baited controls. Trapping frequencies were significantly higher with live lures (Chi-square, $P < 0.001$). (B) Wild *R. norvegicus* caught at the entrance of a live lure enclosure. (C) Wild *R. norvegicus* caught in the trap compartment (right) of a freestanding live lure cage. The lure albino laboratory rat is seen on the left in its nest box.

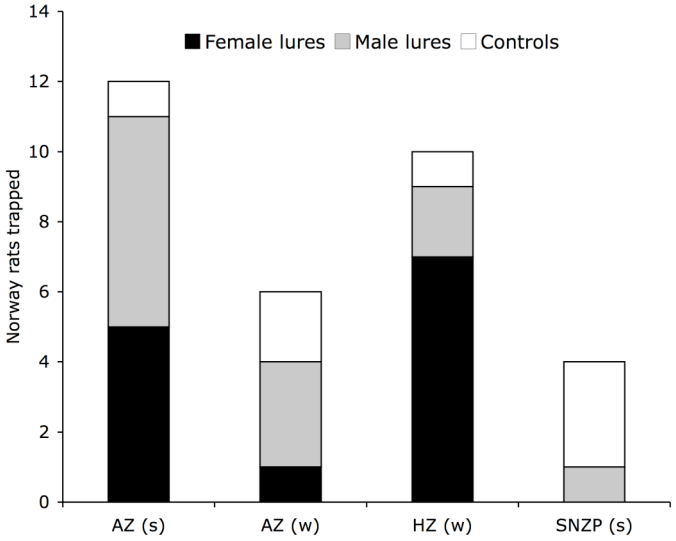

Figure 3.4.2. Wild invasive Norway rats trapped with female and male live lures and food-baited controls during experiment 2 (E2) in the three zoological parks with abundant access to food. Captures were significantly higher with live lures (ANOVA, $P = 0.004$). AZ – Auckland Zoo, HZ – Hamilton Zoo, SNZP – Smithsonian National Zoological Park, (s) – summer, (w) – winter.

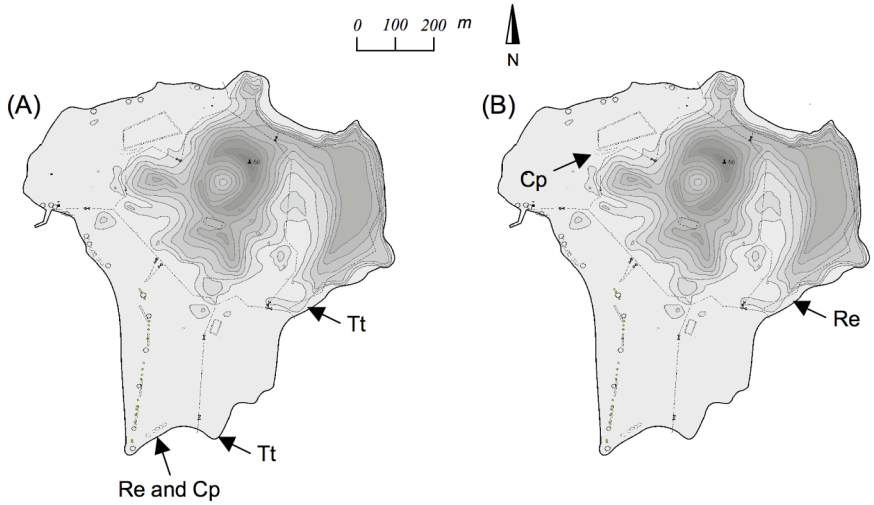

Figure 3.4.3. Map of Browns Island (Motukorea) showing two releasing events (E3). (A) Rat one, and (B) rat two. Both rats were left to explore the island for three nights before trapping devices were activated (see Fig. 3.3.2 for details). The first rat was recaptured during the first night after activation and rat two during the fifth night after activation. Both rats were trapped with lure females. Re – release point; Cp – recapture point; Tt – tracking tunnels with rat footprints.

3.5. Discussion

The detection of sparsely distributed, small invasive mammals can be a challenging task and usually requires considerable effort and a combination of detection methods (Russell et al. 2008b; King et al. 2009). Preliminary studies (Shapira et al. 2013) demonstrated that laboratory rats are effective lures when wild *R. norvegicus* are relatively abundant. The results of this study support my live lure hypothesis and I show that laboratory rats are a more efficient means of detecting and capturing wild *R. norvegicus* at low population densities, including incursion scenarios, and when food is abundant, compared to traps that are baited with food. During E1, only two out of a total of 17 *R. norvegicus* were caught with control traps. The most notable difference between the efficiency of the trapping methods was at S1 where *R. norvegicus* have not been detected in the last three years (but *R. rattus* (Linnaeus 1758) and *Mustela* spp. are caught regularly, J. Staniland, *pers. comm*.). At this site I trapped three male *R. norvegicus* over a period of 15 days.

Rattus norvegicus are highly social, and intraspecific relations between individuals of both sexes plays an important role in its life history (Calhoun 1963). Therefore, the attraction to the lure animals shown by their wild counterparts was perhaps unsurprising. The rats' strong preference for social interactions over food, however, might suggest that when population densities are low, food is probably not a limiting factor, and therefore becomes less attractive as bait. Investigative behaviour in *R. norvegicus* is a dominant trait over foraging when the animals experience unfamiliar surroundings. However, this trade-off does not persist once the animal becomes familiar with the environment (Chance & Mead 1955). E1 took place in a cool temperate climate and as small mammals, especially in colder

climates, must keep high metabolic rates to maintain their body heat (Schmidt-Nielsen 1975), foraging remains a high priority. I suspect, however, that the attraction exhibited by the wild rats to their caged conspecifics probably did change their foraging priorities.

In E1, the willingness to enter devices containing a conspecific combined with the low effectiveness of food-baited traps, suggests that food was relatively abundant in the surrounding habitat and also that attraction to conspecifics has the potential to overcome possible trap neophobia (Inglis et al. 1996). Familiar odours applied to bait stations have been shown to reduce neophobia in wild *R. norvegicus* (Watkins et al. 1999). Here, I suggest that the use of conspecifics might overcome neophobia altogether.

Results from E2, where food in the surrounding habitats was abundant and rat control problematic, are more difficult to interpret. As with E1, live lures were in general more efficient than food-baited controls, especially at AZ during summer and HZ during autumn. The trials at AZ during winter and SNZP during summer however, present anomalies. At both AZ and SNZP, I had low trapping rates despite extensive rat activity that was detected during operations not directly related to the experiment. At AZ, infrared footage revealed that several animals were active around both lure and control traps but avoided entering them (C. Knapp, AZ, *pers. comm*.). At SNZP, when the study was temporarily halted because of the extreme heat, 19 rats were caught with plastic Trapper T-Rex (Bell Laboratories Inc., Madison, WI, USA) and wooden Victor (Woodstream Corp., Lititz, PA, USA) traps (S. Alberts, SNZP, *pers. comm*.). The latter were placed without box covers. SNZP often uses mechanical traps inside yards after zoo animals are removed. However, the lure trapping boxes were used outside exhibits only, as the zoo's veterinarians determined lure rats would need to be "quarantined" from exhibit animals. This prohibited the use of the lure boxes

inside animal yards, where many of the rats have burrows and where past trapping has been shown to be most productive.

The SNZP study did vary from the New Zealand trials, where traps were left in place for considerably longer and for more continuous periods. Because of a shortage of manpower, traps at SNZP were not operated over the weekend periods. In addition, the record-setting heat, which occurred in much of the US during July 2012, made it necessary to remove the rats early during most weekdays. Both these factors reduced the number of days in the trials and the number of trap nights. Although the trap boxes were left in place continuously for the four-week period, the lure rats were only there during the week and when temperatures allowed.

The AZ (winter) and SNZP trapping failures could be the result of rat neophobia (Inglis et al. 1996). However, as the rest of the results suggest that neophobia can be overcome with lure animals, it is more likely that this result occurred because of animals avoiding social interactions. This might be explained by two factors. First, for the SNZP study, most of the rats captured were juveniles for whom social interactions with adult rats (the lures) might be of low importance or even risky. Second, for both sites, it is possible that invasive rat densities were relatively high and hence the novelty of the lure animals is reduced. Shapira et al. (2013) found that in a population with high rat density, live lures and food-baited controls had similar attractiveness in terms of capture frequencies. Overall, in the case of high abundance of food, results are less clear and this stresses the need for additional research on wild rat social interactions in order to improve trapping methodology in these situations.

At E3, owing to logistical constraints (i.e. permit timing and weather limitations), I could perform only three rat releases. Nevertheless, the qualitative results again suggest that

live conspecifics have the potential to reduce trap neophobia. I recaptured two of the released male rats within one to five days of trapping. Using traditional methods, Russell et al. (2008b) found that the mean interception time from release of a male *R. norvegicus* was 13.8 days, but only 59% of the released rats were intercepted within two weeks. Furthermore, with the exception of one individual, Russell et al. (2008a) found that all animals intercepted within five days ate poison rather than being caught in kill traps, again this might be a result of trap neophobia.

In a real incursion scenario, trap effort can be targeted at only a specific position if the rat goes through a tracking tunnel or leaves some other sign. Here, I located the invaders with the VHF transmitter. Detecting an unknown invader can be problematic (Russell et al. 2005; Russell et al. 2008b) and the extensive trapping effort for the third rat, including an active search with a rat sniffing dog, a widely used and reliable rat detecting methodology (Gsell et al. 2010; Shapira et al. 2011), failed. The subsequent capture of a Norway rat presents two scenarios. First, the animal I released evaded capture over an eight-week period. Second, it could be a new invader. The lack of incursion history on Browns Island suggests that the first scenario is more likely and highlights the remarkable ability of these animals to avoid detection.

My prediction of lure traps having a biased sex ratio towards the more mobile males (Innes 2005) was statistically rejected in both E1 and E2. In total, however, I caught more males and the non-significance difference between the sexes seems to be, at least for E1, the result of the relative low number of animals caught. The results from E3 (albeit for only two animals) hint that female conspecifics are more attractive to males. Unfortunately, I could not gather similar data for the behaviour of females. In real incursions the sex of the invader is

unknown and as males are also attracted to other males, the use of both sexes as lures is recommended.

The lure system described here does not reveal the mechanism of attraction and the relative importance of each sense. Pheromones are regularly used to enhance pest insect trapping rates (Burkholder & Ma 1985; Copping & Menn 2000) and conspecific attraction of birds by playbacks is common (Ward & Schlossberg 2004; Hahn & Silverman 2007). In mammals, studies on invasive mustelids have revealed some level of conspecific scent attraction (Clapperton et al. 1994a; Clapperton et al. 1999; Clapperton et al. 2006) as well as visual (mirrors) attraction (Robbins et al. 2007), but live luring has not been trialled. Urine is an important agent in rodent olfactory communication (Cheal 1975; Hurst 1987; Rich & Hurst 1998; Hurst et al. 2001; Hurst 2009) and urine and faeces soaked rats' bedding has been shown to have a positive effect on rat visitation rates (Gsell et al., unpublished data). Vocalizations are also important aspects of *R. norvegicus* social behaviour (Barfield et al. 1979) and I suggest that a multi-modal form of signalling is probably present in my luring system. Scent, as well as playbacks, will probably attract wild rats as well and I suggest that their effectiveness should be tested as alternatives to live animals.

The behavioural traits of invasive and pest species can be used as a valuable tool in conservation practices (Buchholz 2007). In the current study I rely on the behavioural traits of *R. norvegicus* to establish novel trapping set ups and to show that laboratory rats might be efficient lures for invasive counterparts at low densities and when food is abundant. This study provides evidence that caged lure Norway rats attract conspecifics. However, it is important to note that our live lure experiments followed stringent animal welfare guidelines. Lure animals were checked daily for signs of stress, had *ad lib* food and water as well as

shelter and bedding. None of our lure animals showed overt signs of stress and no animal was injured during our trials. Such intense monitoring of welfare means that the large-scale deployment of live lure animals may not be a practical solution for general rodent detection. Nonetheless, we advocate that under special conditions, such as on offshore island that are sanctuaries for rodent-vulnerable species, this approach may provide a further tool for rodent detection and the use of lure rats, with the ethical and labour-intensive costs of caring for them, might be justified if rat incursions can be identified and managed promptly. The ethical costs of this approach must be weighed against the severe negative consequences that may result from the presence of invasive rats and the need for additional measures to detect survivors after eradication attempts. Ultimately, conservation practitioners must make the decision whether the advantages of using live lures can outweigh these disadvantages. As discussed in regard to the third rat release on Browns Island and the SNZP study, the capability of these animals to avoid detection highlights the need for flexible management in response to incursions (i.e. the use of a variety of detecting methods).

Biological control for the protection of natural environments is highly effective against weeds, invertebrates and vertebrates (Hoddle 2002; Saunders et al. 2010; Van Driesche et al. 2010). Vertebrates, in particular, have historically been controlled through predation by other species (Hoddle 2002; Saunders et al. 2010; Wallach et al. 2010), as prey lures (Shivik et al. 2000; Vice et al. 2005), as well as through species-specific diseases (Saunders et al. 2010). The use of conspecifics as biocontrol agents is far less common (Taylor & Katahira 1988; Tidemann 2005; Tsachalidis et al. 2006). The Norway rat, being intensively domesticated while the wild stock has become a worldwide invasive pest, presents the opportunity to use tame individuals to lure their wild counterparts. In the current

study, I have demonstrated the power of conspecific attraction over food bait in wild populations of invasive Norway rats in situations where food in the environment is abundant either because it is supplemented or as a result of low rat population densities. I suggest that the use of laboratory rats as live lures should be considered in future management plans for invasive *R. norvegicus*, especially in island incursions where rapid response is crucial, or in situations where other means of control (e.g. poison) are restricted. I further suggest that conspecific live luring should be tested with other invasive and social pest species.

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3.7. References

Agmo A 2003. Unconditioned sexual incentive motivation in the male Norway rat (*Rattus norvegicus*). Journal of Comparative Psychology 117(1): 3-14.

Alberts JR, Galef BG 1973. Olfactory cues and movement: stimuli mediating intraspecific aggression in wild Norway rat. Journal of Comparative and Physiological Psychology 85(2): 233-242.

Atkinson IAE 1978. Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands. In: Dingwell PR, Atkinson IAE, Hay C ed. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Department of Lands and Survey Pp. 7-30.

Barfield RJ, Auerbach P, Geyer LA, Mcintosh TK 1979. Ultrasonic vocalizations in rat sexual behavior. American Zoologist 19(2): 469-480.

Barnett SA 1958. An analysis of social behaviour in wild rats. Proceedings of the Zoological Society of London 130: 107-152.

Ben-Ami Bartal I, Decety J, Mason P 2011. Empathy and pro-social behavior in rats. Science 334: 1427-1430.

Boreman J, Price E 1972. Social dominance in wild and domestic Norway rats (*Rattus norvegicus*). Animal Behaviour 20(3): 534-542.

Buchholz R 2007. Behavioural biology: an effective and relevant conservation tool. Trends in Ecology & Evolution 22(8): 401-407.

Burkholder WE, Ma M 1985. Pheromones for monitoring and control of stored-product insects. Annual Review of Entomology 30: 257-272.

Calhoun JB 1963. The Ecology and Sociology of the Norway Rat. Bethesda Public Health Service, U.S. Dept. of Health, Education, and Welfare.

Campbell DJ 1978. The effects of rats on vegetation. In: Dingwell PR, Atkinson IAE, Hay C ed. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Department of Lands and Survey. Pp. 99-119.

Chance MRA, Mead AP 1955. Competition between feeding and investigation in the rat. Behaviour 8: 174-182.

Cheal M 1975. Social olfaction: a review of ontogeny of olfactory influences on vertebrate behavior. Behavioral Biology 15(1): 1-25.

Clapperton BK 2006. A review of the current knowledge of rodent behaviour in relation to control devices. Science for Conservation. 55 p.

Clapperton BK, Phillipson MS, Woolhouse DA 1994a. Field trials of slow-release synthetic lures for stoats (Mustela erminea) and ferrets (M. furo). New Zealand Journal of Zoology 21: 279-284.

Clapperton BK, Eason CT, Weston RJ, Woolhouse AD, Morgan DR 1994b. Development and testing of attractants for feral cats, *Felis catus* L. Wildlife Research 21(4): 389-399.

Clapperton BK, McLennan JA, Woolhouse DA 1999. Responses of stoats to scent lures in tracking tunnels. New Zealand Journal of Zoology 26: 175-178.

Clapperton BK, Robbins L, Porter RER, Tallentire K 2006. Testing the attractiveness, palatability and longevity of stoat lure and bait formulations. Wellington, DOC. 1-30 p.

Clavero M, Brotons L, Pons P, Sol D 2009. Prominent role of invasive species in avian biodiversity loss. Biological Conservation 142(10): 2043-2049.

Coomes DA, Mark AF, Bee J 2006. Animal control and ecosystem recovery. In: Allen RB, Lee WG ed. Biological Invasions in New Zealand. Berlin, Springer-Verlag. Pp. 339-353.

Copping LG, Menn JJ 2000. Biopesticides: a review of their action, applications and efficacy. Pest Management Science 56(8): 651-676.

Davis MA 2009. Invasion Biology. Oxford, Oxford University Press.

Dilks P, Towns DR 2002. Developing tools to detect and respond to rodent invasions of islands: workshop report and recommendations. DOC Science Internal Series 59: 5-18.

Donlan CJ, Howald GR, Tershy BR, Croll DA 2003. Evaluating alternative rodenticides for island conservation: roof rat eradication from the San Jorge Islands, Mexico. Biological Conservation 115(1): 29-34.

Epstein PR 1995. Emerging diseases and ecosystem instability: new threats to public health. American Journal of Public Health 85(2): 168-172.

Galef BG 2005. Social learning. In: Whishaw IQ, Kolb B ed. The Behavior of the Laboratory Rat. New York, Oxford University Press. Pp. 363-370.

Galef BG, Allen C 1995. A new model system for studying behavioral traditions in animals. Animal Behaviour 50: 705-717.

Gsell A, Innes J, de Monchy P, Brunton D 2010. The success of using trained dogs to locate sparse rodents in pest-free sanctuaries. Wildlife Research 37(1): 39-46.

Hahn BA, Silverman ED 2007. Managing breeding forest songbirds with conspecific song playbacks. Animal Conservation 10(4): 436-441.

Hoddle MS 2002. Restoring balance: using exotic species to control invasive exotic species. Conservation Biology 18: 38-49.

Howald G, Donlan CJ, Galvan JP, Russell JC, Parkes J, Samaniego A, Wang YW, Veitch D, Genovesi P, Pascal M and others 2007. Invasive rodent eradication on islands. Conservation Biology 21(5): 1258-1268.

Hurst JL 1987. The functions of urine marking in a free-living population of house mice, Mus-domesticus Rutty. Animal Behaviour 35: 1433-1442.

Hurst JL 2009. Female recognition and assessment of males through scent. Behavioural Brain Research 200(2): 295-303.

Hurst JL, Payne CE, Nevison CM, Marie AD, Humphries RE, Robertson DHL, Cavaggioni A, Beynon RJ 2001. Individual recognition in mice mediated by major urinary proteins. Nature 414(6864): 631-634.

Inglis IR, Shepherd DS, Smith P, Haynes PJ, Bull DS, Cowan DP, Whitehead D 1996. Foraging behaviour of wild rats (*Rattus norvegicus*) towards new foods and bait containers. Applied Animal Behaviour Science 47(3-4): 175-190.

Innes JG 2005. Norway rat. In: King CM ed. The Handbook of New Zealand Mammals. Second ed. New York, Oxford University Press. Pp. 174-187.

King CM, McDonald RM, Martin RD, Dennis T 2009. Why is eradication of invasive mustelids so difficult? Biological Conservation 142(4): 806-816.

Long JL 2003. Introduced Mammals of the World. Collingwood, CSIRO. 589 pp.

MacKay JWB, Russell JC, Murphy EC 2007. Eradicating house mice from islands: successes, failures and the way forward. In: Witmer GW, Pitt WC, Fagerstone KA ed. Managing Vertebrate Invasive Species. Pp. 294-304.

Masuda BM, Jamieson IG 2013. The impact of a rat reinvasion and poison operation on survival of reintroduced endemic bird populations on Ulva Island, New Zealand. New Zealand Journal of Ecology in press.

Meerburg BG, Singleton GR, Leirs H 2009a. The Year of the Rat ends - time to fight hunger! Pest Management Science 65(4): 351-352.

Meerburg BG, Singleton GR, Kijlstra A 2009b. Rodent-borne diseases and their risks for public health. Critical Reviews in Microbiology 35(3): 221-270.

Meyer AN 1999. Commensal rodent control: challenges for the new millennium. In: Robinson WH, Rettich F, Rambo GW ed. 3rd International Conference on Urban Pests. Pp. 99-103.

Mills JN, Childs JE 1998. Ecologic studies of rodent reservoirs: Their relevance for human health. Emerging Infectious Diseases 4(4): 529-537.

Murphy EC, Robbins L, Young JB, Dowding JE 1999. Secondary poisoning of stoats after an aerial 1080 poison operation in Pureora Forest, New Zealand. New Zealand Journal of Ecology 23(2): 175-182.

Primack RB 2010. Essentials of Conservation Biology. 5th edition. Sunderland, Sinauer. 601 pp.

Ramsay GW 1978. A review of the effects of rodents on the New Zealand invertebrate fauna. In: Dingwell PR, Atkinson IAE, Hay C ed. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Department of Lands and Survey. Pp. 89-95.

Rich TJ, Hurst JL 1998. Scent marks as reliable signals of the competitive ability of mates. Animal Behaviour 56: 727-735.

Robbins L, Clapperton BK, Tallentire K, Porter RER 2007. Testing the attractiveness and palatability of stoat lures and baits with various sensory cues. Wellington, Department of Conservation.

Robitaille JA, Bovet J 1976. Field observations on social behavior of Norway rat, *Rattus norvegicus* (Berkenhout). Biology of Behaviour 1(4): 289-308.

Russell JC, Clout MN 2005. Rodent incursions on New Zealand Islands. In: Parks J, Statham M, Edwards G ed. Proceedings of the 13th Australian Vertebrate Pest Conference. Pp. 324-330.

Russell JC, Towns DR, Anderson SH, Clout MN 2005. Intercepting the first rat ashore. Nature 437(7062): 1107-1107.

Russell JC, Towns DR, Clout MN 2008a. Review of rat invasion biology: implications for islands biosecurity. Science for Conservation 286. Wellington, Department of Conservation. 53 pp.

Russell JC, Beaven BM, MacKay JWB, Towns DR, Clout MN 2008b. Testing island biosecurity systems for invasive rats. Wildlife Research 35(3): 215-221.

Russell JC, McMorland AJC, MacKay JWB 2010. Exploratory behaviour of colonizing rats in novel environments. Animal Behaviour 79(1): 159-164.

Saunders G, Cooke B, McColl K, Shine R, Peacock T 2010. Modern approaches for the biological control of vertebrate pests: an Australian perspective. Biological Control 52: 288-295.

Schmidt-Nielsen K 1975. Animal Physiology. New York, Cambridge University Press. 685 pp.

Shapira I, Buchanan F, Brunton DH 2011. Detection of caged and free-rangigng Norway rats *Rattus norvegicus* by a rodent sniffing dog on Browns Island, Auckland, New Zealand. Conservation Evidence 8: 38-42.

Shapira I, Shanas U, Raubenheimer D, Brunton D 2013. Laboratory rats as trap lures for invasive Norway rats: field trial and recommendations. New Zealand Journal of Ecology, in press.

Shivik JA, Wright WG, Clark L 2000. Seasonal variability in brown tree snake (*Boiga irregularis*) response to lures. Canadian Journal of Zoology 78(1): 79-84.

Simberloff D 2009. Rats are not the only introduced rodents producing ecosystem impacts on islands. Biological Invasions 11(7): 1735-1742.

St Clair JJH 2011. The impacts of invasive rodents on island invertebrates. Biological Conservation 144(1): 68-81.

Stenseth NC, Leirs H, Skonhoft A, Davis SA, Pech RP, Andreassen HP, Singleton GR, Lima M, Machang'u RS, Makundi RH and others 2003. Mice, rats, and people: the bio-economics of agricultural rodent pests. Frontiers in Ecology and the Environment 1(7): 367-375.

Stoddart DM 1986. The comparative responses of mice and voles to conspecific and heterospecific odors in the field - a lesson in social behavior. Chemical Signals in Vertebrates 4: 533-540.

Taylor CM, Hastings A 2005. Allee effects in biological invasions. Ecology Letters 8(8): 895-908.

Taylor D, Katahira L 1988. Radio telemetry as an aid in eradicating remnant feral goats. Wildlife Society Bulletin 16(3): 297-299.

Tidemann C 2005. Indian mynas - can the problem be controlled? 15th Urban Animal Management Conference. Canberra, Australian Veterinary Association. Pp. 55-57.

Tsachalidis EP, Sokos CK, Birtsas PK, Patsikas NK 2006. The Australian crow trap and the Larsen trap: their capture success in Greece. In: Manolas EI ed. Proceedings of the 2006 Naxos International Conference on Sustainable Management and Development of Mountainous and Island Areas. Island of Naxos, Democritus University of Thrace. Pp. 325-329.

Van Driesche RG, Carruthers RI, Center T, Hoddle MS, Hough-Goldstein J, Morin L, Smith L, Wagner DL, Blossey B, Brancatini V and others 2010. Classical biological control for the protection of natural ecosystems. Biological Control 54: S2-S33.

Veitch CR 2002. Eradication of Norway rats (*Rattus norvegicus*) and house mouse (*Mus musculus*) from Browns Island (Motukorea), Hauraki Gulf, New Zealand. In: Veitch CR, Clout MN ed. Turning the Tide: The Eradication of Invasive Species. Gland and Cambridge, IUCN SSC Invasive Species Specialist Group. Pp. 350-352.

Vice DS, Engeman RM, Vice DL 2005. A comparison of three trap designs for capturing brown treesnakes on Guam. Wildlife Research 32(4): 355-359.

Wallach AD, Johnson CN, Ritchie EG, O'Neill AJ 2010. Predator control promotes invasive dominated ecological states. Ecology Letters 13(8): 1008-1018.

Ward MP, Schlossberg S 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18(2): 519-525.

Watkins RW, Whiterow A, Bull DS, Cowan DP 1999. The use of familiar odors to reduce the impact of container neophobia on the control of Norway rats (*Rattus norvegicus*).

In: Johnston RE, Muller-Schwarze D, Sorensen PW ed. Advances in Chemical Signals in Vertebrates. New York, Kluwer Academic / Plenum. Pp. 655-661.

CHAPTER 4: CONSPECIFIC ATTRACTION IN WILD HOUSE MICE: EFFECTS OF STRAIN, SEX AND DIET

4.1. Abstract

Invasive rodents pose major concerns for human health, agriculture and conservation. House mice *Mus musculus* are one of the most widespread invasive rodents, and require intensive efforts for their control. Control measures rely largely on food baits but difficulties in the eradication of mouse populations necessitate the development of alternative pest control methods. Conspecific attraction is used as a luring method for invasive species control and can be used to attract wild mice into traps. The proximate cause of the live lure attraction might be primarily scent or a more complex array of stimuli emanating from a live animal. I used a Y maze apparatus to test the effect of urine from mice fed high vs. low protein diets on the attraction of male and female conspecific wild mice (focal animals), and tested whether the protein content of the diet of focal animals affected their response. I further compared the strength of attraction of wild mice towards wild and laboratory (Swiss Webster) live lure conspecifics of the opposite sex. Both males and females were marginally more attracted to conspecific scent originating from lure animals previously on high protein diets, regardless of the focal animal's diet. Wild mice were equally attracted to laboratory mice of the Swiss Webster strain and wild mice. However, preference for one side of the maze was significant. Males were more attracted to female lures than females were to male lures. Activity of both sexes near conspecifics was significantly reduced over exposure time. I discuss the implications of these findings for the control of invasive mice.

4.2. Introduction

Invasive rodents are pests worldwide (Long 2003) and pose major threats to human health (Epstein 1995; Mills & Childs 1998; Meerburg et al. 2009a), agricultural crops (Meyer 1999; Stenseth et al. 2003; Meerburg et al. 2009b) and natural ecosystems (Atkinson 1978; Campbell 1978; Ramsay 1978; Simberloff 2009; St Clair 2011). Governmental and non-governmental agencies annually invest considerable resources to eradicate and control invasive and pest rodents (Meyer 1999; Dilks & Towns 2002; Stenseth et al. 2003; Coomes et al. 2006; Meerburg et al. 2009b). Eradications of entire rodent populations have been successful, an example being the aerial poisoning of rats on some offshore islands (Howald et al. 2007). The house mouse *Mus musculus* is harder to eradicate, with 19% of attempts being unsuccessful; the highest failure rate for any widespread invasive rodent species (Howald et al. 2007). The main reason for these failures is the difficulty of targeting all individual mice, which is most likely due to their small home ranges, extremely high reproductive rates and the amount of natural food in the environment (Ruscoe 2001; Ruscoe & Murphy 2005). In human settlements or in agriculture-dominated landscapes, including natural refuges on mainland sites, complete eradication of mice is an unrealistic goal due to fast re-establishment of populations from even a very few survivors or new invaders (Ruscoe 2001; Goldwater 2007; Howald et al. 2007; MacKay et al. 2007). Therefore, long-term control programs to keep populations at a minimum are required.

The most common means of rodent control are poisoning (Towns & Broome 2003; Clapperton 2006; MacKay et al. 2007) and to a lesser extent trapping (Clapperton 2006). Both methods rely on the attractiveness of food baits. The difficulties encountered in

controlling mouse populations (Ruscoe 2001; Howald et al. 2007; MacKay et al. 2007) suggest that alternative control measures should be explored. The trapping and detecting of pest animals using conspecific scent or live conspecifics have proven effective for several species. Mouse scent (urine driven) applied to bait stations has increased the responsiveness of pest mice and enhanced bait take (Volfova et al. 2011). In feral goats, females fitted with GPS collars proved crucial for the detection of remnant populations following culling by hunting (Taylor & Katahira 1988; Campbell et al. 2004; Cruz et al. 2009). Conspecifics are also used to enhance trapability of invasive crows and magpies (Tsachalidis et al. 2006), and Indian mynas (Tidemann 2005), these species being major pests of both agriculture and natural systems. Recently, Shapira et al. (Shapira et al. 2013; In Press) have demonstrated that in the highly social Norway rat *Rattus norvegicus*, laboratory rats used as live lures were more effective than food bait in attracting invasive *R. norvegicus* into traps.

The house mouse is a highly social rodent (Berry 1970; Lidicker 1976; Ruscoe & Murphy 2005), and thus live lures could potentially be used to attract conspecifics into traps. House mice rely heavily on olfactory communication for intraspecific interactions and much of their intraspecific information can be gathered via inspection of conspecific urine (Hurst 1987; Hurst et al. 2001; Thom & Hurst 2004; Cheetham et al. 2007; Hurst 2009). Based on urine, for example, mice are able to discriminate with high resolution between the scent of familiar and unfamiliar individuals (Thom & Hurst 2004; Cheetham et al. 2007; Nunes et al. 2009). Previous work suggests that this is likely to involve molecules of the major histocompatibility complex (MHC) (Yamazaki et al. 1983) and major urinary proteins (MPUs) (Hurst et al. 2001). It is unknown, however, what effect diet has on the attractiveness of mice to conspecifics.

Reliance on scent alone as a lure has two disadvantages. The first is the narrowing of bandwidth by restricting the luring system to a single sensory modality. Vocalization, which has been demonstrated in many studies to be important in mouse communication (Bean 1982; Pomerantz et al. 1983; White et al. 1998; Moles & D'Amato 2000; Musolf et al. 2010), might make a significant contribution in a luring system. A live conspecific lure can provide both olfactory and auditory cues and thus intensify and expand the responsiveness of attraction to wild mice. The second disadvantage is the need for a constant supply of fresh scent samples, which is redundant when using a live animal as lure.

One of the advantages of testing conspecific attractiveness in mice is the availability of laboratory animals for use as attractants. Laboratory mice are much easier to handle and maintain compared to their wild counterparts. However, laboratory mice have been bred for generations under artificial conditions and, being derived from a small pool of ancestors (Beck et al. 2000), their genetic polymorphism is limited and does not represent that of wild house mice (Guénet & Bonhomme 2003). This latter might result, among other things, in behavioural differences (Smith et al. 1994; Blanchard et al. 1998; Augustsson et al. 2005). Differences between laboratory and wild mice might also influence conspecific attraction, as has been demonstrated by the effect of chromosomal incompatibility on attractiveness in closely related wild mice populations (Nunes et al. 2009).

In the current study I tested the effect of diet on attractiveness to conspecific scent cues (urine), and whether the nutritional state of the focal mouse influenced this. I assumed that urine gathered from mice fed a high protein diet would be more attractive to conspecifics, as has been demonstrated in fish (Ward et al. 2011). However, since Shapira et al. (in preparation) demonstrated that, unlike their laboratory counterparts (Sorensen et al.

2008; Sorensen et al. 2010), wild mice do not prioritize dietary protein, I predicted that the preference of focal mice for urine from high-protein fed mice would be independent of the nutritional state of the focal mice. I also tested the attractiveness of wild mice vs. albino Swiss Webster mice to wild mice of the opposite sex. Albino Swiss Webster is a common laboratory strain representing a modified form of the wild house mouse. For conspecific attraction to live lures, I predicted that wild mice would be more attracted to wild conspecifics, because of genetic and ontogenic driven differences between them and laboratory animals. Based on intrasexual interactions in the house mouse (Berry 1970; Berry 1981), I also predicted that male mice would show greater motivation (expressed as activity) to move towards female lures compared to female movement towards male lures, and that activity levels would decrease with duration of exposure.

4.3. Methods

During the following experiments, I used relatively long habituation and test periods for the test animals. Some researchers use much shorter periods of habituation and test times (Kavaliers & Colwell 1995a; Hurst et al. 2001; Nunes et al. 2009; Musolf et al. 2010; Volfova et al. 2011), while others have used similar time frames (Hughes & Banks 2010). Ultimately, I tested the responses of mice with the overall objective of improving practical pest solutions. As such, I designed the experiments in a way that 1) enabled the test animals to become highly comfortable and habituated to their environment (as mice would be in their natural environment) and 2) let the interaction between the test and stimuli animals last for a considerable amount of time (as would be expected if a new scent/animal is introduced to an

established territory). All animals were euthanised at the end of the experiment using isoflurine via airways. Animal treatments were subject to a Massey University Animal Ethics Committee approval, protocols MUAEC 09/40 and 11/08.

4.3.1. Effect of mouse diet on conspecific attraction to scent

Wild-caught house mice were used as focal animals (19 females and 18 males). Mice were trapped within the Tawharanui Open Sanctuary sand dunes (36°21′41.60″ S 174°49′08.83″ E) during the austral winter of 2011 and spring-summer 2011-2012. I used Sherman folding traps (H.B. Sherman Traps, FL, USA) baited with peanut butter and supplied with paper as bedding. Traps were set during the day and captured animals were collected early the following morning. Animals were transferred to Massey University laboratory facilities on the day of capture, where they were housed in individual cages (41L X 25W X 15H cm) and initially supplied daily with *ad libitum* water, rodent pellets (diet 86) and seed mixture. Mice were provided with several shelters and pine wood shavings and shredded paper as bedding. Animals were held under 12L/12D periodic cycle (L – white light, D – red dim light) and an ambient temperature of 22 ± 1.5°C.

I used 14 male laboratory C57 mice as urine donors. Newly weaned animals (21-23 days of age) were obtained from the University of Auckland and were transferred to laboratory facilities at Massey University where they were housed under the same conditions as wild caught mice (above), the only difference being a natural light cycle. At 42-46 days of age, all animals were shifted and confined to one of two types of isocaloric purified diets (TestDiet, Richmond IN, USA): a low protein (P) to carbohydrate (CHO) ratio food (LP;

6.5%P-80.4%CHO; n = 7) or a high P to CHO ratio food (HP; 26%P-58.1%CHO; n = 7) in the form of pellets. All other nutritional components in the diets were identical. Both food types were based on standard rodent diet AIN-93M, recommended by the American Institute of Nutrition (AIN) as the basic diet for the maintenance of adult rodents (Reeves et al. 1993).

To reduce stress and because wild mice produce relatively small amounts of debris, cages with wild mice were cleaned every four weeks. Animals were transferred using glass jars to prevent direct contact and to enable visual health checks. Cages containing laboratory mice were cleaned every two weeks and animals were transferred by hand.

I collected urine from the laboratory animals using a single mouse metabolic cage (MC) (Tecniplast, Rydalmere NSW, Australia). Urine was collected after at least three weeks of diet restriction (HP or LP). Animals were housed individually in the MC for 24 h during which time they were supplied with *ad libitum* water and the relevant diet. Urine samples were stored in vials at -18 °C. I collected urine three times from each mouse with at least a two-week interval between collections. I refer to urine samples as hp if the donor was confined to the HP diet and lp if it was confined to the LP diet.

Preference toward urine samples from the two diets was tested in a Y maze apparatus. The maze was comprised of a home cage (HC, 41L X 25W X 15H cm) housing the focal animal, connected to a single tube that bifurcated into two Y arm tubes (transparent pipes; Ø 4 cm, each 50 cm long). Each Y arm was connected to a stimulus cage (SC, 41L X 25W X 15H cm) with wire mesh cover (Fig. 4.3.1). The two Y arms were mounted with two sets of infrared (IR) sensors (5V phototransistor and 5V emitting diode, generic) at both ends of each arm. The sensors were wired to a computer via a logic circuit (Country Mouse, EH, Israel) and 24 channels I/O card (PC-LabCard, PCI-1757UP, Advantech, Taiwan). I used

Mice-Tracker software (Country Mouse, EH, Israel) to record the number of visits and the time spent in the ECs by the focal animals.

I tested the effect of diet on mouse activity as a function of both the sex and diet of the focal animal (HP females, LP females, HP males, LP males) and the dietary origin of the urine sample (hp, lp). Individual mouse activity was measured for each type of diet restriction (HP and LP). Animals were acclimated to a given food type from 14 to 40 days prior to testing and, after the first test, shifted to the other diet type for the same period before re-testing. The differences in time of diet acclimation resulted from constraints due to apparatus availability. Fourteen days was considered sufficient for diet acclimation, considering the high metabolic rate and associated high relative energy requirement of small mammals such as mice (Pearson 1947).

In each experimental session I tested four to six animals simultaneously in individual apparatuses. Each focal animal cage was connected to the Y apparatus 3-4 h before lights off and mice were free to explore the apparatus for a total of 5-6 h before the start of the experiment. In each experimental session I used three urine samples from three different donors for each diet type. Samples were defrosted at 4 °C for 5-6 hours before being distributed in the SCs. Two hours after lights off, I moved the mice back to their cages and closed the entrances to the Y maze. 80 μl of urine from an individual sample was poured into frozen glass Petri dishes (to slow urine evaporation). The urine samples were assigned randomly to each SC; LP donor on one side and HP donor on the other. After all samples were distributed, the IR sensors were activated and the cage entrances to the Y maze opened. All mice were free to explore their attached apparatus for a further 9.5 hours until the lights were turned on. During that time, the number of visits and time spent in the SCs by the mice

were recorded by the Mice-Tracker. Each apparatus was then dismantled and cleaned thoroughly with sterilizing detergent, rinsed with clean water and air dried before being re-used.

4.3.2. Data analysis

Activity data were analyzed as total values. I calculated time spent in, number of visits to, and time per visit, by mice in the lp and hp urine SCs for each group (HP females, LP females, HP males, LP males). For each factor and group (time, visits, time per visit) I subtracted lp from hp activity values and tested the effects (sex, diet and their interaction) on the activity values using ANOVA.

4.3.3. Effect of mouse strain on conspecific attraction to live lures

I used the offspring (F1) of five wild mouse pairs, trapped at three sites near Albany, New Zealand, as both focal and stimuli animals, and albino Swiss Webster laboratory mice (AgResearch, New Zealand) as stimuli animals only. Wild and laboratory animals were held in different rooms. Males were housed individually and females in sister groups of two to four animals. Cages (41L X 25W X 15H cm for males and 60L X 30W X 40H for females) contained pine wood shavings and several shelters. Animals were provided with *ad libitum* food (rodent diet 86, IFNHH, Massey University, New Zealand) with additional grain mix and water. Animals were held under 12L/12D periodic cycle and 22 ± 1.5 °C.

Attractiveness to live lures was tested in a Y maze apparatus as described above but with different stimuli cages (SC). In this experiment, the SCs (41L X 25W X 15H cm) were divided into a compartment (3/4 of the cage) holding the stimulus animal and a smaller compartment (1/4 of the cage) that was open to the tube (Fig. 4.3.1). The mesh divider prevented physical contact between the focal and stimuli animals.

Wild and laboratory mice were all sexually mature (204 ± 124 and 223 ± 38 days of age, respectively) but with no sexual experience. Wild animals were unfamiliar with the laboratory animals prior to the experiments. Siblings from the same or different litters were never used together as focal and stimuli animals. Within the above constraints, distribution of focal and stimuli animals among the six apparatuses and within each session were random. Assignment of stimulus animals to the two arms was also random. Each mouse was tested twice in the presence of the wild and laboratory animals of the opposite sex, before and after exchanging the SCs at the end of the Y arms.

I tested 24 wild male and 18 wild female mice (focal animals). Focal animals were given an habituation period of approximately 45 hours during which they were able to explore the maze freely. I introduced the stimulus animals to the SCs, a wild mouse on one side and a laboratory mouse on the other side of the maze. To reduce stress associated with placement of the stimulus animals, the exit to the tube from the HC was closed and animals left for six hours to habituate without interference from the focal animals. The experiment was started two hours before the dark phase by opening the entrance to the Y maze and lasted for approximately 37 hours (two dark phases). To detect possible side fixations, I switched the SCs with their resident stimulus mouse to the alternate side of the same apparatus. Side fixation is a known psychological phenomenon in mice (Blednov et al. 2001; Bachmanov et

al. 2002) as well as in other species (Reicher & Holman 1977; Bogren 1984; Erdőhegyi et al. 2007). If a strong side fixation occurs, the test animal will prefer one side regardless of the stimuli. It can be detected if the animal continues to prefer one side even if the stimulus is changed or shifted between sides. I then left the animals to habituate for an additional six hours. Two hours before the next dark phase, I opened the exit to the tube and let the focal animals freely explore the maze for two more dark phases. Each apparatus was then dismantled and cleaned thoroughly with sterilizing detergent, rinsed with clean water and air dried before being re-used.

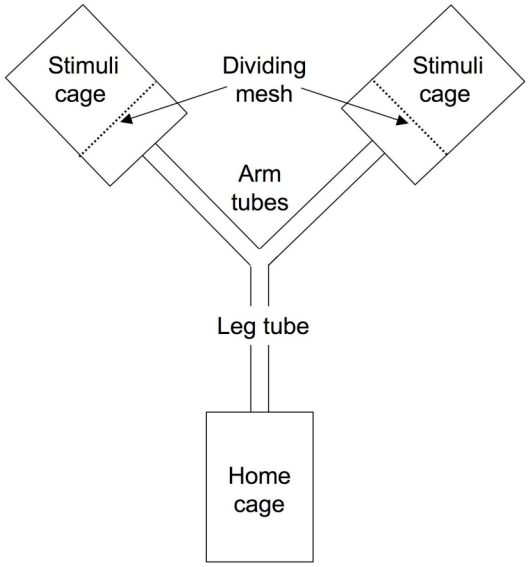

Figure 4.3.1. Experimental apparatus: home cage (HC), access and arm tubes and stimulus cages (SCs). Dividing mesh (-----) separated the focal and stimulus animals in the SCs in the live lure experiment. Smaller SCs without dividers were used for the urine experiment.

4.3.4. Data analysis

Data were analyzed using linear mixed models (LMM) in SPSS. As I had several sets of data for each animal I treated individuals as subjects in the model to avoid pseudo-replication. I

analyzed only the data obtained during the dark phases, as mice are nocturnal and activity during the light phases was very limited and sporadic. I first conducted a full analysis on the effects of gender, treatment (wild and laboratory stimuli), Y arm (before and after changing sides) and dark phase (first and second) on the number of visits and time spent in the SCs by the focal animals. As I found a side fixation, I also conducted a partial analysis on the effects of gender, treatment and dark phase on the number of visits and time spent in the SCs by the focal animals only during the first part of the experiment, before the SCs were swapped. To meet the assumptions of normality, I transformed the data, analyzing the square root of time and the $\log_{10}$ of number of visits.

4.4. Results

Time spent by mice near the hp and lp stimuli urine did not differ between sexes and dietary pretreatment (HP vs. LP) groups (Fig. 4.4.1A). There were no significant overall, sex or diet effects (ANOVA, $F_{1,68} = 2.295$, $P = 0.135$; $F_{1,68} = 0.001$, $P = 0.978$; $F_{1,68} = 0.085$, $P = 0.772$; respectively), nor any interaction effects between sex and diet (ANOVA, $F_{1,68} = 0.471$, $P = 0.495$). There was, however, a significant overall effect on the number of visits made to the hp and lp SCs (Fig. 4.4.1B), with a bias toward hp (ANOVA, $F_{1,68} = 8.508$, $P = 0.005$), but there was no difference in this response between sexes, diet or their interaction (ANOVA, $F_{1,68} = 2.485$, $P = 0.120$; $F_{1,68} = 0.678$, $P = 0.413$; $F_{1,68} = 0.146$, $P = 0.0704$; respectively). Time per visit did not differ significantly between the groups (Fig. 4.4.1C), although HP females showed a tendency to favour hp, whereas the other groups tended towards the lp stimulus. For time per visit there was no overall, sex or diet effect (ANOVA, $F_{1,68} = 0.03$, P

= 0.0.863; $F_{1,68}$ = 0.841, P = 0.363; $F_{1,68}$ = 0.411, P = 0.524; respectively) and there were no interaction effects between sex and diet (ANOVA, $F_{1,68}$ = 1.778, P = 0.187).

Analysis of time spent in the SCs of live lures revealed a significant effect of gender (LMM, $F = 11.394_{1,325}$, P = 0.001), with males being more active than females. There was also a significant effect in the relationships between treatment and Y arm (LMM, $F = 4.865_{1,325}$, P = 0.028), indicating that the animals showed side bias (first and second sides were dependent). The full analysis for the number of visits made to the SCs revealed that the factors significantly affecting the model were gender (LMM, $F = 6.541_{1,325}$, P = 0.011), with males being more active than females, Y arm (LMM, $F = 14.202_{1,325}$, $P < 0.001$), and also phase (LMM, $F = 17.674_{1,325}$, $P < 0.001$), with higher activity during the first dark phase.

When the first scent presentation was analyzed separately, the only factor significantly affecting the model for the time spent in the SCs (Fig. 4.4.2) was gender (LMM, $F = 11.470_{1,160}$, P = 0.001), with males being more active than females. There was a marginal but non-significant effect of treatment (LMM, $F = 3.32_{1,160}$, P = 0.07), with wild stimuli being more attractive. The only factors significantly affecting the model for the number of visits to the SCs (Fig. 4.4.3) were gender (LMM, $F = 5.981_{1,160}$, P = 0.016), with males being more active than females, and phase (LMM, $F = 13.473_{1,160}$, $P < 0.001$), with activity being higher during the first dark phase.

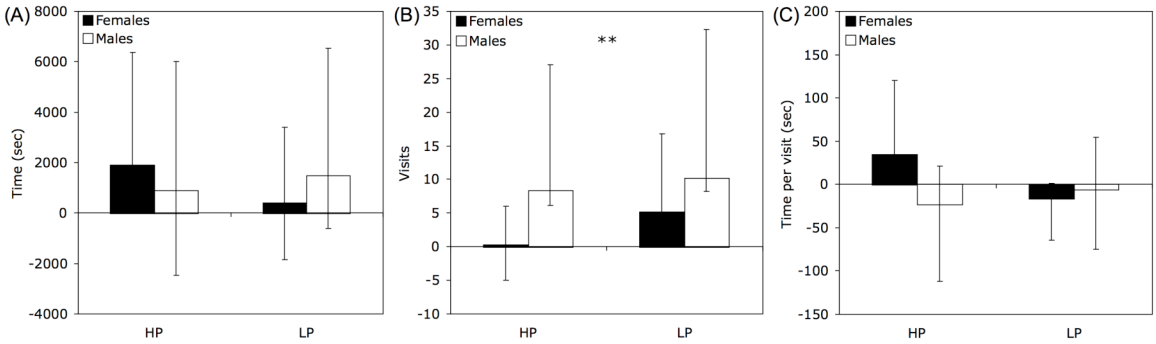

Figure 4.4.1. Activity near hp and lp urine samples in the stimulus cages (SCs) of the four mouse groups (HP females, LP females, HP males, LP males). Columns represent mean (± CI) difference between lp and hp. (A) Time spent in the SCs. (B) Number of visits to the SCs. (C) Time per visit in the SCs. Values above zero represent a preference for hp urine and values below zero represent a preference for lp urine. ** Corresponds to a significant overall effect of sex where $\alpha < 0.01$.

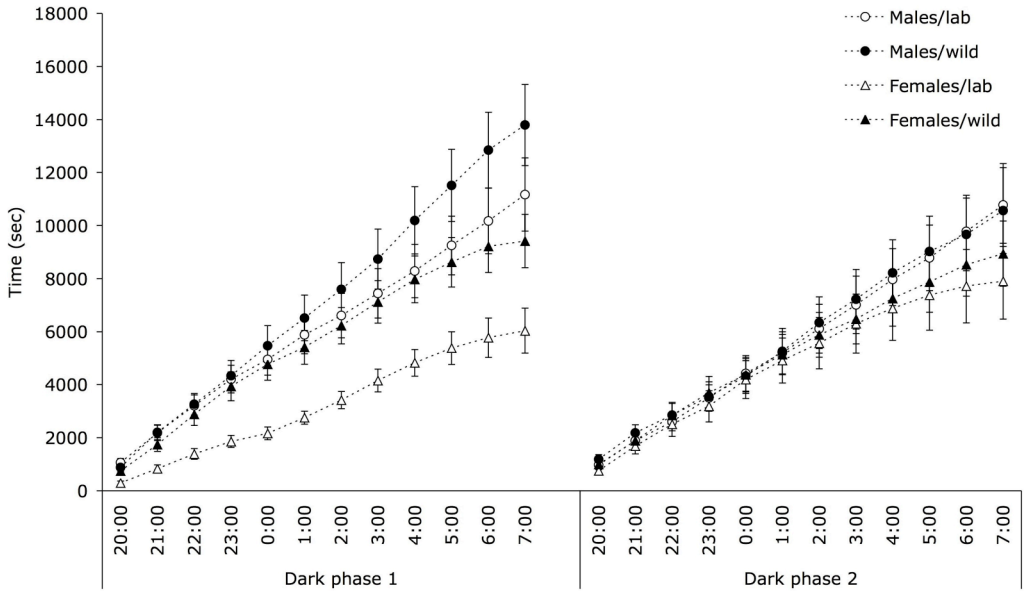

Figure 4.4.2. Mean (± SE) cumulative time spent by wild mice near the opposite sex stimulus cages (lab - laboratory mice, wild - wild mice) during two consecutive dark phases.

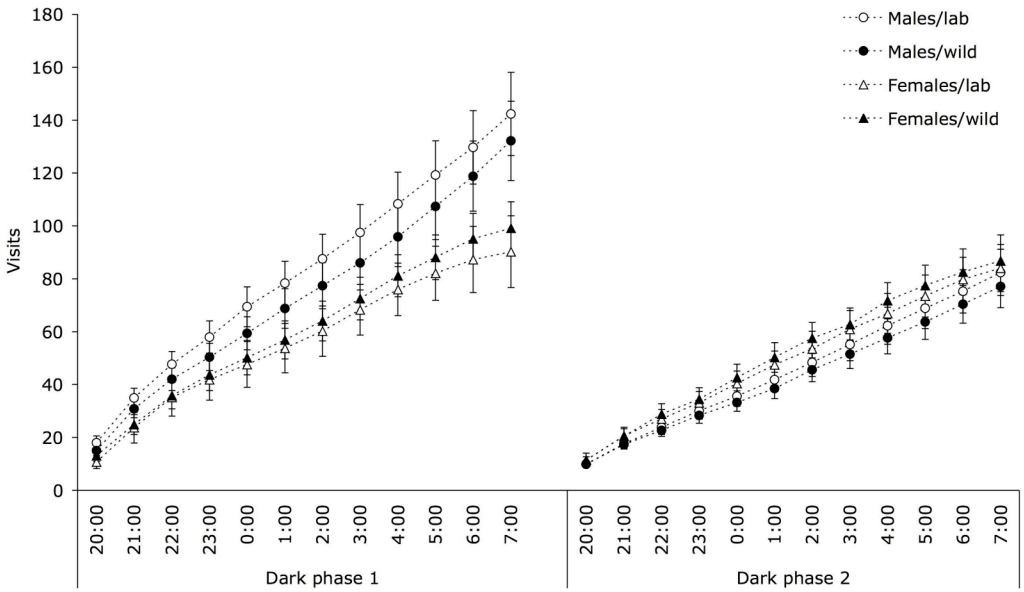

Figure 4.4.3. Mean (± SE) cumulative visits made by wild mice to the opposite sex stimulus cages (lab - laboratory mice, wild - wild mice) during two consecutive dark phases.

4.5. Discussion

All focal animals exhibited preference toward hp over lp urine. This supports my prediction of the higher attractiveness of hp urine regardless of sex and diet of the focal animals. I based this prediction on Ward et al. (2011), showing that mate selection is based on protein (P) values in fish. However, the results show that mice were attracted to high P whether they were male or female, suggesting that this response is not necessarily based on mate attraction. So how do mice interpret hp urine? Shapira et al. (in preparation) showed that both male and female wild mice were targeting low P/CHO in their diet, and therefore it is unlikely that high P/CHO represents higher fitness. The interpretation for attraction of males to high P/CHO in this case might be explained by motivation to confront a subordinate rival (Berry 1970). If mice do prefer low P/CHO ratios in their diet (Shapira et al. in preperation),

then high P/CHO ratios in the urine might inform on low fitness resulting from specific diets. Whatever the reasons, this contradiction between preference for low P/CHO ratio diet (Shapira et al. in preperation) and the higher attraction of high P/CHO ratio urine (this study) should be addressed in further research. As a lure cue, the results suggest that urine-based scent from animals fed with high P/CHO ratio diet might enhance trapability and/or poison intake in wild mice.

Wild house mice found both wild and laboratory mice of the opposite sex attractive in a Y maze. Wild mice were marginally (but not significantly) more attractive than laboratory animals during the first part of the experiment (before swapping the SCs), but analysis of the two test parts showed that side fixation (and possibly time of exposure) had a stronger effect on attractiveness than did the strain of the mouse. When presented with conspecific urine only, house mice discriminate between familiar and unfamiliar conspecifics (Cheetham et al. 2007), recognize kin (Sherborne et al. 2007) and chromosomal incomparability (Nunes et al. 2009), and assess conspecific health (Kavaliers & Colwell 1995b). While female mice have been shown to prefer familiar individuals (with which they had prior contact) based on olfactory transmission only (Cheetham et al. 2007), it appears in the current study that when a live animal was used as the stimulus, no preference for the familiar (the wild mice) over the unfamiliar (the laboratory mice) occurred. This phenomenon might be explained by the multiple cues presented by a live individual in comparison to urine scent alone, and by the long time allowed for the interactions. These multiple cues might include vocalizations (Musolf et al. 2010), behavioural displays and scent cues produced outside of the urinary system such as the Harderian gland (Payne 1994). In this study, the most important factor that may explain the general absence of significant effects in terms of the time and rate of

attraction is probably the complex and direct intraspecific interactions between live animals. It is possible that differences in time spent by the test animals in the Y maze arms were due to avoidance of rather than attraction to the stimulus animals. However, as there were no significant differences, this is hard to assess. Also, the test animals had at all times the option of retreating to their HCs if deterred by the animals in the SCs.

As predicted, males were more active than females both in the total time they spent in the stimulus cages and in the visitation rates. Male house mice are territorial and spend considerable time and energy exploring, guarding and marking their territories (Anderson 1961; Berry 1970; Lidicker 1976; Berry 1981; Jensen et al. 2005). Female house mice are more social and less aggressive than males (Anderson 1961; Berry 1970; Gray et al. 2002), although exploratory behaviour, depending on the study, has been found to be either less than in males (Berry 1970) or similar (Jensen et al. 2003). In this experiment, differences in activity were most apparent during the first dark phase and decreased during the second phase. Mice are complex creatures and fast learners, and non-aggressive relationships with the opposite sex are usually achieved within a few hours (Anderson 1961; Berry 1970). These results show that over longer time periods the effect of gender is reduced. A closer look at the cumulative data shows that males reduce their activity levels, perhaps because of general habituation, or because they learn that physical contact cannot be achieved due to the dividing mesh in the chamber.

Time spent in, and number of visits to, the SCs for both males and females was reduced during the second dark phase. This highlights the importance of novelty for the attraction process and suggests that new animals presented to conspecifics will get more attention at the beginning of the familiarization process (Berry 1970; Jensen et al. 2005;

Levitis et al. 2009). This could clearly affect the levels of trapability as a function of the time of exposure to the target animals. Accordingly, the probability of an animal approaching a given (familiar) conspecific lure will reduce over time.

My results provide support for the possible use of conspecific attraction in mouse control, through using laboratory mice as lures for trapping wild mice. Using an animal as an attractant in traps necessitates a considerable amount of handling (e.g. getting the animal in and out of cages, and feeding regimes). Wild mice are not docile when handled and therefore handling can become difficult and time consuming. Moreover, while laboratory mice are accustomed to small cages and should behave normally in a luring device (given that the size of housing is sufficient), wild mice are likely to become stressed in small cages and this could negatively affect the rates of attraction. Mice have been shown to respond to stress hormones emitted by other mice, (Carr et al. 1970). I suggest that the advantages of using laboratory animals over wild animals outweighs the slight drop in attractiveness and that laboratory mice might serve as live lures to test the efficacy of conspecific attraction over food bait for invasive and pest house mice. I further suggest that the type of diet fed to the luring conspecifics, whether they are to be used as urine donors or as live lures, might also have an effect on the level of attractiveness and thus can be used to enhance their efficacy as lures.

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4.7. References

Anderson PK 1961. Density, social structure, and nonsocial environment in house-mouse populations and the implications for regulation of numbers. Transactions of the New York Academy of Sciences 23: 447-451.

Atkinson IAE 1978. Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands. In: Dingwell PR, Atkinson IAE, Hay C ed. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Department of Lands and Survey Pp. 7-30.

Augustsson H, Dahlborn K, Meyerson BJ 2005. Exploration and risk assessment in female wild house mice (*Mus musculus musculus*) and two laboratory strains. Physiology & Behavior 84: 265-277.

Bachmanov AA, Reed DR, Beauchamp GK, Tordoff MG 2002. Food intake, water intake, and drinking spout side preference of 28 mouse strains. Behavior Genetics 32: 435-443.

Bean NJ 1982. Olfactory and vomeronasal mediation of ultrasonic vocalizations in male-mice. Physiology & Behavior 28(1): 31-37.

Beck JA, Lloyd S, Hafezparast M, Lennon-Pierce M, Eppig JT, Festing MFW, Fisher EMC 2000. Genealogies of mouse inbred strains Nature Genetics 24: 23-25.

Berry RJ 1970. The natural history of the house mouse. Field Studies 3: 219-162.

Berry RJ 1981. Biology of the house mouse. London, Academic Press.

Blanchard RJ, Hebert MA, Ferrari P, Palanza P, Figueira R, Blanchard CD, Stefano P 1998. Defensive behaviors in wild and laboratory (Swiss) mice: the mouse defense test battery. Physiology & Behavior 65: 201-209.

Blednov YA, Stoffel M, Chang SR, Harris RA 2001. Potassium channels as targets for ethanol: Studies of G-protein-coupled inwardly rectifying potassium channel 2 (GIRK2) null mutant mice. Journal of Pharmacology and Experimental Therapeutics 298: 521-530.

Bogren LY 1984. Side preference in women and men when holding their newborn child: psychological background. Acta Psychiatrica Scandinavica 69: 13-23.

Campbell DJ 1978. The effects of rats on vegetation. In: Dingwell PR, Atkinson IAE, Hay C ed. The Ecology and Control of Rodents in New Zealand Nature Reserves. Wellington, Department of Lands and Survey. Pp. 99-119.

Campbell K, Donlan CJ, Cruz F, Carrion V 2004. Eradication of feral goats *Capra hircus* from Pinta Island, Galápagos, Ecuador. Oryx 38: 328-333.

Carr WJ, Martoran.Rd, Krames L 1970. Responses of mice to odors associated with stress. Journal of Comparative and Physiological Psychology 71(2): 223-228.

Cheetham SA, Thom MD, Beynon RJ, Hurst JL 2008. The effect of familiarity on mate choice. In: Hurst JL, Beynon RJ, Roberts SC, Wyatt TD ed. Chemical Signals in Vertebrates 11, New York, Springer. Pp. 271-280.

Clapperton BK 2006. A review of the current knowledge of rodent behaviour in relation to control devices. Science for Conservation. Wellington, Science & Technical Publishing, Department of Copnservation. 55 pp.

Coomes DA, Mark AF, Bee J 2006. Animal control and ecosystem recovery. In: Allen RB, Lee WG ed. Biological Invasions in New Zealand. Berlin, Springer-Verlag. Pp. 339-353.

Cruz F, Carrion V, Campbell KJ, Lavoie C, Donlan CJ 2009. Bio-Economics of large-scale eradication of feral goats from Santiago Island, Galápagos. Journal of Wildlife Management 73: 191-200.

Dilks P, Towns DR 2002. Developing tools to detect and respond to rodent invasions of islands: workshop report and recommendations. Wellington, Department of Copnservation, DOC Science Internal Series 59: 5-18.

Epstein PR 1995. Emerging diseases and ecosystem instability: new threats to public health. American Journal of Public Health 85(2): 168-172.

Erdőhegyi Á, Topál J, Virányi Z, Miklósi Á 2007. Dog-logic: inferential reasoning in a two-way choice task and its restricted use. Animal Behaviour 74: 725-737.

Goldwater N 2007. Ecology of house mice within the Tawharanui Open Sanctuary. Unpublished thesis, University of Auckland, Auckland. 128 p.

Gray SJ, Jensen SP, Hurst JL 2002. Effects of resource distribution on activity and territory defence in house mice, *Mus domesticus*. Animal Behaviour 63: 531-539.

Guénet J-L, Bonhomme F 2003. Wild mice: an ever-increasing contribution to a popular mammalian model. Trends in Genetics 19(1): 24-31.

Howald G, Donlan CJ, Galvan JP, Russell JC, Parkes J, Samaniego A, Wang YW, Veitch D, Genovesi P, Pascal M and others 2007. Invasive rodent eradication on islands. Conservation Biology 21(5): 1258-1268.

Hughes NK, Banks PB 2010. Interacting effects of predation risk and signal patchiness on activity and communication in house mice. Journal of Animal Ecology 79(1): 88-97.

Hurst JL 1987. The functions of urine marking in a free-living population of house mice, *Mus domesticus* Rutty. Animal Behaviour 35: 1433-1442.

Hurst JL 2009. Female recognition and assessment of males through scent. Behavioural Brain Research 200(2): 295-303.

Hurst JL, Payne CE, Nevison CM, Marie AD, Humphries RE, Robertson DHL, Cavaggioni A, Beynon RJ 2001. Individual recognition in mice mediated by major urinary proteins. Nature 414(6864): 631-634.

Jensen SP, Gray SJ, Hurst JL 2003. How does habitat structure affect activity and use of space among house mice? Animal Behaviour 66: 239-250.

Jensen SP, Gray SJ, Hurst JL 2005. Excluding neighbours from territories: effects of habitat structure and resource distribution. Animal Behaviour 69: 785-795.

Kavaliers M, Colwell DD 1995a. Odours of parasitized males induce aversive responses in female mice. Animal Behaviour 50: 1161-1169.

Kavaliers M, Colwell DD 1995b. Discrimination by female mice between the odours of parasitized and non-parasitized males. Proceedings of the Royal Society of London Series B-Biological Sciences 261(1360): 31-35.

Levitis DA, Lidicker WZ, Freund G 2009. Behavioural biologists do not agree on what constitutes behaviour. Animal Behaviour 78(1): 103-110.

Lidicker WZ 1976. Social behaviour and density regulation in house mice living in large enclosures. Journal of Animal Ecology 45(3): 677-&.

Long JL 2003. Introduced Mammals of the World. Collingwood, CSIRO. 589 p.

MacKay JWB, Russell JC, Murphy EC 2007. Eradicating house mice from islands: successes, failures and the way forward. In: Witmer GW, Pitt WC, Fagerstone KA eds. Managing vertebrate invasive species: proceedings of an international symposium. USDA/APHIS Wildlife Services, National Wildlife Research Center, Fort Collins, Colorado, USA Pp. 294-304.

Meerburg BG, Singleton GR, Kijlstra A 2009a. Rodent-borne diseases and their risks for public health. Critical Reviews in Microbiology 35(3): 221-270.

Meerburg BG, Singleton GR, Leirs H 2009b. The Year of the rat ends - time to fight hunger! Pest Management Science 65(4): 351-352.

Meyer AN 1999. Commensal rodent control: challenges for the new millennium. In: Robinson WH, Rettich F, Rambo GW ed. 3rd International Conference on urban pests. Pp. 99-103.

Mills JN, Childs JE 1998. Ecologic studies of rodent reservoirs: Their relevance for human health. Emerging Infectious Diseases 4(4): 529-537.

Moles A, D'Amato FR 2000. Ultrasonic vocalization by female mice in the presence of a conspecific carrying food cues. Animal Behaviour 60: 689-694.

Musolf K, Hoffmann F, Penn DJ 2010. Ultrasonic courtship vocalizations in wild house mice, *Mus musculus musculus*. Animal Behaviour 79: 757-764.

Nunes AC, Mathias MD, Ganem G 2009. Odor preference in house mice: influences of habitat heterogeneity and chromosomal incompatibility. Behavioral Ecology 20(6): 1252-1261.

Payne AP 1994. The Harderian gland: a tercentennial review. Journal of Anatomy 185: 1-49.

Pearson OP 1947. The rate of metabolism of some small mammals. Ecology 28(2): 127-145.

Pomerantz SM, Nunez AA, Bean NJ 1983. Female behavior is affected by male ultrasonic vocalizations in house mice. Physiology & Behavior 31(1): 91-96.

Ramsay GW 1978. A review of the effects of rodents on the New Zealand invertebrate fauna. In: Dingwell PR, Atkinson IAE, Hay C ed. The Ecology and Control of Rodents in New Zealand Nature Reserves. Department of Lands and Survey, Wellington. Pp. 89-95.

Reeves PG, Nielsen FH, Fahey GC 1993. Ain-93 purified diets for laboratory rodents - final report of the American Institute of Nutrition ad hoc writing committee on the reformulation of the Ain-76a rodent diet. Journal of Nutrition 123(11): 1939-1951.

Reicher MA, Holman EW 1977. Location preference and flavor aversion reinforced by amphetamine in rats. Animal Learning & Behavior 5: 343-346.

Ruscoe WA 2001. Advances in New Zealand mammalogy 1990-2000: house mouse. Journal of the Royal Society of New Zealand 31(1): 127-134.

Ruscoe WA, Murphy EC 2005. House mouse. In: King CM ed. The Handbook of New Zealand Mammals. Second ed. New York, Oxford University Press. Pp. 204-221.

Shapira I, Shanas U, Raubenheimer D, Brunton D 2013. Laboratory rats as trap lures for invasive Norway rats: field trial and recommendations. New Zealand Journal of Ecology 37(2): (in press)

Shapira I, Shanas U, Raubenheimer D, Knapp C, Alberts S, Brunton D 2013. Laboratory rats as conspecific biocontrol agents for invasive Norway rats *Rattus norvegicus*. Biological Control 66: 83-91.

Sherborne AL, Thom MD, Paterson S, Jury F, Ollier WER, Stockley P, Beynon RJ, Hurst JL 2007. The genetic basis of inbreeding avoidance in house mice. Current Biology 17(23): 2061-2066.

Simberloff D 2009. Rats are not the only introduced rodents producing ecosystem impacts on islands. Biological Invasions 11(7): 1735-1742.

Smith J, Hurst JL, Barnard CJ 1994. Comparing behaviour in wild and laboratory strains of the house mouse: Levels of comparison and functional inference. Behavioural Processes 32: 79-86.

Sorensen A, Mayntz D, Raubenheimer D, Simpson SJ 2008. Protein-leverage in mice: the geometry of macronutrient balancing and consequences for fat deposition. Obesity 16(3): 566-571.

Sorensen A, Mayntz D, Simpson SJ, Raubenheimer D 2010. Dietary ratio of protein to carbohydrate induces plastic responses in the gastrointestinal tract of mice. Journal of Comparative Physiology B 180(2): 259-266.

St Clair JJH 2011. The impacts of invasive rodents on island invertebrates. Biological Conservation 144(1): 68-81.

Stenseth NC, Leirs H, Skonhoft A, Davis SA, Pech RP, Andreassen HP, Singleton GR, Lima M, Machang'u RS, Makundi RH and others 2003. Mice, rats, and people: the bio-economics of agricultural rodent pests. Frontiers in Ecology and the Environment 1(7): 367-375.

Taylor D, Katahira L 1988. Radio telemetry as an aid in eradicating remnant feral goats. Wildlife Society Bulletin 16(3): 297-299.

Thom MD, Hurst JL 2004. Individual recognition by scent. Annales Zoologici Fennici 41(6): 765-787.

Tidemann C 2005. Indian mynas - can the problem be controlled? 15th Urban Animal Management Conference. Australian Veterinary Association, Canbara. Pp. 55-57.

Towns DR, Broome KG 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. New Zealand Journal of Zoology 30(4): 377-398.

Tsachalidis EP, Sokos CK, Birtsas PK, Patsikas NK 2006. The Australian crow trap and the Larsen trap: their capture success in Greece. In: Manolas EI ed. Proceedings of the 2006 Naxos International Conference on Sustainable Management and Development of Mountainous and Island Areas. Democritus University of Thrace, Island of Naxos. Pp. 325-329.

Volfova R, Stejskal V, Aulicky R, Frynta D 2011. Presence of conspecific odours enhances responses of commensal house mice (*Mus musculus*) to bait stations. International Journal of Pest Management 57(1): 35-40.

Ward AJW, Herbert-Read JE, Simpson SJ 2011. Diets and decisions: the potential use of food protein cues in dietary, sexual and social decisions by mosquitofish. Animal Behaviour 82(4): 783-790.

White NR, Prasad M, Barfield RJ, Nyby JG 1998. 40- and 70-kHz vocalizations of mice (*Mus musculus*) during copulation. Physiology & Behavior 63(4): 467-473.

Yamazaki K, Beauchamp GK, Egorov IK, Bard J, Thomas L, Boyse EA 1983. Sensory distinction between H-2b and H-2bm1 mutant mice. Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences 80(18): 5685-5688.

CHAPTER 5: RESPONSES TO DIRECT VERSUS INDIRECT CUES OF PREDATION AND COMPETITION IN NAÏVE INVASIVE MICE: IMPLICATIONS FOR MANAGEMENT

5.1. Abstract

Many populations of invasive mice *Mus musculus* in New Zealand have experienced the removal of mammalian predators and competitors, with the consequence of mouse population irruptions. The effects of these removals on mouse foraging are largely unknown, yet this information is essential for developing and implementing better mouse control. I investigated the effects of direct and indirect predatory cues on foraging of free-ranging mice at a site where mammalian predators were eradicated 5 years previously. I used 17 stations, each containing four trays of millet seeds mixed thoroughly in sand, with three unfamiliar mammalian (a predator, a competitor, and a herbivore) odour treatments and a control (water), during the four phases of the moon. I measured mouse selectivity for treatment/control trays, giving-up densities (GUDs, a measure of food consumption), and tray encounter rates. Foraging by mice was not affected by odour cues from any of the unfamiliar mammals. Although the study was limited to a single lunar cycle, it appears that moonlight intensity may affect mouse foraging, with higher GUDs being recorded on brighter moon phases (full and waxing > new and waning) during the first night of the trials. Any effect was less pronounced during the second night. Resource encounter rates may also affected, with the proportion of trays foraged being lower during the brighter phases of the moon on both the first and second nights. I suggest that repeating the study over multiple

lunar cycles to confirm this influence and, if confirmed, coordinating management efforts according to the phases of the moon to improve mouse control and reduce bait wastage.

5.2. Introduction

Predators exert strong selection pressure on the foraging behaviours of prey species (Gould 1982; Lima & Dill 1990; Hawlena & Schmitz 2010). Animals generally increase their exposure and conspicuousness to predators when foraging, and may decrease their vigilance when feeding (Sih 1992; Brown & Kotler 2004). Therefore, when predators are present, prey species face a conflict between satisfying their nutritional requirements and minimizing their predation risk (Bernays 1998; Brown & Kotler 2004).

Cues of predation risk might be direct, for example scent cues indicating the presence of a predator, or indirect, representing a general predation risk (e.g. illumination intensity, which might affect exposure in nocturnal foragers). It has been suggested that the use of animal odours as deterrents may have the potential to constrain foraging and breeding of pest animals (Sheriff et al. 2009; Hughes & Banks 2010; McPhee et al. 2010; Webb et al. 2010). However, other studies suggest that this trait is species-specific and that naïve animals may be less receptive to these cues (Dickman 1992; Orrock 2010). Since there are costs both to being too risk averse in the face of these cues (foregone foraging opportunities) and too risk prone (increased predation), there is a strong incentive to continually recalibrate the correlation between cues and predation during the life history of an individual forager (Lima & Dill 1990; Brown & Kotler 2004).

One situation in which this calibration might occur is when prey species have become isolated from their predators. Potential consequences of this include loss of the ability to recognize predators, the neglect of cues indicating their presence, and the loss of anti-predator behaviours (Dickman 1992; Beauchamp 2004; Blumstein & Daniel 2005; Cox & Lima 2006; Orrock 2010). The process of losing anti-predator behaviours could be due either to individual learning (Griffin et al. 2000; Blumstein 2002; Cox & Lima 2006) or, in the longer term, to the effect of relaxed selection on gene pools (Lahti et al. 2009). In the former case, recalibration might involve direct or indirect cues of predation, or both, together with the availability of food, which might shift foraging between different levels of vigilance.

House mice (*Mus musculus*) show responsiveness to predatory cues of mammalian predators with which they are familiar, including cats (Hughes & Banks 2010) and feral cats (*Felis catus*) (Dickman 1992; Arthur et al. 2005) , red foxes (*Vulpes vulpes*), and western quolls (*Dasyurus geoffroii*) (Dickman 1992). The odour of ship rats (*Rattus rattus*) was also found to affect mouse foraging (Hancock 2008). While rats are interspecific competitors of mice (Ruscoe & Murphy 2005), they can also be considered as intraguild predators (O'Boyle 1974). Mice have also been shown to reduce foraging activities during the brighter phases of the moon (Dickman 1992). However, field and laboratory studies show that wild mice can become indifferent to cues of predation in the form of predator odours or illumination intensity (Dickman 1992; Coulston et al. 1993; Bramley 1999; Powell & Banks 2004), even despite the presence of avian predators (Dickman 1992).

Mice are among the most destructive invasive species in New Zealand (Atkinson 2006) but are seldom targeted during pest control operations. They are opportunistic omnivores and highly successful breeders (Ruscoe & Murphy 2005). Growing evidence

shows that invasive mice can damage native vegetation (Ruscoe et al. 2005), and reduce invertebrate (Tann et al. 1991) and vertebrate (Jones et al. 2003) populations. Mouse populations in New Zealand can irrupt both when food sources become abundant, for example after mast years in South Island beech forests (Murphy 1992), and when rat and mustelid populations are intensively controlled (Caut et al. 2007; Goldwater 2007; Ruscoe et al. 2011). The two principal strategies for ongoing pest management are the proactive approach (i.e. preventing establishment of pests in a pest-free environment) and the reactive approach (i.e. management of existing pest populations) (Parkes & Murphy 2003), both of which are used for mouse control in New Zealand. To date, the reactive approach (usually used when complete eradication has not been achieved) has had limited success for mouse control (Ruscoe & Murphy 2005; Goldwater 2007; MacKay et al. 2007), probably because current management of bait stations is not efficient enough.

Several studies have demonstrated that the odours of predators can reduce mouse activity and trappability (Dickman 1992; Coulston et al. 1993; Bramley 1999; Powell & Banks 2004; Arthur et al. 2005; Hancock 2008; Hughes & Banks 2010). However, the feasibility of using the odours of predators and competitors to deter mice as part of a reactive control strategy remains unclear. Key questions related to the use of such a strategy are whether mice in New Zealand retain the ability to recognize cues from predators and competitors when these predators/competitors have been removed, and whether such cues affect their foraging. Also unknown is the possible connection between the effectiveness of mouse control and a potential indirect cue, the illumination associated with the moon cycle.

Here I test the possible impacts of mammalian odours (a specific direct cue of predation or competition) and illumination resulting from moon phase (a general indirect cue

of predation), on the foraging of invasive mice in a mainland site free from mammalian predators and competitors. I aimed to measure the behavioural responses of these mice to predatory and competitive cues and assess the relative importance of these two factors to mouse foraging. I predicted that mouse foraging would be negatively affected by predator/competitor odours and the brighter phases of the moon. I also predicted that the effects of these cues would decrease over time, as mice would get familiar with the food sources and habituate to the unreinforced cues. Based on these results, I identify implications for the management of invasive mice unfamiliar with heterospecific mammals.

5.3. Methods

I investigated foraging decisions in a population of feral mice within the coastal sand dunes (36º22'N, 174º49'E) of the Tawharanui Open Sanctuary, 65 km north of Auckland City. The dune site is dominated by *Muehlenbeckia complexa* shrubs, which provide an effective dense cover for the mice, which prefer these over exposed areas (Arthur et al. 2005). In 2004, a 2.5-km-long predator-deterrent fence was erected at the western end of the peninsula, with the aim of creating a 588-ha pest-free park. An aerial poison drop and ground-based control followed the fence completion and resulted in the eradication of ship rats, Norway rats (*Rattus norvegicus*), cats and mustelids (*Mustela erminea*, *M. nivalis* and *M. furo*), but mice survived the poisoning. Unconstrained by other mammals, mouse populations at Tawharanui irrupted and spread throughout the sanctuary. Goldwater (2007) found that while mice within the park maintained high population densities in all available microhabitats, outside the park, where there are mammalian predators and competitors, there were fewer mice. Moreover, he

found that mice inside the park were significantly larger and heavier than mice outside the park. Although mice can penetrate the fence (Goldwater 2007), the existence of a buffer zone outside the fence, which includes grazed paddocks with limited cover and bait stations targeting pest mammals, restricts immigration and also prevents encounters with predators.

At the time of this study, the mouse population at Tawharanui had been free from predation by mammals for 5 years (M. Maitland, Open Sanctuary Coordinator, pers. comm.), and presumably naïve to mammalian predators. Occasional incidents of rat and mustelid reinvasions have been reported (M. Maitland, pers. comm.), but these are rare and the rats have been rapidly detected and controlled. The only other potential mouse predators at present in the park are two species of birds (Robertson et al. 2007), the strictly diurnal Australian harrier (*Circus approximans*) (Baker-Gabb 1981) and the nocturnal morepork owl (*Ninox novaeseelandiae*) (Haw & Clout 1999). Mice are generally nocturnal, although they occasionally forage during the day (Ruscoe & Murphy 2005).

I used trays of millet seeds, mixed thoroughly in 0.5 L of sand, with scent treatments during four phases of the moon (waxing, full, waning and new) to study the effect of the presence of predator olfactory cues and light intensity on mouse foraging. The study was conducted in 2009 during the austral winter (June and August) when food is scarce and thus mice would potentially be more responsive to supplementary food. Four trays were placed at each of 17 stations (giving 68 trays in total). Trays were set up as sealed boxes (3-L clear plastic boxes with lids, Sistema, New Zealand) to protect the seeds and sand from the weather and to prevent birds from taking seeds. I used clear plastic lids so as to keep trays exposed to illumination from the moon. The mice could enter the trays via two grey plastic pipes (40 mm in diameter and 50 mm long) mounted on opposite sides of each box. Seeds

were sterilized in an autoclave for 50 min at 121°C to prevent germination (Hancock et al. 2004) and then dried in an oven at 70°C for 1 h before weighing to standardized weights (see below).

I used the odours of domestic cat (a predator previously present in the park), the Norway rat (*Rattus norvegicus*; a competitor (Ruscoe & Murphy 2005) and potential intraguild predator (O'Boyle 1974) also previously present), goat (*Capra hircus*; an unfamiliar herbivore and a potential cue for competition, diseases and/or physical disturbance) as treatments, and distilled water as the control. Rat faeces were collected separately from male and female laboratory animals at Massey University, Auckland. Cat faeces were collected from a cattery in Auckland (no discrimination between male and female cats was possible). Goat faeces were collected separately from male and female goats at a private farm near Auckland. All samples were frozen at < −18°C immediately after collection. To standardize the volume of the scent samples, faeces were defrosted overnight at 4°C then mixed with distilled water at a ratio of 1:2.14 by volume and blended into a solution. The solutions were separated into 1-g samples and distributed into 10-ml plastic vials. Vials were frozen again at < −18°C, and defrosted on the night before use in the experiment. Vials containing 2 ml of distilled water were used as controls.

The stations were set out in two east–west transects, one comprising 14 stations and the other three. Stations were set up 25 m apart (the average home range length for mice at another dune site in New Zealand was > 50 m; Miller 1999). Trays placed at each station were spaced 1–1.5 m apart. To habituate the mice to the presence of the trays, trays were placed in the field 7 days prior to the start of the experiment, with 1 g of seeds mixed thoroughly into 0.5 L of sand in the trays.

After the habituation period, I ran the experiment over three consecutive nights for each moon phase (with the empty trays left in place between moon phases). In the afternoon before the first night of each phase, I mixed 3 g of seeds thoroughly into the 0.5 L of sand in the trays and placed the three scent and control vials in the four trays of each station. Upright vials were attached to the inside of the tray with gaffer tape. The treatments were distributed randomly among the trays within each station before each phase to prevent possible orientation effects. The vials were removed at the end of each phase, with new samples being used at the beginning of the next phase. During the phases, trays were checked each morning and, if foraged upon, the seeds were sifted from the sand and placed in a labelled container. New seeds (3 g) were then thoroughly mixed into the sand in the tray. On the third morning of each moon phase, all seeds were removed from the trays. The seeds collected from each foraged tray were dried (as above) and reweighed.

5.3.1. Data Analysis

Due to inclement weather, it was not possible to collect the seeds from the trays during and after the third night of the waning moon. Data from the third night could therefore only be included in analyses comparing the full- and new-moon phases. I used non-parametric tests whenever the data violated the assumption of normality, and for comparisons of proportions.

Preference of mice for each of the treatments was evaluated by calculating the Manly–Chesson Selectivity Index (Chesson 1983). The mean proportion of seeds harvested from a treatment tray was divided by the sum of the means of proportions of seeds harvested from all four treatments trays. I used a one-sample t-test (normally distributed data) or a one-

sample Wilcoxon signed rank test (data not normally distributed) to determine whether selectivity values differed from an expected random proportion of 0.25. Selectivity values >0.25 would indicate preference for the treatment, while values <0.25 would indicate preference against the treatment. Stations where none of the four treatment trays were foraged upon by mice were excluded from this analysis.

I used giving-up densities (GUD) and the proportion of trays foraged to compare levels of foraging by mice. GUD refers to the amount of food a forager leaves behind in a food patch (Brown 1988), and hence gives an indication of the balance reached by the forager between foraging benefits (food gain) and costs, including the perceived risk of predation while feeding. GUD is therefore taken to reflect the density at which it is no longer worth the risk (or the effort) of continuing to exploit the resource. In contrast, the proportion of foraged trays will provide information on the probability that a mouse locates the food and initiates feeding. GUD thus reflects the decision of when to terminate a feeding bout, while the number of food stations that are exploited provides a measure of the probability that a given seed tray was encountered and exploited at least once.

GUDs were measured by the final mass of seeds remaining in the trays. I used Kruskal–Wallis tests to compare GUDs (foraged trays only, treatments pooled) between moon phases for each of the first two foraging nights. To evaluate interactions between moon phases and foraging nights, and differences between foraging nights for each moon phase, I subtracted the second night from the first (for all 68 trays) and performed one-sample Kolmogorov–Smirnov and one-sample t-tests, respectively. A Kruskal–Wallis test was used to compare GUDs (treatments pooled) among the first, second and third foraging nights during full- and new-moon phases. I used Mann–Whitney tests to compare GUDs (treatments

pooled) between full- and new-moon phases for each foraging night separately. To evaluate moon phases and foraging night interactions, I subtracted results for the new moon from those for the full moon for each of the foraging nights and performed a Kruskal–Wallis test on the difference.

Maximum likelihood analysis of variance (MLAV) was used to compare the effect of treatments and moon phases on the proportions of trays foraged by mice during the first and second nights separately. MLAV was also used to test the effects of the first two foraging nights during full- and new-moon phases on the proportion of foraged trays (the third night was excluded from the analysis since all trays were foraged during both these moon phases).

5.4. Results

Only during the first night of waxing and waning moon phases did odour treatments have a significant effect on mouse selectivity. Interestingly, however, the mice showed preference against control trays (one-sample t-test; $t_{14} = -3.45$, $P = 0.004$ and Wilcoxon signed rank test; $P = 0.001$; Fig. 5.4.1A). There were no significant preferences for any of the trays on the second night (Fig. 5.4.1B).

Moon phase had a significant effect on mouse foraging during the first night, with significantly lower GUDs during waning and new moons on the first night (Kruskal–Wallis; $H_3 = 10.038$, $P = 0.018$; Fig. 5.4.2A) and near significant differences during the second night (Kruskal–Wallis; $H_3 = 7.811$, $P = 0.050$; Fig. 5.4.2B). Interactions between the first and second nights were significant for full moon (Kolmogorov–Smirnov; $D = 2.308$, $P = 0.001$)

and waning moon (t-test, t_{67} = 2.879, P = 0.005), and not significant for waxing and new moons (Fig. 5.4.2C).

GUDs were higher during full moon compared with new moon on the first night (Mann–Whitney; U = 239.5, P = 0.024), but not on the second and third nights (Fig. 5.4.2D). During full moon compared with new moon phases, the foraging night (first, second and third) had a significant effect on mouse GUDs (Kruskal–Wallis; H_2 = 12.806, P = 0.001; Fig. 5.4.2D). There was a significant interaction between foraging night and moon phase when foraging during full moon is compared with foraging during new moon (Kruskal–Wallis; H_2 = 15.122, P = 0.001; Fig. 5.4.2E).

Scent had no effect on the number of trays foraged by mice on either the first or second nights (MLAV; $P > 0.1$). Moon phase had an effect on the number of trays foraged by mice, with fewer trays foraged upon during the full moon on the first and second nights (MLAV; χ^2_3 = 22.6, $P < 0.001$; χ^2_3 = 13.24, P = 0.004, respectively; Fig. 5.4.3A, B). There were no interactions between treatment and moon phase on either night (MLAV; χ^2_9 = 6.39, P = 0.700; χ^2_9 = 2.37, P = 0.984, respectively).

Proportions of foraged trays were higher during new moon compared with during full moon on both the first and second nights (MLAV; χ^2_1 = 15.13, $P < 0.001$; Fig. 5.4.4). The proportion of foraged trays was higher on the second night than on the first night (MLAV; χ^2_1 = 7.45, P = 0.006; Fig. 5.4.4). On the third night, all the trays showed signs of foraging during both new and full moons (Fig. 5.4.4).

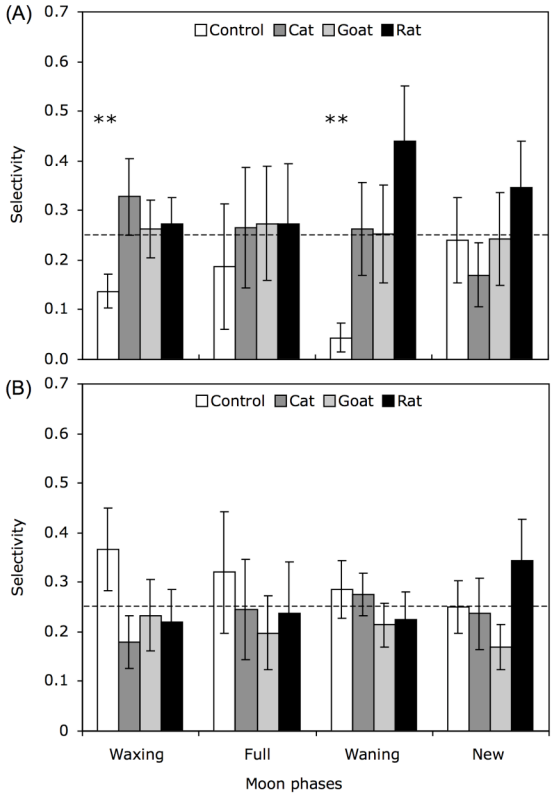

Figure 5.4.1. Effect of odour treatments on mouse selectivity (mean ± SE) on the first (A) and second nights (B), during all moon phases. Selectivity values >0.25 (represented by dashed line) indicate preference for the treatment, while values <0.25 indicate preference against the treatment. Only control trays during waxing and waning moons significantly differ (negatively) from 0.25. ** $P < 0.01$.

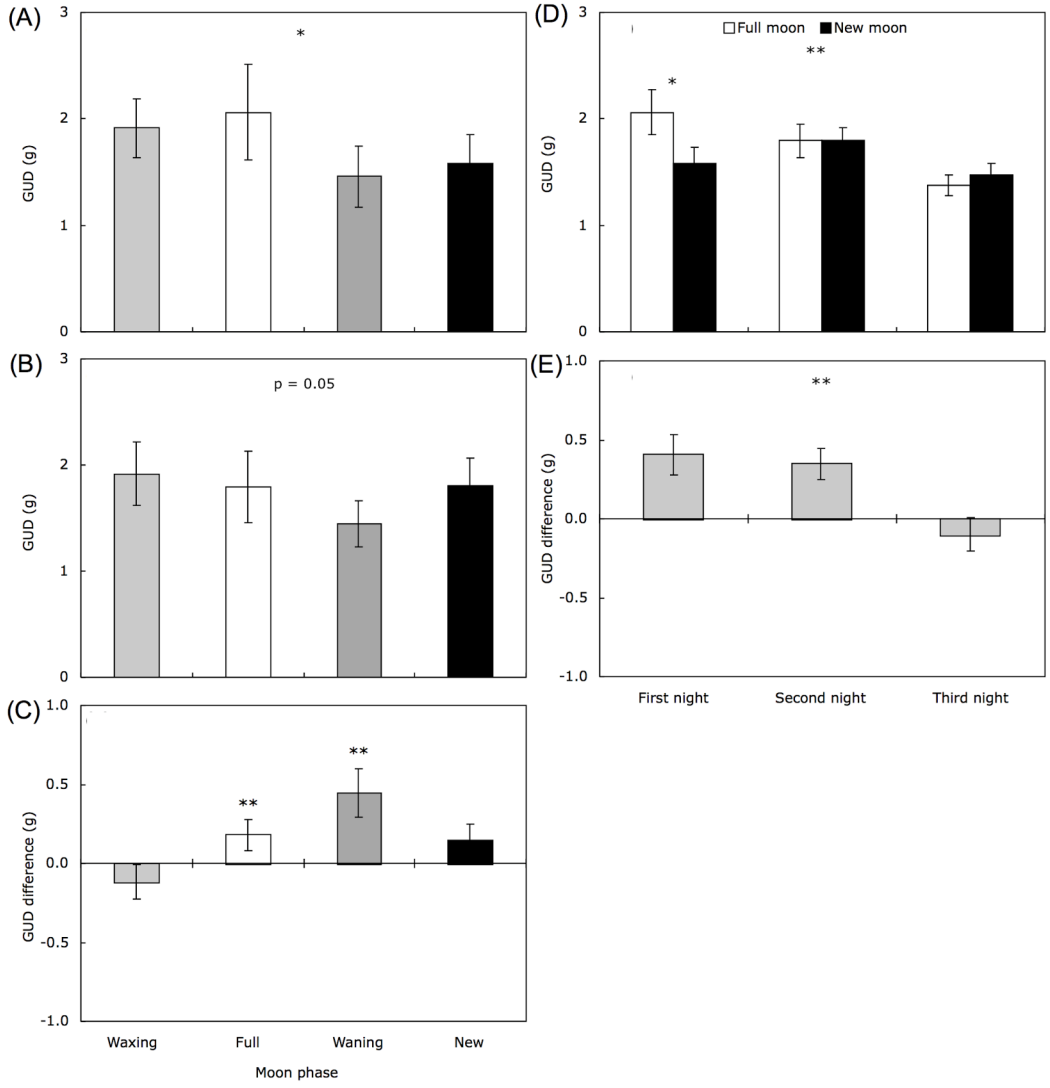

Figure 5.4.2. Effect of moon phase on mouse giving-up densities (GUDs, the density of seeds at which the forager ceases consumption; mean ± SE, treatments pooled) during (A) the first and (B) the second nights (foraged trays only). (C) The interaction between moon phase and foraging nights as indicated by the differences in GUDs between the first and second nights (all trays included). (D) Effects of full- and new-moon phases on mouse GUDs (mean ± SE, treatments pooled) during the first, second and third nights (foraged trays only). (E) The relationship between moon phase and foraging nights is demonstrated by the differences in GUDs between full and new moons during the three nights (all trays included). GUDs were higher during bright phases of the moon and lower during the first night compared with the second night. Both foraging night and the interaction between foraging night and moon phase had an effect on mouse GUDs. **P* < 0.05 and ***P* < 0.01.

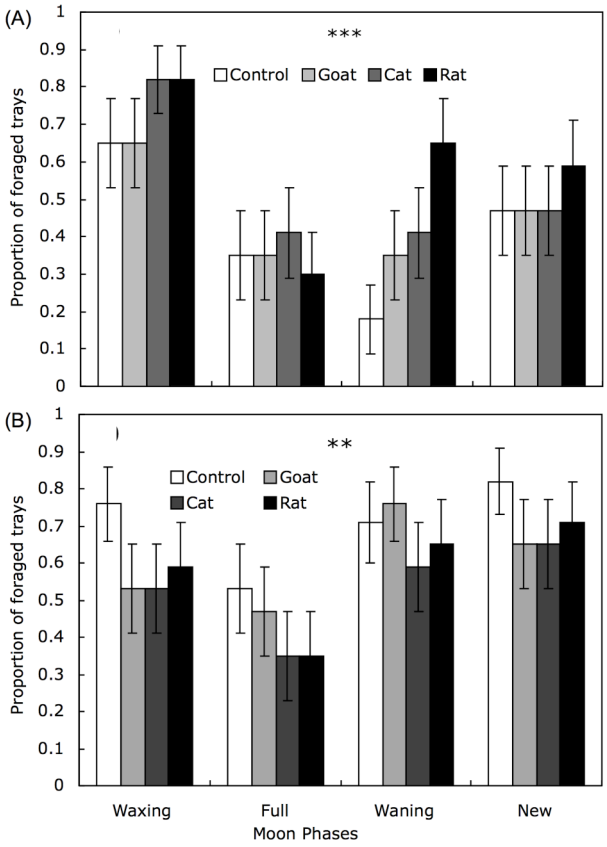

Figure 5.4.3. Effects of scent and moon phase on the proportions of foraged trays (mean ± SE) during (A) the first and (B) the second nights. Moon phase and scent had an effect on mouse foraging, proportions being the lowest during full moon. $^{**}P < 0.01$ and $^{***}P < 0.001$. SE were calculated using SAS PROC CATMOD.

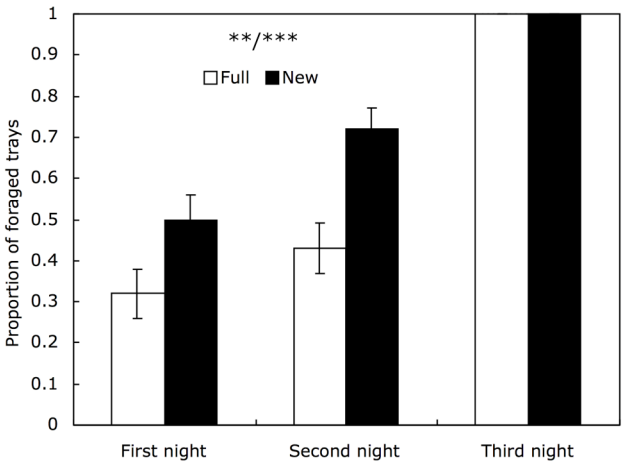

Figure 5.4.4. Effect of full and new moons on the proportion of trays with signs of foraging (mean ± SE, treatments pooled). Proportions were higher during new moons compared with full moons on both the first and second nights, and on the second night compared with the first night. All trays were foraged upon on the third night during both moon phases and hence these values are excluded from the statistical analysis. $^{**}P < 0.01$ and $^{***}P < 0.001$.

5.5. Discussion

I found some evidence that mouse foraging was affected by the presence of scent cues of a mammalian predator, competitor or herbivore; a result that contrasts with previous studies on *Mus musculus*, both naïve and familiar with mammalian predators (Dickman 1992; Bramley 1999; Powell & Banks 2004). Likewise, the only circumstance where selectivity was significant was against control trays, suggesting a degree of attraction to the test odours, possibly as a result of a neophilic response. At the time of this study, populations of mice at Tawharanui Open Sanctuary had been free from mammalian predators for at least 5 years. Although mice do reinvade the park each year (Goldwater 2007), these incursions are from the heavily predator controlled buffer zone outside the park's fence, which means that such invasions are rare and mouse contact with mammalian predators is limited.

In contrast to mammalian odours, the results are consistent with moonlight intensity influencing mouse foraging, with GUDs being lower and visiting rates higher during darker phases. It has been shown that rodents experiencing little or no predatory pressure might not respond to light intensity as a cue for increased predation. Shapira et al. (2008) found that in sites where the presence of nocturnal mammalian predators was very low, desert-dwelling gerbils did not decrease food consumption even during full-moon nights. Dickman (1992) showed that mice inhabiting sites free of mammalian predators were less responsive to moonlight intensity than mice from sites where predators were present. In both cases, however, mammalian predators were historically either very scarce (Shapira et al. 2008) or completely absent (Dickman 2008), although owls and snakes were present. At this study site, mice have co-existed with mammalian predators for many generations, experiencing a mammal-free environment only recently. In addition, owls are present at the site, and might affect mouse responsiveness to brighter phases of the moon.

The effect of illumination intensity on mouse foraging behaviour demonstrates a complex interplay between the vigilance of mice and their foraging strategies. During the first night, trends in mouse foraging were affected by the phases of the moon, and full and waxing moon phases had higher GUDs compared with new and waning phases. Moreover, the lowest GUDs were seen during the waning rather than the new-moon phases. This suggests that after two weeks of relatively low food consumption (waxing and full moon), mice compensated by increasing consumption, resulting in higher GUDs during the new-moon phase. These differences can be attributed to an increase in food consumption during the full moon and a decrease in food consumption during the waning-moon phase. During the second night, however, differences in GUDs between the moon phases were less obvious.

The shift in GUDs during the different moon phases from the first to the second night suggests that mice treated the trays as reliable and secure food sources. The effect was significant enough to decrease the importance of the intensity of moonlight as a cue for predation risk.

Proportions of foraged trays were lowest during the full-moon phase on both the first and second nights. This suggests that light intensity affected encounters by mice with the food stations more than the time they took to extract a given amount of food from the source upon encounter. Comparison of the full- and new-moon phases supports this conclusion; GUDs were similar during the second night but proportions of foraged trays, while increasing in both moon phases, remained higher during the new moon. Cloudy skies might have been the reason for the high GUDs and tray encounter rates recorded on the third night of the full moon. I predict from this study that mice may be generally sensitive to illumination cues.

My findings suggest that the scents tested here are likely to be ineffective as deterrents for naïve invasive mice. Although responses to predator odour can be species specific (Jędrzejewski et al. 1993), I suspect that this finding will apply to a much wider range of mammalian odours. It should be noted that I used the odours of domesticated animals that had not had access to mice as prey. However, domestic cats are predators of wild rodents (Woods et al. 2003) and laboratory rats are the same species (*R. norvegicus*) as the Norway rat and it has been demonstrated that predator scent can alter prey behaviour even in a synthesized form (Boag & Mlotkiewicz 1994).

However, the effect of illumination on foraging by invasive mice appears to be significant and could be used to contribute to mouse control protocols. The most common method of mouse control in New Zealand is poisoning (Towns & Broome 2003; Clapperton

2006), but it is time-consuming to maintain bait stations and replenish bait. At the same time, reducing the quantity and spread of poison are strategies used to minimize harm to non-target species (Eason & Spurr 1995; Murphy et al. 1998; Eason et al. 2002). My results indicate that moonlight intensity has a greater effect on the probability that foraging will continue after the animal has encountered a food source than on the animal's GUD; mice varied their spatial activity more than the times they spent at a food source during brighter phases of the moon. Hence, consideration should be given to the distances between bait stations. The standard grids in New Zealand for mice traps and bait stations are 50 x 50 m or 25 x 25 m (King et al. 1996; Choquenot & Ruscoe 2000; Harper 2010; MacKay et al. 2011). In this study, I found that even a 25 x 25 m grid is significantly less effective when illumination conditions are unfavourable (i.e. light nights) than when they are favourable (i.e. dark nights). Moreover, as the maximum home range of mice is small relative to other invasive rodents, especially in high density populations and high productivity habitats (average home range of 0.6 ha and range length of 57.6 m ± 10.3 m was reported from other sites in New Zealand, Ruscoe & Murphy 2005), and extraction efficiency is high (this study), long distances between stations might target the mice that are foraging close to the station, but some individuals might never encounter a bait station.

This study was conducted during winter, when food was relatively scarce, and in a habitat that provided dense cover. Cover has been found to be an important factor in mouse activity levels and foraging (Dickman 1992; Arthur et al. 2005). These studies report that mice were more active in areas with greater habitat complexity and higher percentages of land cover. My results showing reduced activity during brighter phases of the moon are likely to be exacerbated in areas where cover is less dense. In addition, following baiting

regimes in accordance with the moon cycle could benefit management even more in productive seasons when bait consumption is often lower than it is in winter. I suggest this approach requires a more robust design: independent placement of trays and repetition over multiple lunar cycles.

Incorporating an animal's behavioural traits into management decisions can be a powerful tool in conservation (Holway & Suarez 1999) and this is true for the management of the house mouse (Clapperton 2006). I suggest that using a greater density of bait stations and shifting bait applications toward the darker phases of the moon (i.e. refilling stations at waning moon) would target more mice and that these mice would consume greater amounts of poison bait. This would increase poison control efficacy while reducing bait waste. Further research comparing existing baiting regimes with the ones suggested here would demonstrate whether incorporating mouse foraging traits into management practices is feasible.

5.6. Acknowledgements

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5.7. References

Arthur AD, Pech RP, Dickman CR 2005. Effects of predation and habitat structure on the population dynamics of house mice in large outdoor enclosures. Oikos 108: 562–572.

Atkinson IAE 2006. Introduced mammals in a new environment. In: Allen RB, Lee WG eds Biological Invasions in New Zealand. Ecological Studies 186. Berlin, Springer-Verlag. Pp. 49–66.

Baker-Gabb DJ 1981. The diet of the Australasian harrier (*Circus approximans*) in Manawatu-Rangitikei sand country, New Zealand. Notornis 28: 241–254.

Beauchamp G 2004. Reduced flocking by birds on islands with relaxed predation. Proceedings of the Royal Society B – Biological Sciences 271: 1039–1042.

Bernays EA 1998. The value of being a resource specialist: behavioral support for a neural hypothesis. American Naturalist 151: 451–464.

Blumstein DT 2002. Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. Journal of Biogeography 29: 685–692.

Blumstein DT, Daniel JC 2005. The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society B – Biological Sciences 272: 1663–1668.

Boag B, Mlotkiewicz JA 1994. Effect of odor derived from lion faeces on behavior of wild rabbits. Journal of Chemical Ecology 20: 631–637.

Bramley GN 1999. Habitat use and responses to odours by rodents in New Zealand. Unpublished PhD thesis, University of Waikato, Hamilton, New Zealand. 260 pp.

Brown JS 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22: 37–47.

Brown JS, Kotler BP 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7: 999–1014.

Caut S, Casanovas JG, Virgos E, Lozano J, Witmer GW, Courchamp F 2007. Rats dying for mice: modelling the competitor release effect. Austral Ecology 32: 858–868.

Chesson J 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64: 1297–1304.

Choquenot D, Ruscoe WA 2000. Mouse population eruptions in New Zealand forests: the role of population density and seedfall. Journal of Animal Ecology 69: 1058–1070.

Clapperton BK 2006. A review of the current knowledge of rodent behaviour in relation to control devices. Science for Conservation 263. Wellington, Department of Conservation. 55 pp.

Coulston S, Stoddart DM, Crump DR 1993. Use of predator odors to protect chick-peas from predation by laboratory and wild mice. Journal of Chemical Ecology 19: 607–612.

Cox JG, Lima SL 2006. Naiveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. Trends in Ecology & Evolution 21: 674–680.

Dickman CR 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73: 313–322.

Dickman CR 2008. Indirect interactions and conservation in human-modified environments. Animal Conservation 11: 11–12.

Eason CT, Spurr EB 1995. Review of the toxicity and impacts of brodifacoum on non target wildlife in New Zealand. New Zealand Journal of Zoology 22: 371–379.

Eason CT, Murphy EC, Wright GRG, Spurr EB 2002. Assessment of risks of brodifacoum to non-target birds and mammals in New Zealand. Ecotoxicology 11: 35–48.

Goldwater N 2007. Ecology of house mice within the Tawharanui Open Sanctuary. Unpublished MSc thesis, University of Auckland, Auckland, New Zealand. 128 pp.

Gould JL 1982. Ethology: The mechanisms and evolution of behavior. 1st edn. New York, Norton. 544 pp.

Griffin AS, Blumstein DT, Evans CS 2000. Review: Training captive-bred or translocated animals to avoid predators. Conservation Biology 14: 1317–1326.

Hancock B 2008. The influence of ship rats (*Rattus rattus*) on the habitat preferences of the house mouse (*Mus musculus*). Unpublished MSc thesis, Victoria University of Wellington, New Zealand. 117 pp.

Hancock JH, Wilkerson JB, Moody FH, Newman MA 2004. Seed-specific placement of in-furrow fungicides for control of seedling disease in cotton. Crop Protection 23: 789–794.

Harper GA 2010. Habitat use by mice during winter on subantarctic Auckland Island. New Zealand Journal of Ecology 34: 262–264.

Haw JM, Clout MN 1999. Diet of morepork (*Ninox novaezeelandiae*) throughout New Zealand by analysis of stomach contents. Notornis 46: 333–345.

Hawlena D, Schmitz OJ 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. Proceedings of the National Academy of Sciences (USA) 107: 15503–15507.

Holway DA, Suarez AV 1999. Animal behavior: an essential component of invasion biology. Trends in Ecology & Evolution 14: 328–330.

Hughes NK, Banks PB 2010. Interacting effects of predation risk and signal patchiness on activity and communication in house mice. Journal of Animal Ecology 79: 88–97.

Jędrzejewski W, Rychlik L, Jędrzejewska B 1993. Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. Oikos 68: 251–257.

Jones AG, Chown SL, Gaston KJ 2003. Introduced house mice as a conservation concern on Gough Island. Biodiversity and Conservation 12: 2107–2119.

King CM, Innes JG, Flux M, Kimberley MO 1996. Population biology of small mammals in Pureora Forest Park: 2. The feral house mouse (*Mus musculus*). New Zealand Journal of Ecology 20: 253–269.

Lahti DC, Johnson NA, Ajie BC, Otto SP, Hendry AP, Blumstein DT, Coss RG, Donohue K, Foster SA 2009. Relaxed selection in the wild. Trends in Ecology & Evolution 24: 487–496.

Lima SL, Dill LM 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619–640.

MacKay JWB, Russell, JC, Murphy, EC 2007. Eradicating house mice from islands: successes, failures and the way forward. In: Witmer GW, Pitt WC, Fagerstone KA eds Managing Vertebrate Invasive Species. Proceedings of an International Symposium. Fort Collins, CO, USDA/ APHIS/WS, National Wildlife Center. Pp. 294–304.

MacKay JWB, Murphy EC, Anderson SH, Russell JC, Hauber ME, Wilson DJ, Clout MN 2011. A successful mouse eradication explained by site-specific population data. In: Veitch CR, Clout MN, Towns DR eds Island Invasives: Eradication and Management. Gland, Switzerland, IUCN. Pp. 198–203.

McPhee ME, Segal A, Johnston RE 2010. Hamsters use predator odors as indirect cues of predation risk. Ethology 116: 517–523.

Miller AP 1999. Ecological energetics of feral house mice (*Mus musculus*) inhabiting coastal sand dunes. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.

Murphy EC 1992. The effects of a natural increase in food-supply on a wild population of house mice. New Zealand Journal of Ecology 16: 33–40.

Murphy EC, Clapperton BK, Bradfield PMF, Speed HJ 1998. Brodifacoum residues in target and non-target animals following large-scale poison operations in New Zealand podocarp-hardwood forests. New Zealand Journal of Zoology 25: 307–314.

O'Boyle M 1974. Rats and mice together: The predatory nature of the rat's mouse killing response. Psychological Bulletin 81: 261–269.

Orrock JL 2010. When the ghost of predation has passed: do rodents from islands with and without fox predators exhibit aversion to fox cues? Ethology 116: 338–345.

Parkes J, Murphy E 2003. Management of introduced mammals in New Zealand. New Zealand Journal of Zoology 30: 335–359.

Powell F, Banks PB 2004. Do house mice modify their foraging behaviour in response to predator odours and habitat? Animal Behaviour 67: 753–759.

Robertson CJR, Hyvönen P, Fraser MJ, Pickard CR 2007. Atlas of Bird Distribution in New Zealand 1991–2004. Wellington, The Ornithological Society of New Zealand. 533 pp.

Ruscoe WA, Murphy EC 2005. House mouse. In: King CM ed. The Handbook of New Zealand Mammals. 2nd edn. Melbourne, Oxford University Press. Pp. 204–221.

Ruscoe WA, Elkinton JS, Choquenot D, Allen RB 2005. Predation of beech seed by mice: effects of numerical and functional responses. Journal of Animal Ecology 74: 1005–1019.

Ruscoe WA, Ramsey DSL, Pech RP, Sweetapple PJ, Yockney I, Barron MC, Perry M, Nugent G, Carran R, Warne R, Brausch C, Duncan RP 2011. Unexpected consequences of control: competitive vs. predator release in a four-species assemblage of invasive mammals. Ecology Letters 14: 1035–1042.

Shapira I, Sultan H, Shanas U 2008. Agricultural farming alters predator–prey interactions in nearby natural habitats. Animal Conservation 11: 1–8.

Sheriff MJ, Krebs CJ, Boonstra R 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. Journal of Animal Ecology 78: 1249–1258.

Sih A 1992. Prey uncertainty and the balancing of antipredator and feeding needs. American Naturalist 139: 1052–1069.

Tann CR, Singleton GR, Coman BJ 1991. Diet of the house mouse, *Mus domesticus*, in the mallee wheatlands of north- western Victoria. Wildlife Research 18: 1–12.

Towns DR, Broome KG 2003. From small Maria to massive Campbell: Forty years of rat eradications from New Zealand islands. New Zealand Journal of Zoology 30: 377–398.

Webb JK, Pike DA, Shine R 2010. Olfactory recognition of predators by nocturnal lizards: safety outweighs thermal benefits. Behavioral Ecology 21: 72–77.

Woods M, McDonald RA, Harris S 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. Mammal Review 33:174–188.

CHAPTER 6: FIRST ENCOUNTERS OF WILD HOUSE MICE WITH NOVEL RAT SCENT: RISK-TAKING FEMALES AND CAUTIOUS MALES?

6.1. Abstract

Interspecific competition and predator prey interactions are key factors for an individual's survival. Therefore, subordinate competitor or prey species have strong incentives to continually recalibrate the correlation between cues indicating the presence of competitors/predators and the exploitation of available resources. I tested for behavioural responses of rat-naïve wild mice (*Mus musculus*) upon first encounter with novel scent cues of rats (*Rattus spp*., competitors and potential predators of mice) during two consecutive nights in a Y maze apparatus. My aim was to learn whether these cues affect foraging and activity decisions made by mice. When all mice were analysed together, I found no or weak responses to rat scent. This result however, masked unanticipated behavioural differences between male and female mice. During the first night, male food selectivity (between treatment and control cages) was positive for control while female selectivity was slightly positive for treatment. Males spent more time in, and made more visits to, control compared with treatment cages, while no difference was found for females. During the second night however, both males and females showed no preference for either treatments or controls. Female harvest rates (the time spent finding, handling and consuming seeds) were higher than those of males during the first night and lower (but not significantly) during the second night, whereas male harvest rates remained constant. I show here that in rat-naïve wild mice, initial response to novel rat scent is sex and time related, and regardless of whether these are

general responses to the novelty of the scent or specific responses to rat scent, the behavioural differences between the sexes are striking. I suggest that these differences might be the result of different evolutionary pressures on males and females, and that quick adjustments in responses through time relate to rapid learning by mice.

6.2. Introduction

Interspecific competition and predator prey interactions are key drivers for the structure of communities and populations, and are crucial factors for the fate of individuals (Schoener 1983, Lima & Dill 1990, Krebs 2001). Taxonomically close species usually exhibit similar niche requirements and if sharing the same habitat, the potential for competitive exclusion (Gause 1934, Burns & Strauss 2011), and/or intraguild predation (Polis, Myers & Holt 1989, Polis & Holt 1992, Arim & Marquet 2004) increases. Since there are costs both to being too risk averse (foregone resource opportunities) and to being too risk prone (direct encounter with a competitor/predator), there is a strong incentive for subordinate individuals to continually recalibrate the correlation between cues indicating the presence of competitors/predators and the exploitation of available resources (Brown 1988, Kotler & Brown 1990, Mitchell *et al.* 1990, Polis & Holt 1992, Fedriani *et al.* 2000). How animals resolve this conflict is a factor that is likely under strong selection pressure, and of fundamental interest to understanding the demography, activity patterns and time budgets of animals in their natural habitats (Schoener 1974, Polis et al. 1989, Ziv *et al.* 1993, Bernays 1998, Abramsky, Rosenzweig & Subach 2001).

Predator-prey and competitive interactions can be the result of direct interactions between two or more species (Lawrence 1979, Lima & Dill 1990, Pinter-Wollman *et al.* 2006). These interactions can also be indirect, and mediated for example by cues such as scent (Orrock, Danielson & Brinkerhoff 2004, Apfelbach *et al.* 2005, Liesenjohann & Eccard 2008, Hughes & Banks 2010). Scent marks may be used to infer on the presence of a predator or competitor and affect behavioural decisions. Recognition of scent cues can be innate (Müller-Schwarze 1972, Boag & Mlotkiewicz 1994, Apfelbach et al. 2005) and in such cases, they will occur irrespective of individual familiarity. Appropriate responses to scent may also require individual learning, and hence the responses may change depending on previous experience (Dickman 1992, Blumstein 2002, Apfelbach et al. 2005, Blumstein & Daniel 2005, Shapira *et al.* 2013).

Invasive species are usually a threat to native species through predation and/or competition (Davis 2009). However, predation and competition also occur within guilds of invasive species (Jones *et al.* 2011, Ruscoe *et al.* 2011), and may determine the relative abundance and thus the effect of each species on the ecosystems they invade (Caut *et al.* 2007, Le Corre 2008, Harper & Cabrera 2010). In New Zealand, several small invasive mammals coexist and are subject to predator-prey interactions and interspecific-competition (Ruscoe et al. 2011). The house mouse *Mus musculus* and rats of the genus *Rattus* (*R. rattus*, *R. norvegicus* and to a lesser extent *R. exulans*) are part of this guild in many New Zealand habitats, where they form the mesopredator level (Fitzgerald & Gibb 2001, Ruscoe et al. 2011). In these communities, the house mouse is under predation pressure from mustelids and competition from the rat species (Miller & Miller 1995, Ruscoe & Murphy 2005, Ruscoe et al. 2011). O'Boyle (1974) argued that the mouse-killing response by rats is predatory, and

that predator-prey interactions exist between rats and mice. This argument, while still not experimentally validated in the field, does have observational support (J. Innes; J. Peace; I. Shapira; *pers. comm.*). Irrespective, research suggests that competition has a more profound effect than predation on mouse populations within New Zealand's invasive mammal communities (Caut et al. 2007, Ruscoe et al. 2011).

Competition in sympatric rodent species is reduced in many cases by spatial or temporal niche partitioning (Shkolnik 1971, Schoener 1974, Kotler & Brown 1990, Ovadia *et al.* 2001). In New Zealand, rats negatively affect mouse population densities and when rats are eradicated or heavily controlled, mice populations undergo significant growth (Innes *et al.* 1995, Miller & Miller 1995, Goldwater 2007). The underlying mechanisms of rat-mouse interactions in New Zealand, whether direct or indirect, and the relative roles of predation and competition are, however, largely unknown. In many of otherwise successful mammalian eradication attempts in New Zealand, mouse eradication has failed (Towns & Broome 2003, Goldwater 2007, MacKay, Russell & Murphy 2007), resulting in mouse populations that are free from other mammalian predators and competitors.

While studies have demonstrated that mice familiar with their predators/competitors tend to avoid food sources with these scents (Dickman 1992, Hancock 2008), other studies show that predator-naïve mice may also exhibit reluctance to approach such scents (Dickman 1992, Shapira et al. 2013). In contrast, Ferrero et al. (2011) observed responses in predator-naïve laboratory bred mice to a single chemical, 2-phenylethylamine, produced by predators. In the current study I tested behavioural responses of wild rat-naïve mice to rat scent in a controlled laboratory setup. My aim was to observe whether rat-naïve wild house mice recognise and respond aversively to the unfamiliar scent of rats. I did not have rat-

experienced mice as a control group, and hence could not test for the naiveté of mice *per se.* Therefore, the behavioural patterns of the mice used in this study might be the result of general naiveté toward novel scent rather than specific responses towards rat scent. However, my tests provide insights about the patterns of behaviour that might be expected from rat-naïve mice elsewhere.

I predicted that mice will respond negatively to rat scent upon first contact, and that when given a choice between containers with rat scent versus control, mice would prefer to forage in the control containers. Mice rapidly explore their environment and are fast learners of existing conditions (Berry 1970). Thus, I further predict that as exposure time increases without enforcement of the scent cues (i.e. a live rat), any negative effect of scent on mice activity will decline. To ensure maximum statistical power of my design, and to explore possible differences between the sexes, I analysed responses for all mice combined as well as separately for males and females.

6.3. Methods

I used laboratory bred (F1) wild house mice (18 males and 18 females) as the focal animals. These were the offspring of five pairs of wild-caught animals from three rural sites near Auckland, New Zealand (two at 36º43’59.97” S 174º41’40.33 E and 36º42’31.51” S 174º40’53.21 E and one at 36º33’35.93” S 174º28’22.47 E). Breeding mice were cross-paired between sites to avoid inbreeding. Focal animals were 200 – 380 days old at the time of the experiments. Males were housed in individual cages (41L x 25W x 15H cm) and females in sister groups of 2-4 animals per cage (60L x 30W x 40H cm) under ambient

temperature of 21±1.5 Cº and in a light regime of 12L/12D (L – white light, D – red dim light). Mice were provided with *ad libitum* grain-based rodent pellets (86 rodent diet, Massey University Palmerston North, New Zealand) and water with a weekly addition of bird-grain mixture. *Mus musculus* is an invasive species in New Zealand and is considered a serious pest. Hence, all mice were euthanised at the conclusion of the experiment using isoflurane via airways.

I collected faeces from invasive wild rats (*R. rattus* and *R. norvegicus*) that were live trapped for other purposes. Faeces from *R. norvegicus* were obtained from beneath cages where wild animals had been trapped overnight. Faeces from *R. rattus* were obtained from beneath cages in which wild caught animals were held for several days. To standardise the scent treatments, I mixed faeces from multiple male and female rats. Faeces samples likely contained small traces of urine, as total separation of the two extractions was unrealistic. Urine could potentially infer stress status of these caged rats and hence affect the reaction of mice (Henry 1992). However, because faeces may also contain stress hormones (Palme et al. 2005), specific effects due to urine traces are unlikely. The faecal solutions were soaked with cotton balls, which were then frozen at -18° C until the experiment commenced. Cotton balls were thawed at 4° C for 5-6 hours prior to the start of each test. For controls I used distilled water soaked cotton balls. These were also frozen and thawed in the same manner.

To test the effect of rat scent on food consumption and activity patterns of mice, I used a Y-maze design that gave the test animal a choice of control or treatment. Each maze had a home cage (HC, 41L x 25W x 15H cm) housing the focal animal, connected to an access tube with two arms (transparent pipes; Ø 4 cm, each 50 cm long). Each arm was connected to a test cage (TC, 41L x 25W x 15H cm). Y arms were mounted with infrared

(IR) sensors (5V Phototransistor and 5V Emitting Diode, generic) at each end of the tube. The sensors were wired to a computer via logic circuit (Eanygo Software, EH, Israel) and a 24-channel I/O card (PC-LabCard, PCI-1757UP, Advantech, Taiwan). I used the Mice-Tracker software (Eanygo Software, EH, Israel) to record the number of visits to, and the time spent in, the TCs by the focal animals.

For each treatment (scent of *R. rattus* and *R. norvegicus*), I used separate groups of nine male and nine female mice. Animals were randomly assigned to one of the two treatment groups. During the experiment, mice were given *ad libitum* water, bedding, and shelter in the HCs. HCs were half covered with cardboard for shading. Each experimental session lasted 48 h, and I used up to six apparatus simultaneously. Seed trays (plastic containers, 22.4 L x 15.8 W x 7.8 H cm) with 0.5 L of sand were placed at the far end of each TC prior to the experiment. A single mouse was placed in an HC and was free to explore the apparatus for two hours before being confined in the HC for 1 hour prior to the start of the experiment. Millet seeds (3 g) were mixed thoroughly with the sand in the seed trays. Treatment and control samples were randomly assigned to each TC and placed in plastic dishes just inside the TC. The HCs were then re-opened. To control for possible side fixation by the mice, I switched treatment and control sides in the apparatuses after 24 hours. The procedure described above was then repeated for the same mice on night two with fresh treatment and control samples. Seeds remaining in trays were extracted by sifting and a new batch of 3 g added. The experiment ended after an additional 24 hours. Remaining seeds from both days were kept for later analysis. The Animal Ethics Committee of Massey University, New Zealand approved all animal treatments (MUAEC Protocol 09/40).

6.3.1. Data Analysis

In all cases, responses to *R. norvegicus* and *R. rattus* treatments did not differ. Therefore, I pooled the results from these treatments to increase the statistical power of the different tests. I calculated the Manly-Chesson selectivity index (Chesson 1983) for treatments versus controls, based on the amount of seeds harvested by mice. I divided the proportion of seeds harvested from the controls by the sum of proportions of seeds harvested from the controls and treatments and tested whether the values where different from 0.5 (where values above 0.5 indicate preference for foraging in control containers and values below 0.5 indicate preference for foraging in treatment containers). I analysed selectivity for both nights of foraging for all mice combined and for males and females separately using one-sample t-tests.

Mice in this experiment showed strong nocturnal habits and therefore, I used only the dark phase in the analysis of activity. For each individual mouse, I calculated the mean time spent in, and number of visits to, the TCs. I then extracted the treatment values from the control values for all mice combined and for males and females separately, and compared the results with zero using one-sample t-tests (where values above zero indicate preference for activity in control containers and values below zero indicate preference for activity in treatment containers).

I estimated mouse harvest rates and compared them between the sexes, using a modification of Holling's disc equation (Kotler & Brown 1990). Applying the disc equation assumes that harvesting seeds requires two defined activities: searching for the seeds and, upon finding, handling them. When searching, the assumption is that mice encounter seeds in

proportion to the density of seeds in the seed trays. The proportionality constant that determines this encounter rate is defined as the attack rate (a), and it is subject to the ability of the forager to search for seeds, in this case within a sand substrate. After a seed is encountered, the time required for the forager to extract it from the substrate, peel it, and place it in its mouth is defined as handling time (h). Under these assumptions, the following equation gives the immediate rate at which seeds are harvested from a seed tray:

$$t = (1/a) \ln (N_0 / N_f) + h (N_0 - N_f)$$

where: t represents the time spent foraging in a TC, N_0 the initial density of seeds, and N_f the final density of seeds. The first term on the right hand side of the equation represents the search time for the seeds and the second term on the right hand side represents handling time of seeds encountered. The equation was used in a least-square multiple-regression analysis where time spent in the TCs was treated as the dependent variable and $\ln(N_0/N_f)$ and (N_0-N_f) as independent variables. To avoid using the natural logarithm in the equation on zero values in cases where no seeds were harvested from the trays, I transformed zero values to 0.001 (g), which corresponds with approximately zero harvesting rates. Time spent in the TCs (rat treatments combined) was first ln transformed to meet the model's assumption of normality, then means were back-transformed to calculate the attack rates a [the reciprocal of the coefficient $\ln(N_0/N_f)$] in units of seconds and handling time h [the coefficient of (N_0-N_f)] in units of sec/g for male and female foraging on both nights. I used analysis of covariance (ANCOVA) to test whether males and females differed from each other in respect to attack rates and handling times. I used time spent in the TCs (ln transformed to meet the assumption of normality) as the dependent variable and tested the direct effect of sex and the interactions

between sex and each covariate for each of the foraging nights. All statistical tests were done using SPSS Statistics software with a 0.05 level of significance.

6.4. Results

All mice combined did not exhibit selectivity towards either treatments or controls during either the first or second nights (one-sample t-test; t = -0.207, df = 35, P = 0.837; t = 0.765, df = 35, P = 0.449; respectively; Fig. 6.4.1). Males showed significant preference for controls during the first but not the second night (one-sample t-test; t = 2.35, df = 17, P = 0.031; t = 0.70, df = 17, P = 0.494; respectively; Fig. 6.4.1). Females showed a close to significant preference for treatments during the first but not the second night (one-sample t-test; t = -2.09, df = 17, P = 0.052; t = 0.45, df = 17, P = 0.66; respectively; Fig. 6.4.1).

All mice combined exhibited a close to significant preference to spend more time in the controls during the first night and did not have a side preference during the second night (one-sample t-test; t = 1.784, df = 35, P = 0.083; t = -0.561, df = 35, P = 0.578; respectively; Fig. 6.4.2). Males spent significantly more time in the controls during the first but not the second night (one-sample t-test; t = 2.937, df = 17, P = 0.009; t = 1.049, df = 17, P = 0.309; respectively; Fig. 6.4.2). Females did not exhibit any preference for either controls or treatments during either the first or second nights (one-sample t-test; t = 0.911, df = 17, P = 0.375; t = -0.808, df = 17, P = 0.43; respectively; Fig. 6.4.2).

All mice combined exhibited a marginally significant preference to visit the controls during the first night and did not have a side preference during the second night (one-sample t-test; t = 2.033, df = 35, P = 0.05; t = 0.867, df = 35, P = 0.392; respectively; Fig. 6.4.3).

Males made significantly more visits to the controls during the first but not the second night (one-sample t-test; t = 3.48, df = 17, P = 0.003; t = -0.263, df = 17, P = 0.796; respectively; Fig. 6.4.3). Females did not show a visiting preference to either controls or treatments during both the first and second nights (one-sample t-test; t = -0.275, df = 17, P = 0.787; t = -1.094, df = 17, P = 0.289; respectively; Fig. 6.4.3).

There was a significant effect of sex on harvest rates across both treatment and control TCs during the first night and a near significant effect during the second night (ANCOVA; $F_{2,71}$ = 6.096, P = 0.016; Fig. 6.4.4A; $F_{1,70}$ = 3.601, P = 0.062 ; Fig. 6.4.4B; respectively). During the first night, the interaction between sex and the covariate $\ln(N_0/N_f)$ (representing search time) was significant (ANCOVA; $F_{2,71}$ = 5.091, P = 0.009) and the interactions between sex and the covariate (N_0-N_f) (representing handling time) were not (ANCOVA; $F_{2,71}$ = 1.055, P = 0.354). During the second night, the interaction between sex and the covariant (N_0-N_f) was significant (ANCOVA; $F_{2,70}$ = 4.951, P = 0.01) and the interaction between sex and the covariate $\ln(N_0/N_f)$ was not (ANCOVA; $F_{2,70}$ = 0.798, P = 0.455). The regression analysis for the first night revealed values of a (attack rates) and h (handling time) that were significantly different from zero for both females and males (R^2 = 0.408, $F_{2,32}$ = 11.026, P < 0.001; R^2 = 0.206, $F_{2,32}$ = 4.291, P = 0.022; respectively). Estimates of attack rates and handling times for females were 1.37 x 10^{-3}/s and 733 s/g, respectively, and 2.04 x 10^{-3}/s and 1354 s/g, respectively, for males. The regression analysis for the second night revealed values of a and h that were significantly different from zero for females but not for males (R^2 = 0.262, $F_{2,32}$ = 5.692, P = 0.008; R^2 = 0.078, $F_{2,32}$ = 1.349, P = 0.274; respectively). Estimates of attack rates and handling times for females were 3.75 x 10^{-3}/s and 2798 s/g, respectively, and for males 1.17 x 10^{-3}/s and 1284 s/g, respectively.

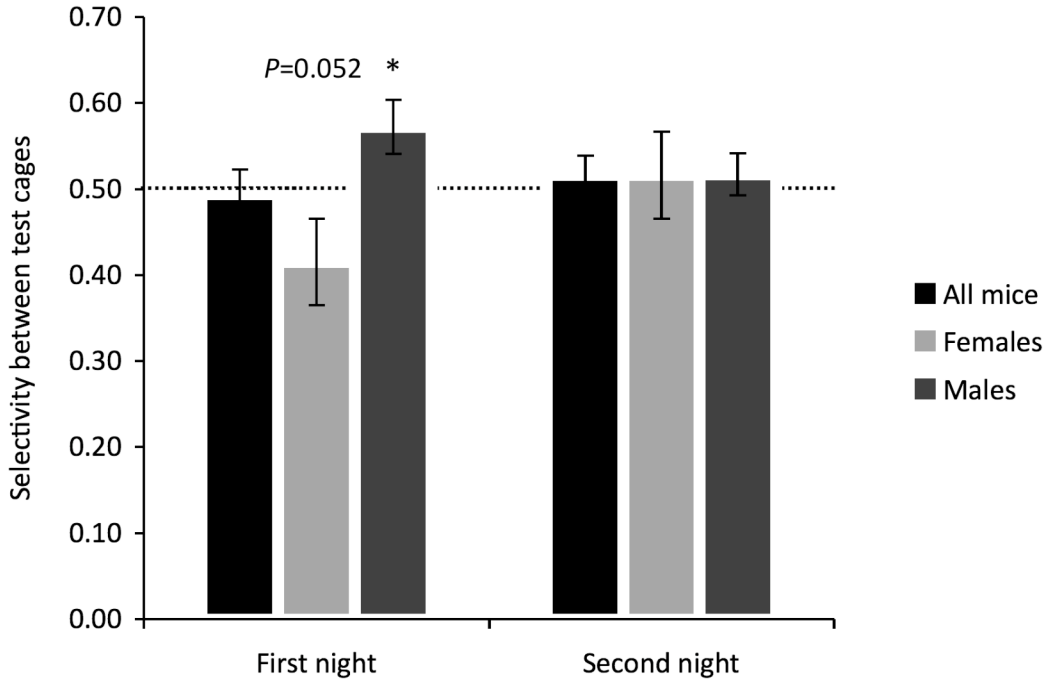

Figure 6.4.1. Mean (± SE) selectivity (between control and treatment test cages) of all mice combined (n = 36) and of females (n = 18) and males (n = 18) separated. Values close to 0.5 indicate a lack of preference between treatment and control; values above 0.5 indicate a preference for control; values below 0.5 indicate a preference for treatment. * Corresponds to $\alpha < 0.05$, non-significant when not indicated.

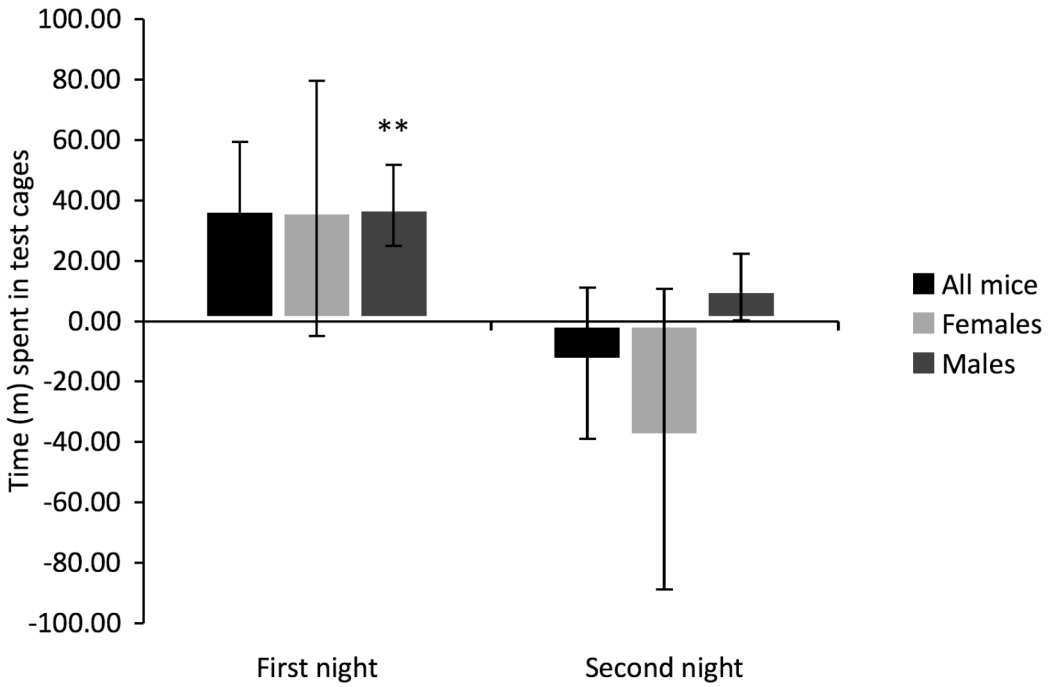

Figure 6.4.2. Mean (± SE) differences from 0.5 in time spent in the test cages between control and treatment by all mice combined (n = 36) and by females (n = 18) and males (n = 18) separated. Values close to zero indicate a lack of preference between treatment and control; values above zero indicate a preference for control; values below 0.5 indicate a preference for treatment. ** Corresponds to $\alpha < 0.01$, non-significant when not indicated.

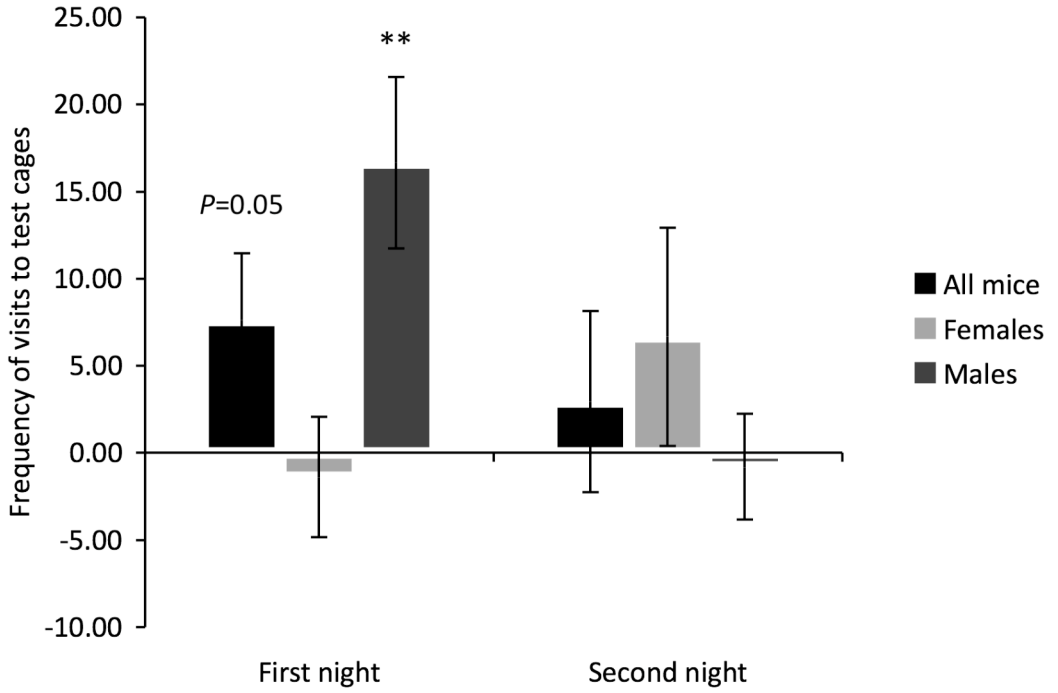

Figure 6.4.3. Mean (± SE) differences from zero in the number of visits to the test cages between control and treatment made by all mice combined (n = 36) and by females (n = 18) and males (n = 18) separated. Values close to zero indicate a lack of preference between treatment and control; values above zero indicate a preference for control; values below 0.5 indicate a preference for treatment. ** Corresponds to $\alpha < 0.01$, non-significant when not indicated.

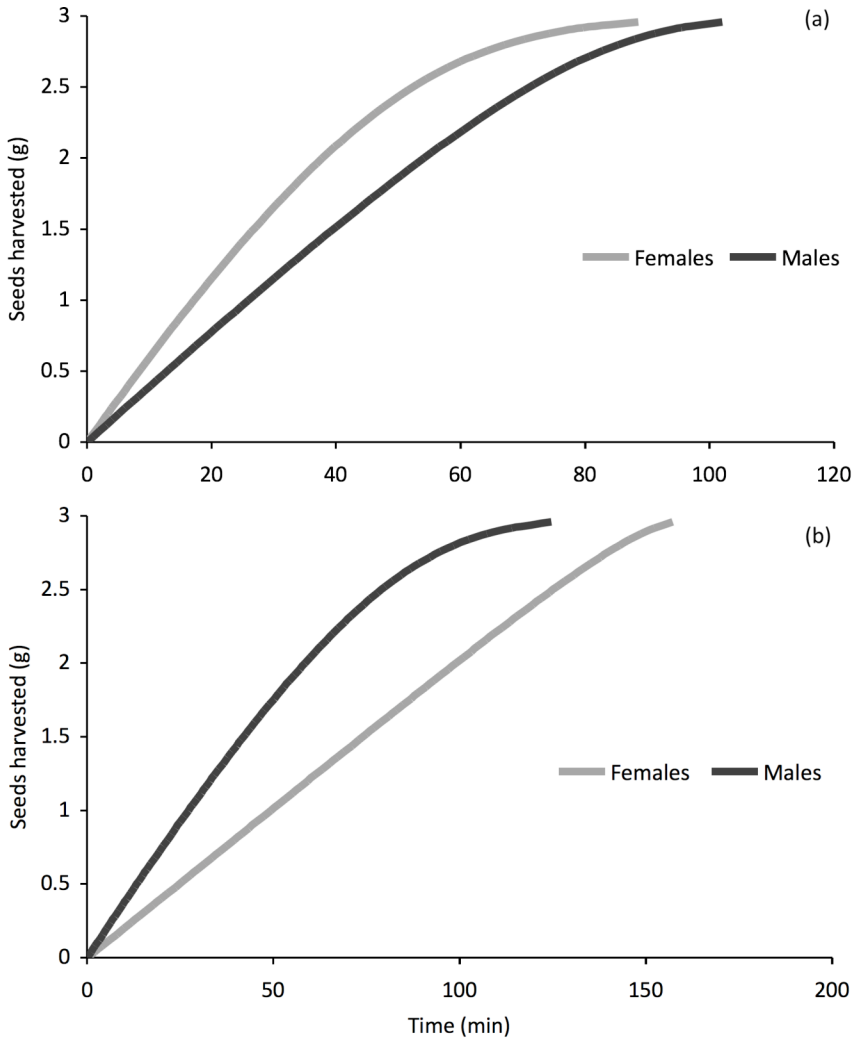

Figure 6.4.4. Mass (g) of seeds harvested by female and male house mice as a function of the time spent foraging during the first (A) and second (B) nights. Lines were calculated from the data obtained in this study by analysing harvest rates and foraging times made by mice with multiple linear regression using the equation $t = (1/a) \ln (N_0 / N_f) + h (N_0 - N_f)$; where t is time spent foraging, N_0 is the initial density of seeds, N_f is the final density of seeds, a is the attack rate (sec^{-1}) and h is handling time (sec/g).

6.5. Discussion

Interspecific competition and predator-prey interactions can affect population dynamics and the fate of individuals (Schoener 1983, Lima & Dill 1990, Krebs 2001) and therefore,

flexible and appropriate behavioural responds to cues of competitors and predators can benefit subordinate competitors and prey species. Here I found that in rat-naïve house mice, apparent lack of response to rat scent [a dominant competitor (Caut et al. 2007, Ruscoe et al. 2011) and a potential predator (O'Boyle 1974)] was masked by unexpected and contrasting behavioural differences between the sexes. When all mice were analysed together, rat scent had no or only a weak effect on their foraging and activity. However, when males and females were analysed separately, I found that males exhibited a strong negative response to rat scent. Conversely, females exhibited no response or at times, positive responses to rat scent.

During the first night of foraging, male mice foraged more extensively, spent more time and made more frequent visits to control TCs compared with treatment TCs. Females exhibited no preference in regard to time spent and visit frequencies and, in contrast to the males, exhibited preference to forage in treatment TCs over control TCs. These curious results are unexpected and do not have any precedent in the literature. Any interpretation therefore, is largely speculative and further research is needed to determine the underlying mechanism of this phenomenon. Nonetheless, I suggest that more males are more spatially active (Berry 1970, Berry 1981) and have greater overall feeding opportunities, and therefore may choose to avoid risky food sources. Females are more spatially restricted, are central place foragers and keep close to the vicinity of their nest, and may need to exploit any local foraging opportunity, albeit a potentially risky one. The different housing techniques for males and females (see above), could potentially have an effect on the behavioural differences. In natural (or naturally simulated) conditions, females exhibit intra-sex

gregarious behaviour while males are more solitary (Berry 1970; Berry 1981). Therefore, I argue that these housing differences are probably of minor effect if at all.

For both sexes, any observable effects ceased after the first night suggesting that in the absence of cue enforcement (e.g. the existence of an actual rat), the fast learning mice (Berry 1970, Berry 1981) quickly habituated to the situation. Furthermore, the changes in activity patterns between the two nights exhibited by the females (see Figs 2 & 3), suggest a degree of side fixation. This further supports the relative lack of interest in the scent cues by the females.

Harvest rates were significantly different between males and females during the first foraging night and reveal an interesting foraging trade-off. Males were more efficient foragers than females during the first night, which can be explained by the over exploitation of one food source (control). This trend was reversed during the second night and might represent female foraging compensation for the first night, as changes in female behaviour were primarily responsible for this difference. Both sexes exploited the seeds in the trays with lower efficiency during the second night, which is consistent with a decreased effect of scent. Males and females thus appear capable of the same exploitation efficiency and the effort they expend depends on the context. As the Holling disc equation predicts, mice show diminishing returns in harvest rates with the time spent exploiting their trays (i.e. mouse harvest rates declined relative to the time spent foraging).

Rodents are the most abundant vertebrate order and although many rodent species compete over resources in the same habitat, the actual mechanism of competition avoidance is not always clear (Grant 1972, Kotler & Brown 1990, Mitchell et al. 1990, Schröpfer & Klenner-Fringes 1991, Ziv et al. 1993, Abramsky et al. 2001, King, Foster & Miller 2011). In

two species of spiny mice (*Acomys*), the dominant species apparently alters behavioural responses by the subordinate species through scent alone (Haim & Rozenfeld 1993). In this case, niche separation will occur without direct interactions. In sympatric rat species (*Rattus spp.*), competition is correlated with body size (Yom-Tov, Yom-Tov & Moller 1999) and in part might depend on different foraging skills (King et al. 2011); nonetheless, it is essentially unknown how these dominance relationships are determined.

Mouse populations undergo substantial increases when rats are excluded or heavily controlled in habitats previously shared by both species (Miller & Miller 1995, Caut et al. 2007, Goldwater 2007). Field studies show that mouse foraging is influenced by the presence of rat scent when mice are rat-experienced (Hancock 2008) but not when they are rat-naïve (Shapira et al. 2013). The results of the current study reveal a complex system in which responses to cues of competition and predation differ between the sexes. This can potentially explain the lack of significant response of mice to rat (and other mammals) scent Shapira et al. (2013) found in field experiments, where the number and sex ratio of wild mice were unknown.

Mice in this study were rat-naïve and as such, the response (or lack of response) to the rat scent might have been driven by its novelty rather than reaction to the detection of a rat. Irrespectively of the driver, the behavioural differences between the sexes observed here are a novel phenomenon, and one that may have a substantial effect on individual survivorship in a natural situation. These differences suggest that male and female mice might undergo different evolutionary pathways with regard to novel and/or risky cues. Clearly, the roles of scent within mice-rat guilds, and their potential effects on mice behaviour, require further research.

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6.7. References

Abramsky, Z., Rosenzweig, M. L. & Subach, A. (2001). The cost of interspecific competition in two gerbil species. *J. Anim. Ecol.* **70,** 561-567.

Apfelbach, R., Blanchard, C. D., Blanchard, R. J., Hayes, R. A. & McGregor, I. S. (2005). The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neurosci. Biobehav. Rev.* **29,** 1123-1144.

Arim, M. & Marquet, P. A. (2004). Intraguild predation: a widespread interaction related to species biology. *Ecol. Lett.* **7,** 557-564.

Bernays, E. A. (1998). The value of being a resource specialist: behavioral support for a neural hypothesis. *Am. Nat.* **151,** 451-464.

Berry, R. J. (1970). The natural history of the house mouse. *Field Stud.* **3,** 219-262.

Berry, R. J. E. (1981) *Biology of the house mouse*. London: Academic Press.

Blumstein, D. T. (2002). Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *J. Biogeogr.* **29,** 685-692.

Blumstein, D. T. & Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. *P. Roy. Soc. B.* **272,** 1663-1668.

Boag, B. & Mlotkiewicz, J. A. (1994). Effect of odor derived from lion faeces on behavior of wild rabbits. *J. Chem. Ecol.* **20,** 631-637.

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22,** 37-47.

Burns, J. H. & Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. *P. Natl. Acad. Sci. USA*. **108,** 5302-5307.

Caut, S., Casanovas, J. G., Virgos, E., Lozano, J., Witmer, G. W. & Courchamp, F. (2007). Rats dying for mice: modelling the competitor release effect. *Austral. Ecol.* **32,** 858-868.

Chesson, J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology.* **64,** 1297-1304.

Davis, M. A. (2009) *Invasion Biology*. Oxford: Oxford University Press.

Dickman, C. R. (1992). Predation and habitat shift in the house mouse, *Mus domesticus*. *Ecology.* **73,** 313-322.

Fedriani, J. M., Fuller, T. K., Sauvajot, R. M. & York, E. C. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia.* **125,** 258-270.

Ferrero, D. M., Lemon, J. K., Fluegge, D., Pashkovski, S. L., Korzan, W. J., Datta, S. R., Spehr, M., Fendt, M. & Liberles, S. D. (2011). Detection and avoidance of a carnivore odor by prey. *P. Natl. Acad. Sci.USA*. **108,** 11235-11240.

Fitzgerald, B. M. & Gibb, J. A. (2001). Introduced mammals in a New Zealand forest: long-term research in the Orongorongo Valley. *Biol. Conserv.* **99,** 97-108.

Gause, G. F. (1934) *The struggle for existence*. New York: Dover.

Goldwater, N. (2007). *Ecology of house mice within the Tawharanui Open Sanctuary*. Unpublished MSc Thesis. University of Auckland, Auckland.

Grant, P. R. (1972). Interspecific competition among rodents. *Annu. Rev. Ecol. Syst.* **3,** 79-106.

Haim, A. & Rozenfeld, F. M. (1993). Temporal segregation in coexisting acomys species - the role of odor. *Physiol. Bhave.* **54,** 1159-1161.

Hancock, B., (2008). *The Influance of Ship Rats (Rattua rattus) on the Habitat Preferences of the House Mouse (Mus musculus)*. Unpublished MSc Thesis. Victoria University of Wellington, Wellington.

Harper, G. A. & Cabrera, L. F. (2010). Response of mice (*Mus musculus*) to the removal of black rats (*Rattus rattus*) in arid forest on Santa Cruz Island, Galápagos. *Biol. Invasions.* **12,** 1449-1452.

Henry, J. P. (1992). Biological basis of the stress response. *Integr. Psychol. Behav. Sci.* **27,** 66-83.

Hughes, N. K. & Banks, P. B. (2010). Interacting effects of predation risk and signal patchiness on activity and communication in house mice. *J. Anim. Ecol.* **79,** 88-97.

Innes, J., Warburton, B., Williams, D., Speed, H. & Bradfield, P. (1995). Large scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North island, New Zealand. *New. Zeal. J. Ecol.* **19,** 5-17.

Jones, C., Pech, R., Forrester, G., King, C. M. & Murphy, E. C. (2011). Functional responses of an invasive top predator *Mustela erminea* to invasive meso-predators *Rattus rattus* and *Mus musculus*, in New Zealand forests. *Wildl. Res.* **38,** 131-140.

King, C. M., Foster, S. & Miller, S. (2011). Invasive European rats in Britain and New Zealand: same species, different outcomes. *J. Zoo. (Lond.)* **285,** 172-179.

Kotler, B. P. & Brown, J. S. (1990). Rates of seed harvest by 2 species of gerbilline rodents. *J. Mammal.* **71,** 591-596.

Krebs, C. J. (2001) *Ecology: the experimental analysis of distribution and abundance,* 5th edn. New York: Benjamin Cummings.

Lawrence, R. L. (1979). Direct and indirect effects of n-species competition. *Oecologia.* **43,** 355-364.

Le Corre, M. (2008). Cats, rats and seabirds. *Nature.* **451,** 134-135.

Liesenjohann, T. & Eccard, J. A. (2008). Foraging under uniform risk from different types of predators. *BMC Ecol.* **8,** 1-9.

Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation - a review and prospectus. *Can. J. Zool.* **68,** 619-640.

MacKay, J. W. B., Russell, J. C. & Murphy, E. C., (2007). Eradicating house mice from islands: successes, failures and the way forward. In: *Managing Vertebrate Invasive Species:* 294-304. G. W. Witmer, W. C. Pitt & K. A. Fagerstone (Eds.). Fort Collins, Colorado: University of Nebraska.

Miller, C. J. & Miller, T. K. (1995). Population dynamics and diet of rodents on Rangitoto island, New Zealand, including the effect of a 1080 poison operation. *New. Zeal. J. Ecol.* **19,** 19-27.

Mitchell, W. A., Abramsky, Z., Kotler, B. P., Pinshow, B. & Brown, J. S. (1990). The effect of competition on foraging activity in desert rodents: theory and experiments. *Ecology.* **71,** 844-854.

Müller-Schwarze, D. (1972). The responses of young black-tailed deer to predator odors. *J. Mammal.* **53,** 393-394.

O'Boyle, M. (1974). Rats and mice together: the predatory nature of the rat's mouse-killing response. *Psychol. Bull.* **81,** 261-269.

Orrock, J. L., Danielson, B. J. & Brinkerhoff, R. J. (2004). Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behav. Ecol.* **15,** 433-437.

Ovadia, O., Ziv, Y., Abramsky, Z., Pinshow, B. & Kotler, B. P. (2001). Harvest rates and foraging strategies in Negev Desert gerbils. *Behav. Ecol.* **12,** 219-226.

Palme, R., Rettenbacher, S., Touma, C., El-Bahr, S. M. & Möstl, E. (2005). Stress hormones in mammals and birds: comparative aspects regarding metabolism, excretion, and noninvasive measurement in fecal samples. *Ann. N. Y. Acad. Sci.* **1040,** 162–171.

Pinter-Wollman, N., Dayan, T., Eilam, D. & Kronfeld-Schor, N. (2006). Can aggression be the force driving temporal separation between competing common and golden spiny mice? *J. Mammal.* **87,** 48-53.

Polis, G. A. & Holt, R. D. (1992). Intraguild predation - the dynamics of complex trophic interactions. *Trends Ecol Evol,* **7,** 151-154.

Polis, G. A., Myers, C. A. & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* **20,** 297-330.

Ruscoe, W. A. & Murphy, E. C., (2005). House mouse. In: *The Handbook of New Zealand Mammals:* 204-221. C. M. King (Ed.). New York: Oxford University Press.

Ruscoe, W. A., Ramsey, D. S. L., Pech, R. P., Sweetapple, P. J., Yockney, I., Barron, M. C., Perry, M., Nugent, G., Carran, R., Warne, R., Brausch, C. & Duncan, R. P. (2011).

Unexpected consequences of control: competitive vs. predator release in a four-species assemblage of invasive mammals. *Ecol. Lett.* **14,** 1035-1042.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science.* **185,** 27-39.

Schoener, T. W. (1983). Field experiments on interspecific competition. *Am. Nat.* **122,** 240-285.

Schröpfer, R. & Klenner-Fringes, B. (1991). Minimizing interspecific competition by different foraging strategies in two North African desert rodents. *Acta. Theriol.* **36,** 109-117.

Shapira, I., Walker, E., Brunton, D. & Raubenheimer, D. (2013). Responses to direct versus indirect cues of predation and competition in naïve invasive mice: implications for management. *New. Zeal. J. Ecol.* **37,** 33-40.

Shkolnik, A. (1971). Diurnal activity in a small desert rodent. *Int. J. Biometeor.* **15,** 115-120.

Towns, D. R. & Broome, K. G. (2003). From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. *New. Zeal. J. Zoo.* **30,** 377-398.

Yom-Tov, Y., Yom-Tov, S. & Moller, H. (1999). Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *J. Biogeogr.* **26,** 947-958.

Ziv, Y., Abramsky, Z., Kotler, B. P. & Subach, A. (1993). Interference competition and temporal and habitat partitioning in 2 gerbil species. *Oikos.* **66,** 237-246.

CHAPTER 7: PRIORITIZING ENERGY OVER MACRONUTRIENT BALANCE IN WILD *MUS MUSCULUS*: IMPLICATIONS FOR MOUSE DOMESTICATION AND INVASIVENESS

7.1. Abstract

Previous research into macronutrient balancing in the house mouse *Mus musculus*, a species that is both a ubiquitous invasive species and a model laboratory animal, has shown that mice from a laboratory-bred strain balance their intake of protein (P) and carbohydrate (CHO), and when fed imbalanced diets prioritize P. However, in the wild, mice are subject to very different ecological challenges and selection pressures, giving rise to the question of whether wild and laboratory-selected mice of the same species regulate the intake of macronutrients in the same way. I used similar protocols as were previously used on laboratory mice and measured the pattern of macronutrient regulation in invasive mice captured from the wild in temperate New Zealand. When presented with a combination of two isocaloric nutritionally complementary foods (high protein = HP, low protein = LP), the wild-caught mice self-selected a diet with an extremely low P:CHO ratio compared with what has been measured for laboratory mice. When shifted to a diet constrained to either LP or HP, the wild-caught mice did not prioritize protein but placed equal weighting on the two macronutrients. When shifted again to choice, the mice did not homeostatically compensate for the previous period of enforced imbalance, but composed a diet with macronutrient balance that was more similar to the previous constrained diet compared with their first choice. These results show that the pattern of macronutrient selection is sensitive to ecological circumstances, and

associate an opportunistic strategy with successful invasion by a small mammal in a temperate environment.

7.2. Introduction

Dietary balance is fundamental to animal performance, dictating the development, growth, maintenance and reproduction success of individuals (Barboza et al. 2009). It is therefore not surprising that many animals have independently evolved the ability to regulate the intake and utilization of different macronutrients to balance their diet (Raubenheimer & Simpson 1997; Simpson & Raubenheimer 2012).

Recent experiments showed that laboratory mice (NMRI strain) offered a combination of protein (P) and carbohydrate (CHO) complementary foods selected a diet relatively high in protein (approximately 1:2 P:non-P energy). When restricted to a single nutritionally imbalanced diet that prevented them from simultaneously satisfying their P and CHO requirements they prioritized protein energy (PE) over non-protein energy (NPE) (Sorensen et al. 2008; Sorensen et al. 2010). Such protein prioritization has also been found in humans (Simpson et al. 2003; Gosby et al. 2011), a similarity that led Sorensen *et al*. (2008) to suggest that mice offer a good model for studying energy intake and obesity in humans. What might account for the similarity in the pattern of macronutrient balancing between mice and humans?

An intriguing possibility is that protein prioritization is associated with ecological similarities between the two species. Like humans, house mice are ecological generalists that have colonized a wide range of habitats. The wild house mouse *Mus musculus* likely

originated in central Asia, and as a result of both self-colonization and human introduction can now be found worldwide (Long 2003). In most regions where they are now present, mice are considered to be pests and inflict considerable damage to agriculture, human health and natural ecosystems, all of which have significant economic implications (Long 2003; Stenseth et al. 2003; MacKay 2010). A likely contributor to the invasive success of both mice and humans is their dietary flexibility. Wild house mice exhibit extreme flexibility in their food selection and can thrive on a broad variety of food items, natural and man-made (Long 2003; Ruscoe & Murphy 2005; MacKay 2010). Interestingly, like humans and mice, a third extreme generalist invasive omnivore, the German cockroach (*Blatella germanica*), also shows protein prioritization (Jones & Raubenheimer 2001; Raubenheimer & Jones 2006).

On the other hand, field studies have shown that the largely frugivorous spider monkey, *Ateles chamek,* which is not a habitat generalist and has a highly restricted distribution range, also shows protein prioritization (Felton et al. 2009). Further, the pattern of macronutrient regulation is not a fixed property of a species, but has been shown to adapt over a small number of generations to nutritional characteristics of the environment (Warbrick-Smith et al. 2009), giving rise to the question of whether laboratory-bred lineages of mice are representative of what might be expected of wild invasive strains of mice.

My aim in this chapter is to test, firstly, whether a strain of house mice that has successfully become established and persisted in the wild over several generations shows the protein-prioritization pattern of macronutrient regulation that has previously been observed in laboratory-bred mice (Sorensen et al. 2008; Sorensen et al. 2010). Secondly, I reasoned that if the pattern differs between laboratory-bred and field-captured, then this provides a within-

species comparison to indicate how macronutrient selection corresponds with the ecological characteristics of the adopted environment of the wild invasive strain.

7.3. Methods

Male and female invasive wild house mice *Mus musculus,* were trapped during the austral spring of 2011 and summer 2012 in Tawharanui Open Sanctuary sand dunes (36°21'41.40" S 174°49'06.14" E) north of Auckland, New Zealand. Mice first invaded New Zealand as stowaways on Australian and European ships in the early 1820s. By the beginning of the twentieth century, mice were spread throughout the whole of New Zealand, occupying most habitat types up to 1200-1300 m in altitude (Ruscoe & Murphy 2005). The animals used in this study thrive in temperate climate with temperatures as low as 5°C during the austral winter. With other mammalian predators removed from the study site during 2005, mice are not likely to be limited by predation. However, they are potentially limited by food availability as demonstrated elsewhere (Tann et al. 1991; Murphy 1992).

I used aluminum Sherman traps (models SFA and XLF15, H.B. Sherman Traps, Tallahassee FL, USA) supplied with shredded paper bedding and baited with peanut butter. Traps were laid during the daytime, left over night and recovered the following morning. Immediately after capture, animals were transferred to an animal facility (Massey University, Albany) where they were individually housed in standard plastic cages (41L X 25W X 15H cm with metal wire mesh lids) for acclimatization (minimum 14 days prior to experiment). Mice were supplied with *ad libitum* water and grain-based rodent pellets (IFNHH, Massey University, Palmerston North, New Zealand) with the addition of millet seeds every second

day and held under an ambient temperature of 21±1°C and light regime of 12L/12D. Cages contained pine wood shavings, shredded paper and several shelters. *M. musculus* is an invasive pest species in New Zealand and hence animals were culled at the end of the experiments.

To test macronutrient regulation by the mice I used two isocaloric, purified foods in the form of pellets, one with high P to CHO ratio (HP, 26% protein by weight) and one with low P to CHO ratio (LP, 6.5% protein by weight) content (AIN -93M with either P 6.5% or 26%, respectively, TestDiet, Richmond IN, USA). Fat content was similar in both foods as were all other non-nutritional components (Table 7.3.1 summarizes the nutritional composition of the two foods). Foods were based on standard rodent diet AIN -93M, recommended by the American Institute of Nutrition (AIN) as a basic diet for the maintenance of adult rodents, which includes 13% P (Reeves et al. 1993).

During the food choice experiments I used 17 mice (11 males and 6 females, randomly assigned to treatments). I presented the mice with three consecutive diet treatments after 10 days of acclimatization under the conditions described above. To assess self-selected preference, each mouse was offered an initial choice (C1) between the two foods (LP and HP) over 18 days. It was assumed based on the composition of the standard rodent diet AIN -93M and the results of Sorensen *et al*. (Sorensen et al. 2008; Sorensen et al. 2010) that this protein range would span the target diet (the preferred position in nutrient space by mice), and the experimental mice would therefore be able to achieve this by mixing their intake of the two foods. I measured the consumption of each food type by each individual in three-day intervals. To measure how the mice trade-off the intake of P versus CHO where diet composition constrains them from reaching their target diet (i.e. as selected in C1), on day 19

the mice were placed on a constrained diet (CD) consisting either of LP (n=9) or HP (n=8). During CD, I measured the consumption by each individual mouse during nine days in three-day intervals, and then left the mice on their respective constrained diet for a further 16-20 days. To test whether mice compensated for the previous period of macronutrient imbalance (excess P or excess CHO), following CD I provided them with a second choice (C2) between HP and LP foods for nine days and measured the consumption of each food type by each individual in three-day intervals (Table 7.3.2 summarizes the experiment's timeline).

In all of the treatments, initial quantities of each food type given to the mice were between 13 and 16 g of pellets, which represented *ad libitum* supply per three days. After each weighing, I added additional pellets as needed. Water was supplied freely throughout the experiment. Weighing (±0.01 g) was done using an open scale (Model Scout Pro, Ohaus, Pine Brooks NJ, USA).

Early observations revealed that mice did not hoard food and were highly efficient in collecting any spillover. I could therefore confidently attribute the decrease in pellet mass during the experiments to consumption by the animals. At all stages of the experiment I quantified the amount of food consumption by extracting the remaining mass of pellets from the initial mass given to each individual mouse. Intakes of P and CHO were derived by multiplying the amount of pellet eaten by the percentage (kJ) of each macronutrient in the respective pellet types. In the choice phases (C1 and C2) total P and CHO intakes were then derived by adding the intakes of each nutrient from the two foods.

To compare relative body fat percentage, I used 40 mice. Animals were culled after 14-30 days of constraint diets (HP or LP foods). The gut of dead mice was removed and the carcasses were dried to constant mass (total of 130 h) in a vacuum oven at 60°C. Dried

carcasses were ground in a sterile coffee mill and dried again for 36 h at 60°C. For analysis of body fat percentage, complete samples were extracted three times with petroleum ether and then reweighed to obtain fat content by mass difference.

Table 7.3.1. Nutritional profile of purified isocaloric high protein (HP) and low protein (LP) foods*.

Food	% Protein (g / kJ)	% Carbohydrates (g / kJ)	% Fat (g / kJ)	Total energy (kJ/g)
HP	26 / 27.9	58.1 / 62.3	4.1 / 9.8	15.45
LP	6.5 / 6.8	80.4 / 83.6	4.1 / 9.6	15.95

- Based on rodent diet AIN -93M
-

Table 7.3.2. Experimental timeline*.

Phase	Initial choice (C1)	Constrained diet (CD)	Second choice (c2)
Duration	18 days	25-29 days**	9 days

* Second and third phases started immediately after the relevant phase ended

** Consumption measured for the first nine days only.

7.3.1. Data analysis

I used the geometric framework (Raubenheimer et al. 2009; Simpson & Raubenheimer 2012) to explore the regulation of P and CHO consumption by the mice in the three phases of the experiment. This framework is based on a Cartesian space, where each axis represents a nutrient, where the animal's optimal nutritional state (the "intake target") and its current nutritional state, are represented by points or areas in this space. Foods are represented by lines that radiate from the origin, called "nutritional rails", with a slope that is determined by the balance of the nutrients the food contains. When an animal feeds, it ingests the nutrients in the same proportion as they are present in the chosen food, and its nutritional state thus

changes along the trajectory that is the same as that of the nutritional rail of that food. By mixing its intake from two foods, however, it can move to any point in the area bounded by the respective rails. The animal can therefore achieve its intake target either by selecting a nutritionally balanced food (i.e. one with a rail that passes through the target), or by mixing its intake in the appropriate proportions from two nutritionally imbalanced foods, provided the area between the rails for these contains the intake target. Such foods which jointly encompass the intake target are "nutritionally complementary" with respect to each other. However, if the animal derives its intake from a single nutritionally imbalanced food, then it cannot reach the target, but must settle on a compromise between over-ingesting one of the nutrients and under-ingesting the other. The compromise reached in this situation is an important metric reflecting the nutritional priorities of the animal (Raubenheimer & Simpson 1997).

Using this framework, I assessed 1) the preferred macronutrient intake selected by mice when allowed to mix their intake from HP and LP (C1), 2) the relative priority assigned to P and CHO when they were provided with either HP or LP and thus constrained from achieving the target intake (CD), and 3) whether the mice compensated for the period of diet constraint (CD) when subsequently allowed to select an intake from the two complementary foods HP and LP (C2).

I used Repeated Measure ANOVA to detect changes in P and CHO consumption through time during C1. I used independent Student *t*-tests to compare total energy intake during CD, P and CHO consumption during the first nine days between C1 and C2 (before and after CD) for separated and accumulated energy intake values, accumulated values of P to CHO ratios during C1 and C2, total energy intake between the HP and LP groups during

the three treatments, cumulative total energy intake across the treatments, and the cumulative energy intake from P and CHO across the three treatments. I used ANOVA to test the effect of sex and food type on mice body fat composition and compared relative fat percentage between males and females restrained to either HP or LP foods.

7.4. Results

During C1, mice exhibited a trend of reduced P intake and increased CHO intake through time, thus further increasing the CHO:P ratio (Fig. 7.4.1). After nine days, almost 50% of the mice ceased consumption from the HP pellets altogether, and as a consequence the mean P consumption was very close to the P percentage of the LP diet. Interestingly, however, throughout this phase of the experiment two mice regulated to a higher P intake by consuming more HP than LP pellets. Repeated Measure ANOVA revealed that the decrease in P consumption from day three through to day 18 was significant ($F_{5,80} = 9.244$; $P < 0.001$).

In the second phase of the experiment (CD), both the mice on LP and HP regulated the same amount of energy after three, six and nine days (Independent *t*-test, n.s., Fig. 7.4.2). A comparison of the intakes between C2 and C1 revealed that energy intakes did not differ between foods and treatments (Independent t-test, n.s., Fig. 7.4.3A). However, macronutrient confinement during CD changed the macronutrient regulation of the mice (Fig. 7.4.3B), but this change was not, as I had predicted, compensatory. Mice that had been confined to the HP diet subsequently consumed more P during C2 compared with C1, whereas mice that had been confined to LP diet consumed less P during C2 compared with C1. Subtracting P consumed in C2 from C1 revealed that in days 6 and 9 these trends were significant

(Independent samples *t*-test; t = -2.994, df = 15, P = 0.009; t = -2.669, df = 15; P = 0.018; respectively) and that this effect was not transitory, but intensified from day 3, in which there was a non-significant trend.

Cumulative values representing P and CHO consumption during nine days on C1, CD and C2 showed that CD affected P consumption on C2 relative to C1. The trajectories show that the trends of macronutrient regulation were stable through time. Extracting the cumulated values of P and CHO consumed in C2 from C1 revealed that during days six and nine HP mice consumed more P than LP mice after the diet confinement (Independent *t*-test; t = -2.354, df = 15, P = 0.033; t = -2.533, df = 15, P = 0.023; respectively), whereas consumption of P during day three and of CHO during the whole time did not differ between the HP and LP groups (Independent t-test; n.s.). Comparisons of P to CHO ratios between HP and LP groups in C1 and C2 as cumulated values during nine days in three days intervals show that in C1, HP and LP mice (offered diet choice after acclimatization) did not differ (Independent t-test; n.s.), but in C2 (offered diet choice after single diet confinement) HP mice had a greater P to CHO ratio then LP mice during the three checks (Independent t-test; t = 2.489, df = 15, P = 0.025; t = 2.465, df = 15, P = 0.026; t = 2.395, df = 15; P = 0.03; respectively). Energy intake (represented by cumulative values) during the first nine days was again similar between HP and LP mice (Independent *t*-test; n.s.) except on the day three of C1+CD and day three of C1+CD+C2 where HP mice had higher energy intake (Independent *t*-test; t = -2.354, df = 15, P = 0.033; t = -2.533, df = 15, P = 0.023; respectively).

Geometric framing of cumulative total energy intake from all days (C1 = 18, CD = 9, C2 = 9) revealed that P consumption by LP and HP mice was similar during C1 but differed

during C2 (after CD). However, this difference was not compensatory, as predicted, but counter-compensatory, with HP mice increasing their P consumption and LP mice decreasing it. Cumulative total energy intake did not differ between HP and LP mice across the three treatments (Independent t-test; n.s.). Cumulative energy intake from P and CHO separately, however, revealed that during CD and C2 HP mice consumed more energy from P relatively to LP mice (Independent *t*-test; $t = 3.847$, $df = 15$, $P = 0.002$; $t = 4.055$, $df = 15$, $P = 0.001$; respectively). P and CHO consumption during C1 and CHO during CD and C2 did not did not differ between the two groups (Independent *t*-test; n.s.).

Sex, but not food type or the interactions between sex and food type, affected mice body fat composition (ANOVA; $F = 6.264_{1,36}$; $P = 0.017$; n.s.; n.s.; respectively). In both groups (LP and HP), females had significantly higher body fat percentage than males (Fig. 7.4.4).

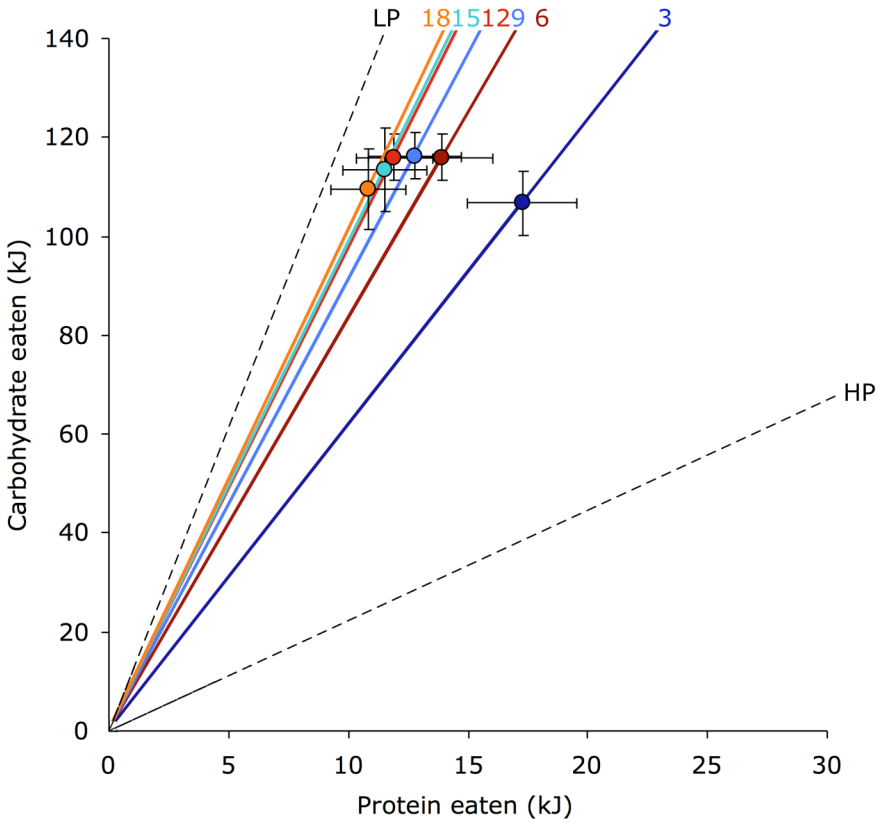

Figure 7.4.1. Geometric representation of macronutrient energy (kJ) selection (mean ± s.e.) by mice (n = 17) offered a choice between high protein (HP) and low protein (LP) contents isocaloric foods, shown for 18 days in three-day intervals. Black dots represent the target of protein (P) to carbohydrate (CHO) ratio consumed by the mice. Full lines represent the predicted trajectories for P to CHO ratios. Numbers correspond with the day of consumption check (3 - 18). Dashed lines represent the trajectories for the pure foods (HP and LP).

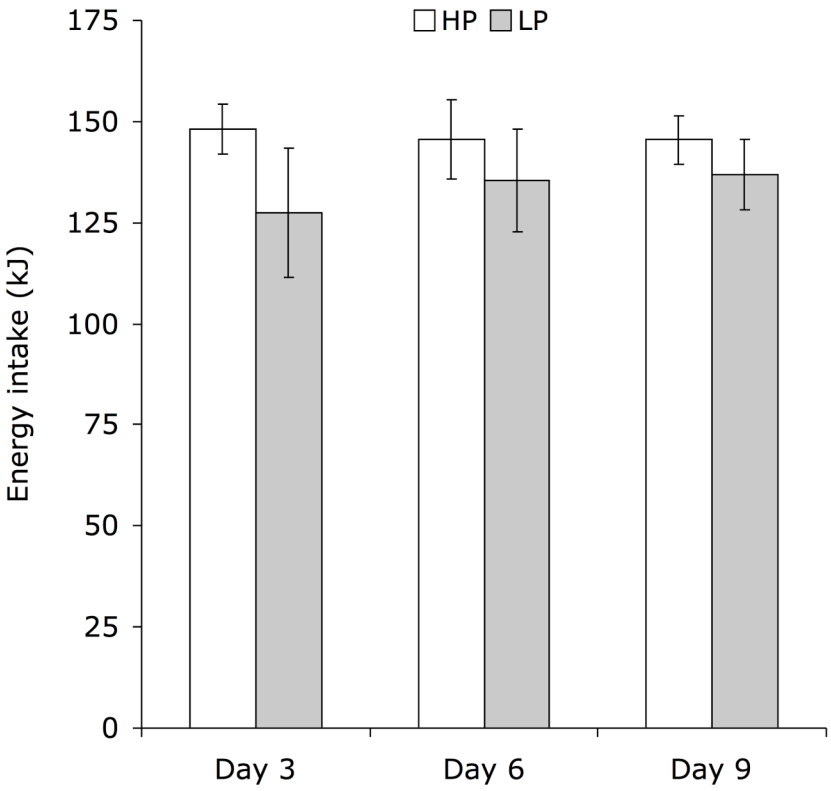

Figure 7.4.2. Total energy (kJ) intake (mean ± s.e.) by mice confined to either high protein (HP, n = 8) or low protein (LP, n = 9) foods during three, six, nine days.

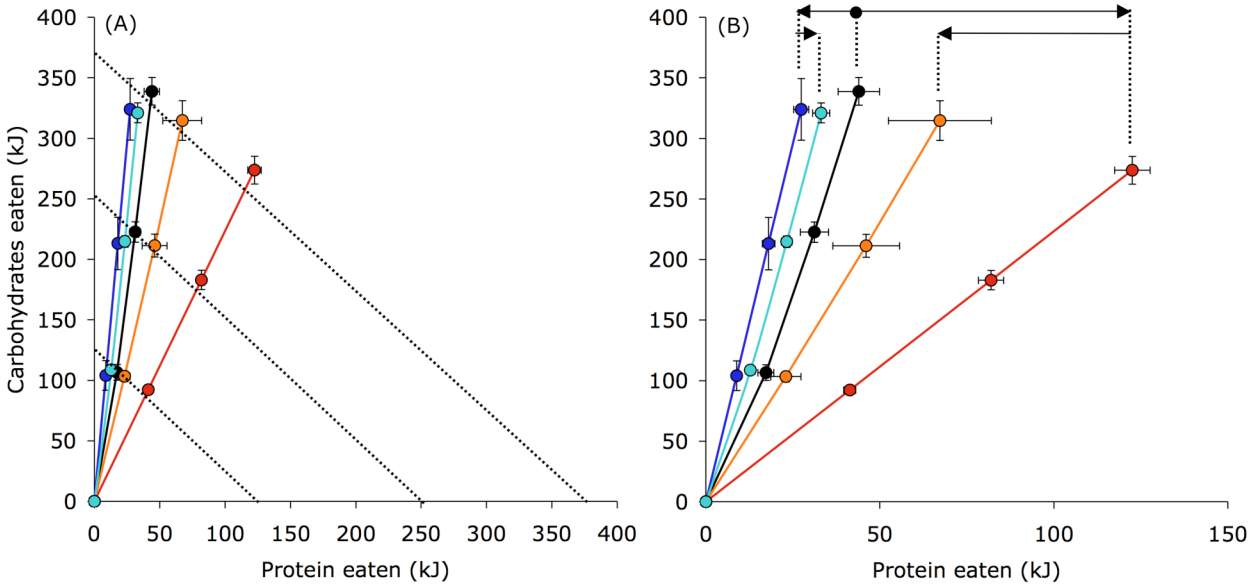

Figure 7.4.3. Geometrical representation of protein (P) and carbohydrates (CHO) energy (kJ) selection as cumulative values for the three checks on days 3, 6 and 9 (mean ± s.e.) in mice offered initial choice (C1) between high protein (HP) and low protein (LP) foods (black), followed by constrained diet (CD) to either the LP (blue) or HP (red) foods, and by subsequent choice (C2) shown for former LP (turquoise) and HP (orange) mice. In (A) Diagonal dashed lines correspond with gross energy intake at the Y (CHO) and X (P) axes (for all days this represent similar energy consumption from both sources throughout the treatments). In (B) Top arrows represent nutritional direction from C1 to CD. Lower arrows represent nutritional direction from CD to C2 (i.e. the direction of macronutrients selection between the treatments).

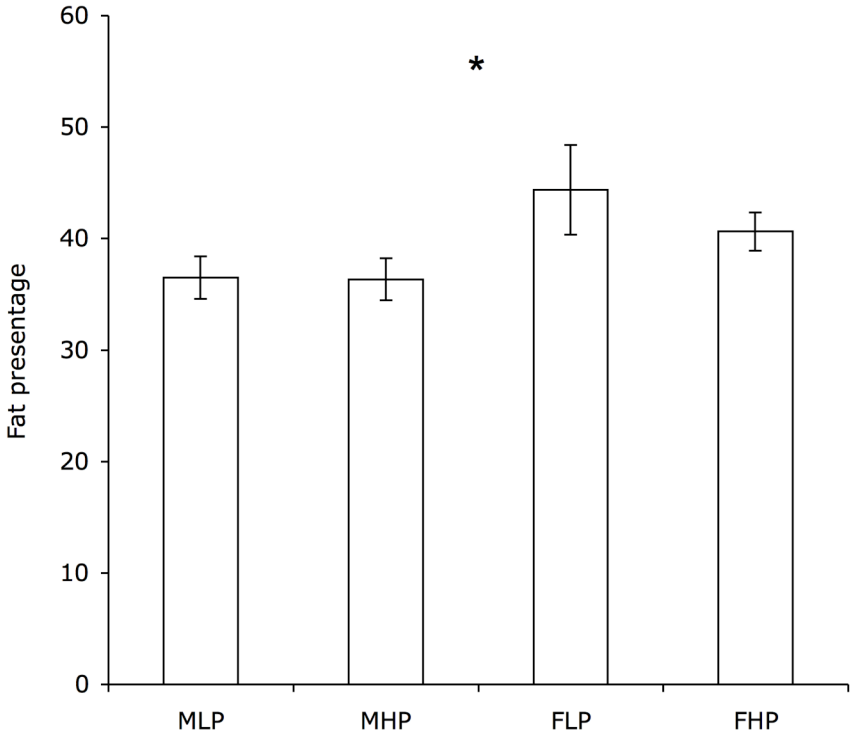

Figure 7.4.4. Relative body fat composition represented as fat percentage (mean ± s.e.), of male (M) and female (F) mice (n=40) fed *ad libitum* on isocaloric foods of either high (HP) or low (LP) protein content.* $P = 0.017$.

7.5. Discussion

My results show that the wild house mice used in this study, regardless of the diet they were offered, maintained a constant total energy intake throughout each experiment. They also prioritized energy intake through macronutrient regulation toward a low P:CHO diet both when on a restricted diet and when given diet choice. These results contrast with macronutrient studies showing that laboratory mice prioritize protein over total energy intake (Sorensen et al. 2008; Sorensen et al. 2010). Almost all strains of laboratory mice are descendants of a very few ancestors and exhibit high levels of genetic homogeneity (Beck *et al.* 2000). Together with the notion that nutritional priorities in the laboratory are highly

affected by laboratory feeding regimes (Warbrick-Smith *et al.* 2009), it is reasonable to assume that prioritizing protein over energy intake in laboratory mice, as demonstrated with the NMRI strain (Sorensen et al. 2008; Sorensen et al. 2010), is a general property of laboratory mice. In any case the results of the current study indicate that this property of laboratory mice was not inherited from their wild ancestors.

Although the mice maintained a constant total energy intake, they did exhibit preference toward low P:CHO diet when given the choice between the LP and HP foods. Moreover, as demonstrated in the first phase of the experiment (C1), mice lowered their P intake through time until their macronutrient regulation was almost identical to the nutrient values of the LP food. In reality this means that while some animals were still feeding from both types of food, others ceased consumption of the HP food completely. Proteins are important components in most animals' diet and are crucial for both development and sustainability (Reeves et al. 1993; Simpson & Raubenheimer 2005; Barboza et al. 2009; Cheeke & Dierenfeld 2012). I predicted that energy intake would be prioritized over protein, but regulating such low levels of protein, especially when foods are isocaloric is puzzling. Hawlena and Schmitz (2010) found that when stressed with predation risk, grasshoppers elevated their carbohydrate consumption. My mice were not under those conditions, but these wild animals were housed in relatively small cages kept in social . This may have unintentionally imposed stressors that drove the animals to increase carbohydrate consumption. Manipulating food resources in more natural field conditions should reveal whether this regulation is a general property or a result of long-term captive condition, already shown to have the potential to induce behavioural changes in wild-derived mice (Fonio et al. 2012).

My predication that mice offered a second choice (after diet confinement) would return to the same nutritional target point as in the first choice (before diet confinement) was rejected. Instead, mice were apparently affected by the constrained diet and during the second choice reached a new nutritional target point that was closer to the values of the pure diet (either HP or LP) compared with the first choice. This phenomenon infers that regulating macronutrient is, despite the tendency to prioritize energy intake, a significant property. Sorensen *et al*. (2010) showed that laboratory mice demonstrated gut function flexibility depending on the diet they were fed and that gut organs differ between groups of mice restricted to different diets. Since the mice in this study were able to withstand protein loads more then 3.5 times higher than the loads they appear to prefer during the choice experiments to achieve the levels of energy intake they desired, it would be safe to assume that wild mice guts have at least the same physiological performances as their laboratory counterparts, if not exceeding them. However, as these physiological adjustments can be energetically costly, choosing a nutritional target point that is closer to the point that the body was restricted to is, energetically speaking, logical.

Relative body fat percentages further demonstrate that total energy intake was more important than macronutrient composition and that mice are able to generate the same amount of fat regardless of the P:CHO ratio in their diet. This is probably more important when mice inhabit colder environments where accumulation of body fat can be crucial for survival in small mammals (Schmidt-Nielsen 1975). In laboratory mice, animals transferred from hot environment (21°C) to cold environment (-3°C) lost weight (Barnett 1965). However, mice born in cold environment (-3°C) had more than twice the body fat of mice born in hot environment (21°C) (Barnett 1973). Krebs and Singleton (1993) have found that

body fat in mice *M. musculus* was not correlated with indices of condition. However, here we measure body fat content not as an indication for general condition but as a comparative measure of using different energy sources to accumulate fat. The ability to accumulate fat from diets with a broad spectrum of P:CHO ratios means that the type of foods available in the environment and through the seasons is less of a limiting factor, as long as the quantities are sufficient to maintain the required energy intake levels. Females accumulated more fat relative to males, but did so regardless of the diet they were confined to, as was the case with the males. This shows that the energy regulation strategy of mice was effective, at least for the accumulation of body fat.

My data support the prediction that generalist-feeding animals should show greater behavioural and physiological flexibility in their responses to nutrient imbalance compared with specialists (Raubenheimer & Simpson 2003). By prioritizing energy, or rather by not being confined to strict regulation of protein, as is the case with laboratory mice (Sorensen *et al.* 2008), wild mice are able to effectively use whatever food types are available in their environment. This trait might also explain, at least partially, their outstanding success as invasive species. Determining a set of traits that would predict invasiveness is tricky, mainly because other factors such as environmental characteristics influence chances for a successful invasion process (Davis 2009). However, I can argue that the more flexible the species in its requirements, potentially the more environments would be suitable. The role of macronutrient regulation in that respect is so far poorly understood, but I suggest that when coupled with other relevant factors, generalist feeding might be a reliable predictor of invasiveness. Because control measures for many invasive species relay on food as bait, I argue that the feeding characteristics and macronutrient/energy regulation of an invasive

species is probably highly relevant for its control. Moreover, with a better knowledge of a species' feeding preferences and the specific opportunities in the environment it invaded, it should be possible to increase the rates of poison bait take.

Interpretation of the geometric pattern presented here could mean that mice do regulate macronutrients and not energy by weighing excesses and deficits of the two nutrients equally, as shown in insects (Raubenheimer & Simpson 1997, 2003). For the mice here though, I argue that the cumulative evidence suggests that energy is primary, because:

1) the high CHO ratio selected in C1, and the progressive trend towards higher CHO indicates that mice do not care much for P. 2) Mice did not compensate for the constrained diet, but again consumed the same amount of energy, which shows little concern for a specific balance of macronutrients. 3) During C2 mice ate more of the diet to which they had been confined previously, suggesting that they switch preference to the familiar, which can also be interpreted as an opportunistic strategy. 4) Across the whole experiment the mice consumed very different P:CHO balances, but very similar energy. 5) Despite different P:CHO intakes, body fat composition was very similar, suggesting that mice were also physiological opportunists, capable of using both CHO and P as efficient energy sources.

In the current study I investigated for the first time macronutrient regulation in wild house mice. My findings suggest that nutritional properties of laboratory and wild mice are different and, while the former exhibit specialist feeding behaviours, the latter is an extreme generalist. These findings shed more light on the different evolutionary pathways that wild and laboratory mice have gone through since their separation. Given the fact that I caught the test animals in the wild, I cannot determine the extent to which the patterns I measured are due to individual experience or natural selection. Further nutritional comparisons between

wild and laboratory mice, especially concerning cross-generation dietary confinements, should emphasis these differences and help reveal their mechanisms. Significant behavioural differences between laboratory and wild mice are likely to have implications for human-related research (Fonio et al. 2012). This is especially important as laboratory mice are being widely used as models for humans across many disciplines. The current study is also the first attempt to connect macronutrient regulation and invasiveness. It has already been shown that enlarged brains, which are thought to enhance behavioral plasticity, potentially in adaptive ways (Rensch 1956; Jerison 1973; Wyles et al. 1983; Dunbar 1992; Reader & Laland 2002), are a predictor of the successful introduction of both birds and mammals into novel environments (Sol & Lefebvre 2000; Sol et al. 2005; Sol et al. 2008). We suggest here that the importance of behavioural plasticity in the ability of a species to successfully invade new environments might also be related to nutritional habits. More research in this direction will help us to understand the complex nutritional relationships between the invader and its environment, and potentially benefits rodent control.

7.6. Acknowledgments

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7.7. References

Barboza PS, Parker KL, Hume ID 2009. Integrative Wildlife Nutrition. Berlin, Springer-Verlag. 615 p.

Barnett BA 1973. Maternal processes in the cold-adaptation of mice. Biological Reviews 48: 477-508.

Barnett SA 1965. Adaptation of mice to cold. Biological Reviews 40: 5-51.

Beck JA, Lioyd S, Hafezparast M, Lennon-Pierce M, Eppig JT, Festing MFW, Fisher EMC 2000. Genealogies of mouse inbred strains. Nature Genetics 24: 23-25.

Cheeke PR, Dierenfeld ES 2012. Comparative Animal Nutrition and Metabolism. Cambridge, Cambridge University Press. 339 p.

Davis MA 2009. Invasion Biology. Oxford, Oxford University Press. 288 p.

Dunbar RIM 1992. Neocortex size as a constraint on group-size in primates. Journal of Human Evolution 22(6): 469-493.

Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley WJ, Wood JT, Wallis IR, Lindenmayer DB 2009. Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology 20(4): 685-690.

Fonio E, Benjamini Y, Golani I 2012. Short and long term measures of anxiety exhibit opposite results. Plos One 7(10): e48414.

Gosby AK, Conigrave AD, Lau NS, Iglesias MA, Hall RM, Jebb SA, Brand-Miller J, Caterson ID, Raubenheimer D, Simpson SJ 2011. Testing protein leverage in lean humans: a randomised controlled experimental study. Plos One 6: e25929.

Hawlena D, Schmitz OJ 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. Proceedings of the National Academy of Sciences of the United States of America 107(35): 15503-15507.

Jerison HJ 1973. Evolution of the Brain and Intelligence. New York, Academic Press. 482 p.

Jones SA, Raubenheimer D 2001. Nutritional regulation in nymphs of the German cockroach, *Blattella germanica*. Journal of Insect Physiology 47: 1169-1180.

Krebs CJ, Singleton GR 1993. Indices of condition for small mammals. Ausralian Journal of Zoology 41: 317-323.

Long JL 2003. Introduced Mammals of the World. Collingwood, CSIRO. 589 p.

MacKay JWB 2010. *Mus musculus*. Retrieved May 10th 2012, from, updated September 17, 2010: http://www.issg.org/database/species/ecology.asp?si=97&fr=1&sts=&lang=EN

Murphy EC 1992. The effects of a natural increase in food supply on a wild population of house mice. New Zealand Journal of Ecology 16(1): 33-40.

Raubenheimer D, Simpson SJ 1997. Integrative models of nutrient balancing: application to insects and vertebrates. Nutrition Research Reviews 10: 151-179.

Raubenheimer D, Simpson SJ 2003. Nutrient balancing in grasshoppers: behavioural and physiological correlates of dietary breadth. Journal of Experimental Biology 206(10): 1669-1681.

Raubenheimer D, Jones SA 2006. Nutritional imbalance in an extreme generalist omnivore: tolerance and recovery through complementary food selection. Animal Behaviour 71: 1253-1262.

Raubenheimer D, Simpson SJ, Mayntz D 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. Functional Ecology 23(1): 4-16.

Reader SM, Laland KN 2002. Social intelligence, innovation, and enhanced brain size in primates. Proceedings of the National Academy of Sciences 99(7): 4436-4441.

Reeves PG, Nielsen FH, Fahey GC 1993. Ain-93 purified diets for laboratory rodents - final report of the American Institute of Nutrition ad hoc writing committee on the reformulation of the Ain-76a rodent diet. Journal of Nutrition 123(11): 1939-1951.

Rensch B 1956. Increase of learning capability with increase of brain-size. American Naturalist 90(851): 81-95.

Ruscoe WA, Murphy EC 2005. House mouse. In: King CM ed. The Handbook of New Zealand Mammals. 2nd ed. New York, Oxford University Press. Pp. 204-221.

Schmidt-Nielsen K 1975. Animal Physiology. New York, Cambridge University Press. 685 p.

Simpson JS, Batley R, Raubenheimer D 2003. Geometric analysis of macronutrient intake in humans: the power of protein? Appetite 41: 123-140.

Simpson SJ, Raubenheimer D 2005. Obesity: the protein leverage hypothesis. Obesity Reviews 6(2): 133-142.

Simpson SJ, Raubenheimer D 2012. The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity. New Jersey, Prinston University Press. 260 p.

Sol D, Lefebvre L 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90(3): 599-605.

Sol D, Bacher S, Reader SM, Lefebvre L 2008. Brain size predicts the success of mammal species introduced into novel environments. American Naturalist 172: S63-S71.

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America 102(15): 5460-5465.

Sorensen A, Mayntz D, Raubenheimer D, Simpson SJ 2008. Protein-leverage in mice: the geometry of macronutrient balancing and consequences for fat deposition. Obesity 16(3): 566-571.

Sorensen A, Mayntz D, Simpson SJ, Raubenheimer D 2010. Dietary ratio of protein to carbohydrate induces plastic responses in the gastrointestinal tract of mice. Journal of Comparative Physiology B 180(2): 259-266.

Stenseth NC, Leirs H, Skonhoft A, Davis SA, Pech RP, Andreassen HP, Singleton GR, Lima M, Machang'u RS, Makundi RH and others 2003. Mice, rats, and people: the bio-economics of agricultural rodent pests. Frontiers in Ecology and the Environment 1(7): 367-375.

Tann CR, Singleton GR, Coman BJ 1991. Diet of the house mouse, *Mus domesticus*, in the Mallee Wheatlands of North Western Victoria. Wildlife Research 18(1): 1-12.

Warbrick-Smith J, Raubenheimer D, Simpson SJ, Behmer ST 2009. Three hundred and fifty generations of extreme food specialisation: testing predictions of nutritional ecology. Entomologia Experimentalis Et Applicata 132(1): 65-75.

Wyles JS, Kunkel JG, Wilson AC 1983. Birds, behavior, and anatomical evolution. Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences 80(14): 4394-4397.

CHAPTER 8: DISCUSSION

8.1. Behavioural conservation

The understanding and improvement of conservation practices directly through the study of animal behavioural processes (Clemmons & Buchholz 1997; Caro 1999) is an emerging science and is rapidly growing (Ulfstrand 1996; Clemmons & Buchholz 1997). In a recent paper, Berger-Tal et al. (2011) suggested a conceptual framework for the integration of animal behaviour and biological conservation. They suggested a triangle consisting of three basic themes: (1) anthropogenic impacts (direct and indirect) on animal behaviour that in turn impact biodiversity, (2) the use and consideration of animal behaviour in practical conservation management, and (3) behavioural indicators to other behavioural processes that are of conservation concern. They further recognize three key behavioural domains that are relevant to both fitness and conservation across taxa: (1) patterns of movement and space-use, (2) foraging and predator–prey interactions, and (3) social behaviour and reproduction. The interactions between the conservation themes and the behavioural domains represent a system of feedbacks that ideally can benefit biodiversity and species conservation through the management of animal behaviour (Fig. 8.1.1.).

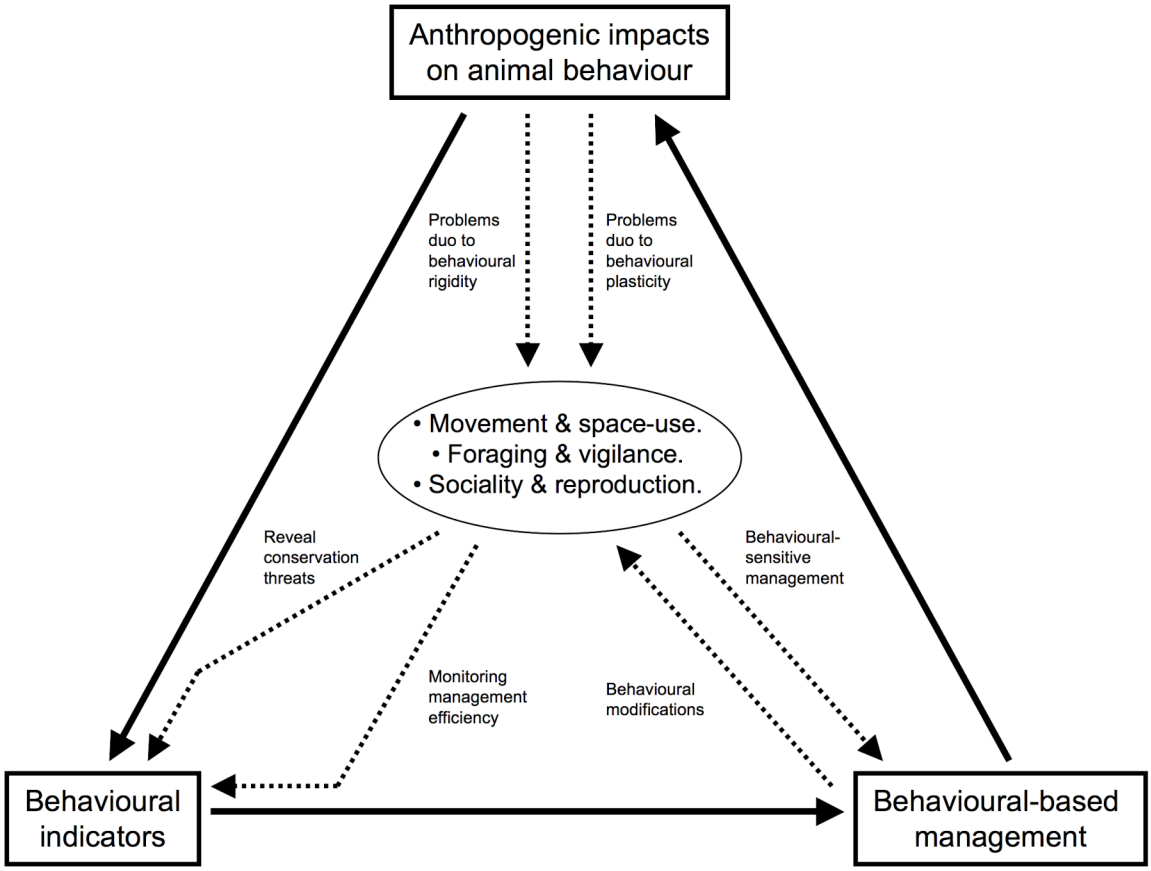

Figure 8.1.1. Schematic presentation of the behavioural conservation framework, adapted from Berger-Tal et al. (2011). The framework consists of three basic interrelated conservation themes (squares) and behavioural domains (circle). Black arrows represent interactions between the conservation themes. Gray arrows represent the pathways that connect each theme to the behavioural domains.

This framework was designed to address actions for species under conservation management. However, it can also be applied to the management of invasive species; indeed the behavioural domains suggested above are equally relevant for invasive species. Spatial behaviour, foraging, interspecific and intraspecific interactions, and reproduction biology are all essential components for the success of an invasive species in its new environment. The conservation themes appear to fit this scenario with only minor adjustments. Behavioural

indicators are used to assess the species' state, as well as the state of the environment it invaded, and behavioural-based management is of course the core of the framework. In the Berger-Tal et al. (2011) model, behavioural-based actions are aimed for the benefit of species' conservation. When considering invasive species management, we should only change it to behavioural-based actions for the focal species' control.

Anthropogenic impacts on animal behaviour, whether direct or indirect, are the one theme that requires the most adjustment, primarily because it represents a contradictory consequence i.e. control rather than conservation of a species. For conservation, positive effects should increase species survival and negative effects reduce it. For control, positive effects should reduce species survival and negative effects increase it. Thus, if in conservation management the aim is to reduce negative anthropogenic effects on a species, in the control of invasive species the aim is to increase negative anthropogenic effects on a species.

The relationships and feedbacks within the model should remain the same however, as the principle remains to enhance, through the understanding of behavioural processes, the impact of management (conservation or control) on target species. The impact of invasive species on the environment is severe (Meffe & Ronald 1997; Davis 2009; Primack 2010) and thus control management is practiced by most conservation agencies, governmental and non-governmental. Animal behaviour has a key role in the conservation of threatened species (Clemmons & Buchholz 1997; Sutherland 1998; Linklater 2004; Buchholz 2007; Moore et al. 2008; Blumstein & Fernandez-Juricic 2010). There are studies exploring control implications and conservation benefits based on invasive species behaviour (Russell et al. 2008; Mattos & Orrock 2010; Russell et al. 2010; King & Powell 2011; MacKay et al. 2011;

Price & Banks In Press) but in general, the importance of invasive species behaviour in direct relation to their control is not extensively implemented, although many researchers emphasis its significant and advocate its promotion (Wace 1986; McClelland 2002; Sowls & Byrd 2002; Amori & Clout 2003; Courchamp et al. 2003; Towns & Broome 2003; Clapperton 2006; Moore et al. 2008).

In my opinion, to maintain an effective and continuous control of invasive species, managers will have to acquire profound knowledge of the behaviour of the species they target. This can be achieved only through fundamental behavioural research of invasive species that is directly related to improvements of their control. In this thesis I have attempted to do just this. In the following sections, I will summarise the principal results from the research chapters, discuss possible implications for invasive species control and identify future directions for research.

8.2. Conspecific attraction using live lures

Conspecific attraction in the form of pheromones has been widely used, primary with insects, to enhance pests trapping rates (Burkholder & Ma 1985; Copping & Menn 2000). In vertebrates, attracting birds with conspecific playbacks is common as a conservation tool (Ward & Schlossberg 2004; Hahn & Silverman 2007) and the use of mouse urine has been shown to enhance trapability of conspecifics (Volfova et al. 2011). However to date, there are only a handful of examples for the use of live animals as attractants to invasive conspecifics (Taylor & Katahira 1988; Tidemann 2005; Tsachalidis et al. 2006). This is especially perplexing because social interactions are a significant component in the life

histories of many species (Gould 1982; Pusey 2005) and contact for reproduction is essential in most (Sadava et al. 2011). The power of conspecifc attraction has therefore a great, unexplored potential for the detection and capture of invasive species.

My live lure studies with the Norway rat *R. norvegicus* demonstrate the potential power of conspecific attraction. Based on the social behaviour of Norway rats I developed and established efficient trapping and detecting methodology, demonstrating that laboratory rats can act as bio-control agents for their invasive counterparts. In almost all of the cases tested, lure rats were more effective than food bait for detecting invasive rats. This is, with lure rats fewer traps were required to capture the same number (Chapter 2), or significantly more (Chapter 3) wild conspecifics compared with food-baited traps. There were few scenarios in which lure rats did not prove to be more efficient, but no scenarios where lure animals were not *at least* equally efficient as food-baited controls.

Deployment of field-based conspecifics as live lures year round is probably impractical, as live animals require relatively high maintenance and can be costly compared to food baits. However, for specific scenarios, this method might prove a viable and valuable additional tool to standard methods: (1) island incursions where rapid response is crucial and bait avoidance common; (2) enforcement of specific control measures such as seasonal control for the protection of bird nesting; (3) any situation where other means of control are restricted (e.g. poison) and specific animals are known to avoid other control measures.

I have suggested that conspecific live luring should be tested with other invasive and pest species and I propose the house mouse *Mus musculus* is a further good candidate. I have demonstrated that there was no significant difference between the attractiveness of wild versus laboratory mice to wild mice (Chapter 4). This finding is encouraging because the use

of wild animals as caged lures can be tiresome for the operator and stressful for the animal. With laboratory mice as the attractants, further research looking at the power and efficacy of live conspecific attraction in mice, especially compared to food baits can be conducted with relative ease. Experiments should probably begin testing the attraction of lure mouse when invasive mice populations are at low densities, a situation that makes it difficult to target the animals using standard methods.

My studies concentrated on the applied side of conspecific attraction. There are however, open questions regarding the mechanisms involved in the attraction that, in addition to providing biological knowledge, can potentially increase the efficacy of the luring method. These include: (1) understanding the trade-offs between foraging and social interactions, (2) defining the trends of attraction within and across genders and between young and adult animals (differences in the attraction to females and males were minor, but trends inferring that females are stronger attractants were identified), and (3) specific measures of the power of lure animals to help target invasive animals overcome trap neophobia.

8.2.1. Issues concerning Animal Ethics

Under Part 6 of the Animal Welfare Act (1999), the manipulation of animals for research, testing or teaching requires approval from the organisation's Animal Ethics Committee. The purpose of Part 6 is to ensure that the use of animals in research, testing and teaching is confined to cases in which there is good reason to believe that (the original section 3 deals with non human hominids and thus was omitted):

1) The findings of the research, or testing or the results of the teaching will enhance

understanding of humans, animals, or the natural or productive environment.

2) The anticipated benefits of the research, testing, or teaching outweigh the likely harm to the animals.
3) All reasonable steps must be taken to meet the physical, health, and behavioural needs in accordance with both good practice and scientific knowledge, except where this is not possible because of the nature of the work, in which case any pain or distress must be reduced to the minimum possible in the circumstances.
4) Where animals are ill or injured they must receive, where practicable, treatment to alleviate unreasonable or unnecessary pain and distress caused by illness and injury, except where this is not possible because of the nature of the work, in which case any pain or distress must be reduced to the minimum possible in the circumstances.
5) Decision makers must promote efforts to reduce the numbers of animals used, refine techniques to minimise harm and maximise benefits, and replace animals with non-living or non-sentient alternatives where appropriate.

In the case of using animals for research, or in my case, for the enhancement of control practices, dealing with sections 1-2 is crucial because it raises the fundamental question of the justification for using and manipulating animals in the first place. It is important to understand that this very basic question is not at all scientific, but rather a moral one. It depends greatly on our view of the natural world. Do we believe all species are equal or do we decide that some species are more important than others regardless what might be the reason? In the heart of this lay the very basic debate between two different philosophies: *nature conservation* and *animal rights*. Nature conservation is a relatively new science, based

on an environmental ethic statement first formulated by Aldo Leopold (1949), and which basically consider the natural world as something of greater importance than a mere pantry. It can be generalised that the main concern of the conservationist is the *survival of a species* (Hutchins & Wemmer 1987). Animal rights individuals and movements are even newer developments (Hutchins & Wemmer 1987), their main concern is basically lay in the *individual level* (Muth & Jamison 2000). And while conservation, by definition is anthropocentric (e.g. it is *we* who decide on the priorities, which might result in the survival of one species on the expense of another), animal rights activists tend to adopt egalitarianism, which is the extension of the concept of rights (in the sense of immanent rights) to the non-human species (Hutchins & Wemmer 1987; Muth & Jamison 2000). As these are *relative* moral decisions, it cannot be rationalised: moral values are by definition different between different people (Wiggins 1990). Therefore, the very basic decision of whether or not to use, in this case live animals as conspecific lures, must be considered in light of ones beliefs.

My view is that satisfying animal right activists by complying with the limitations of sections 3-5 from part 6 of the Animal Welfare Act cited above is not possible. From the point of view of pure animal rights, there is no justification for putting an animal though possible suffering to improve the killing effort of another. Though, at this stage it is still possible to do so by law. Bad publicity is not, in my opinion, a sufficient reason not to use live lures. However, it is important to consider the use of these lures under the Animal Welfare Act. This I believe was achieved with my lure trap design. My live lure experiments followed stringent animal welfare guidelines. Lure animals were provided with *ad lib* food and water as well as shelter and bedding and were checked daily. None of my lure animals showed overt signs of stress and no animal was injured during my trials. Such intense

monitoring of welfare means however, that large-scale deployment of live lures should be heavily considered as a practical solution for general rodent detection. Nonetheless, I have shown that under special conditions, such as on offshore island that are sanctuaries for rodent vulnerable species, this approach may provide an efficient tool for rodent detection and the use of lure rats with the ethical and labour intensive costs of caring for them may be justified if rat incursions can be identified and managed promptly. The bottom line is that in New Zealand, the principle decision of targeting an invader regardless of ethical costs has already been made. Ultimately, decision makers must choose whether the advantages of using live lures can outweigh the disadvantages.

8.3. Predatory and competitive cues and vigilance behaviour

The use of heterospecific odours as deterrents has been suggested to have the potential to constrain spreading, foraging, and breeding of other animals (Sheriff et al. 2009; Hughes & Banks 2010; McPhee et al. 2010; Webb et al. 2010; Ferrero et al. 2011). Other studies however, suggest that this is a species-specific trait and thus naïve animals may be less receptive to these cues (Dickman 1992; Orrock 2010). Since there are costs both to being too risk averse in the face of these cues (i.e. foregoing foraging opportunities) and too risk prone (i.e. increased predation or competition), there is a strong incentive for foragers to continually recalibrate the correlation between the cues and the actual risk (Lima & Dill 1990; Brown & Kotler 2004). Rodents are rapid learners (Calhoun 1963; Berry 1970; Berry 1981; Galef & Allen 1995; Galef 2005) and therefore, to achieve meaningful effect (i.e.

change the animals' behaviour), cues should be reliable (i.e. represent a real risk) or strongly significance to the life history of a species (Roberts et al. 2012).

In the field, naïve mice (Chapter 5) did not exhibit any significant change in their foraging in the presence of direct cues of predation/competition in the form of heterospecific scent. Illumination intensity on the other hand, as demonstrated in other rodent species (Kotler 1984; Dickman 1992; Hughes et al. 1994; Orrock et al. 2004; Shapira et al. 2008), affected foraging mice, but the effect decreased over time. When tested in laboratory conditions (Chapter 6), where many factors can be under control, I found that rat scent affected male mice negatively but did not affect females and the effect declined with time. This surprising result suggests that these trends might have been present in the field (Chapter 5) but could not be detected because the sex ratio and number of wild animals visiting the experimental apparatus could not be controlled.

The effect of illumination, in which mice consume less and apparently foraged to lesser distances when light intensity of the moon increases, can probably be used by managers to enhance bait take by adjusting bait regimes to the cycle of the moon. As a side effect, it can also save bait waste by deploying bait when it has more chance of being taken. Future research should look at direct comparisons between random and moon phase oriented bait spread to determine the most efficient regime in terms of bait take and bait waste.

The use of scent as a deterrent for invasive mice is probably too implausible. However, further research can unveil the mechanisms of scent deterrents in mice. Intraspecific communication in mice depends heavily on scent (Rich & Hurst 1998; Hurst et al. 2001; Thom & Hurst 2004; Sherborne et al. 2007). Recently it has been demonstrated that a single component in male mouse urine, the sex protein darcin, can condition preference and

assist both female and male mice to remember their location even after the urine is removed (Roberts et al. 2012). In contrast, quantitative HPLC analysis across 38 mammalian species demonstrate enriched 2-phenylethylamine production by numerous carnivores, and this compound have been found to be an effective deterrent of both mice and rats, (Ferrero et al. 2011). Whether this compound or a different substance can achieve the opposite reaction showed by Roberts et al. (2012) (i.e. conditioning of site avoidance) is yet unknown.

8.4. Macronutrient selection and invasiveness

To maximize their fitness (i.e. achieve optimal development, growth, maintenance, and reproduction) animals must be able to regulate a balanced diet (Barboza et al. 2009; Simpson & Raubenheimer 2012). We can assume that, when invading a novel environment, a generalist feeder will have better chances to survive and establish than a specialist. It is therefore not surprising that the house mouse, a highly successful invasive species, is prioritizing energy over macronutrients (Chapter 7), a characteristic trait of general feeders (Raubenheimer & Simpson 2003). Yet, until now, no attempts have been made to connect macronutrient selection and invasiveness. This property of mouse ecology is especially relevant because it might have implications not only for our understanding of the processes of invasion, but also for the development of better control methods.

Mice inhabit, through introduction, most parts of the world and are considered one of the worst vertebrate pests, negatively affecting agriculture, human health and natural ecosystems, with significant economic implications (Long 2003; Stenseth et al. 2003; MacKay 2010). Most of the control measures taken against mice are food based (Howald et

al. 2007), and yet, a profound knowledge of their diet preferences and needs is missing. I suggest two further steps in the research on wild mice nutrition. Firstly we need to study the effect of parental nutrition during pregnancy on macronutrient selection in the offspring. This should help in understanding the role that heredity plays in mice nutrition and infer whether nutritional improvement of bait should be based specifically on the knowledge of available foods in a specific environment and season or whether it is a general property. Secondly, we should conduct field based experiments comparing commercial bait with different ratios of macronutrient to determine bait efficacy.

Another important future direction is the role diet plays in conspecific attraction (Chapters 4 and 7) and specifically why mice are selecting a low protein diet while are more attracted to the urine of conspecifics on a high protein diet. Macronutrient selection and conspecific attraction seem to have a complex interaction and a better understanding of these interactions might enhance our understanding of control methods for mice populations.

8.5. Epilogue

“Conservation behaviour' is a young discipline that investigates how proximate and ultimate aspects of the behaviour of an animal can be of value in preventing the loss of biodiversity”. This quote from Buchholz (2007), while referring primary to the behaviour of the animals under threat, is relevant to the control of invasive animals. In my thesis I have aimed to contribute to this field. I believe that the key to effective, long-term, and ultimately successful control of invasive species lies within a deep understanding of their behaviour.

8.6. References

1999. Animal Welfare Act. New Zealand Government, Wellington. Pp. 1-162.

Amori G, Clout MN 2003. Rodents on islands: a conservation challenge. In: Singleton GR, Hinds IA, Krebs CJ, Spratt DM ed. Rats, mice and people: rodent biology and management. Canbara, Australian Centre for International Agricultural Research. Pp. 63-67.

Barboza PS, Parker KL, Hume ID 2009. Integrative Wildlife Nutrition. Berlin, Springer-Verlag.

Berger-Tal O, Polak T, Oron A, Lubin Y, Kotler BP, Saltz D 2011. Integrating animal behavior and conservation biology: a conceptual framework. Behavioural Ecology 22: 236-239.

Berry RJ 1970. The natural history of the house mouse. Field Studies 3: 219-162.

Berry RJE 1981. Biology of the House Mouse. London, academic Press.

Blumstein DT, Fernandez-Juricic E 2010. A Primer of Conservation Behavior. Sunderland (MA), Sinauer Associates.

Brown JS, Kotler BP 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7(10): 999-1014.

Buchholz R 2007. Behavioural biology: an effective and relevant conservation tool. Trends in Ecology & Evolution 22(8): 401-407.

Burkholder WE, Ma M 1985. Pheromones for monitoring and control of stored-product insects. Annual Review of Entomology 30: 257-272.

Calhoun JB 1963. The Ecology and Sociology of the Norway Rat. Bethesda, U.S. Dept. of Health, Education, and Welfare, Public health Service.

Caro T 1999. The behaviour–conservation interface. Trends in Ecology & Evolution 14: 366–369.

Clapperton BK 2006. A review of the current knowledge of rodent behaviour in relation to control devices. Science for Conservation 263, DOC, Wellington. 55 p.

Clemmons JR, Buchholz R 1997. Linking conservation and behavior. In: Clemmons JR, Buchholz R ed. Behavioral Aporoaches to Conservation in the Wild. Cambridge, Cambridge University Press. Pp. 3-22.

Copping LG, Menn JJ 2000. Biopesticides: a review of their action, applications and efficacy. Pest Management Science 56(8): 651-676.

Courchamp F, Chapuis JL, Pascal M 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78(3): 347-383.

Davis MA 2009. Invasion Biology. Oxford, Oxford University Press.

Dickman CR 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73(1): 313-322.

Ferrero DM, Lemon JK, Fluegge D, Pashkovski SL, Korzan WJ, Datta SR, Spehr M, Fendt M, Liberles SD 2011. Detection and avoidance of a carnivore odor by prey. Proceedings of the National Academy of Sciences of the United States of America 108(27): 11235-11240.

Galef BG 2005. Social learning. In: Whishaw IQ, Kolb B ed. The Behavior of the Laboratory rat. New York, Oxford University Press. Pp. 363-370.

Galef BG, Allen C 1995. A new model system for studying behavioral traditions in animals. Animal Behaviour 50: 705-717.

Gould JL 1982. Ethology: The Mechanisms and Evolution of Behavior. New York, Norton.

Hahn BA, Silverman ED 2007. Managing breeding forest songbirds with conspecific song playbacks. Animal Conservation 10(4): 436-441.

Howald G, Donlan CJ, Galvan JP, Russell JC, Parkes J, Samaniego A, Wang YW, Veitch D, Genovesi P, Pascal M and others 2007. Invasive rodent eradication on islands. Conservation Biology 21(5): 1258-1268.

Hughes JJ, Ward D, Perrin MR 1994. Predation Risk and Competition Affect Habitat Selection and Activity of Namib Desert Gerbils. Ecology 75(5): 1397-1405.

Hughes NK, Banks PB 2010. Interacting effects of predation risk and signal patchiness on activity and communication in house mice. Journal of Animal Ecology 79(1): 88-97.

Hurst JL, Payne CE, Nevison CM, Marie AD, Humphries RE, Robertson DHL, Cavaggioni A, Beynon RJ 2001. Individual recognition in mice mediated by major urinary proteins. Nature 414(6864): 631-634.

Hutchins M, Wemmer C 1987. Wildlife conservation and animal rights: are they compatible? Advances in Animal Welfare Science 3: 111-137.

King CM, Powell RA 2011. Managing an invasive predator pre-adapted to a pulsed resource: a model of stoat (Mustela erminea) irruptions in New Zealand beech forests. Biological Invasions 13(12): 3039-3055.

Kotler BP 1984. Effects of illumination on the rate of resource harvesting in a community of desert rodents. American Midland Naturalist 111(2): 383-389.

Leopold A 1949. A Sand County Almanac. New York, Oxford University Press.

Lima SL, Dill LM 1990. Behavioral decisions made under the risk of predation - a review and prospectus. Canadian Journal of Zoology-Revue Canadienne De Zoologie 68(4): 619-640.

Linklater WL 2004. Wanted for conservation research: behavioral ecologists with a broader perspective. Bioscience 54: 352-360.

Long JL 2003. Introduced Mammals of the World. Collingwood, CSIRO. 589 p.

MacKay JWB 2010. *Mus musculus*. Retrieved May 10th 2012, from, updated September 17, 2010: http://www.issg.org/database/species/ecology.asp?si=97&fr=1&sts=&lang=EN

MacKay JWB, Murphy EC, Anderson SH, Russell JC, Hauber ME, Wilson DJ, Clout MN 2011. A successful mouse eradication explained by site-specific population data. In: Veitch CR, Clout MN, Towns DR ed. Island Invasives: Eradication and Management. Gland, IUCN.

Mattos KJ, Orrock JL 2010. Behavioral consequences of plant invasion: an invasive plant alters rodent antipredator behavior. Behavioral Ecology 21(3): 556-561.

McClelland PJ 2002. Island quarantine—prevention is better than cure. In: Veitch CR, Clout MN ed. Turning the Tide: the Eradication of Invasive Species. Gland and Cambridge, IUCN SSC Invasive Species Specialist Group. Pp. 173-181.

McPhee ME, Segal A, Johnston RE 2010. Hamsters use predator odors as indirect cues of predation risk. Ethology 116(6): 517-523.

Meffe GK, Ronald CC 1997. Principles of Conservation Biology. 2nd ed. Massachusetts, Sinauer Associates Inc.

Moore JA, Bell BD, Linklater WL 2008. The debate on behavior in conservation: New Zealand integrates theory with practice. BioScience 58: 454-459.

Muth RM, Jamison WV 2000. On the destiny of deer camps and duck blinds: the rise of the animal rights movement and the future of wildlife conservation. Wildlife Society Bulletin 28: 841-853.

Orrock JL 2010. When the ghost of predation has passed: do rodents from islands with and without fox predators exhibit aversion to fox cues? Ethology 116: 338-345.

Orrock JL, Danielson BJ, Brinkerhoff RJ 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behavioral Ecology 15(3): 433-437.

Price CJ, Banks PB 2012. Exploiting olfactory learning in alien rats to protect birds' eggs. Proceedings of the National Academy of Sciences USA. 109: 19304-19309.

Primack RB 2010. Essentials of Conservation Biology. 5th ed. Sunderland, Sinauer. 601 p.

Pusey AE 2005. Social systems. In: Bolhuis JJ, Giraldeau L-A ed. The Behavior of Animals. Malden (MA), Blackwell Publishing. Pp. 315-341.

Raubenheimer D, Simpson SJ 2003. Nutrient balancing in grasshoppers: behavioural and physiological correlates of dietary breadth. Journal of Experimental Biology 206(10): 1669-1681.

Rich TJ, Hurst JL 1998. Scent marks as reliable signals of the competitive ability of mates. Animal Behaviour 56: 727-735.

Roberts SA, Davidson AJ, McLean L, Beynon RJ, Hurst JL 2012. Pheromonal induction of spatial learning in mice. Science 338: 1462-1465.

Russell JC, Towns DR, Clout MN 2008. Review of rat invasion biology: implications for islands biosecurity. Science for Conservation. 53 p.

Russell JC, McMorland AJC, MacKay JWB 2010. Exploratory behaviour of colonizing rats in novel environments. Animal Behaviour 79(1): 159-164.

Sadava D, Hillis DM, Heller CH, Berenbaum MR 2011. Life: The Science of Biology. 9th ed. Sundeland (MA), Sinauer Associates.

Shapira I, Sultan H, Shanas U 2008. Agricultural farming alters predator-prey interactions in nearby natural habitats. Animal Conservation 11(1): 1-8.

Sherborne AL, Thom MD, Paterson S, Jury F, Ollier WER, Stockley P, Beynon RJ, Hurst JL 2007. The genetic basis of inbreeding avoidance in house mice. Current Biology 17(23): 2061-2066.

Sheriff MJ, Krebs CJ, Boonstra R 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. Journal of Animal Ecology 78(6): 1249-1258.

Simpson SJ, Raubenheimer D 2012. The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity. New Jersey, Prinston University Press.

Sowls AI, Byrd GV 2002. Preventing rat introductions to the Pribilof Islands, Alaska, USA. In: Veitch CR, Clout MN ed. Turning the Tide: the Eradication of Invasive Species. Gland and Cambridge, IUCN SSC Invasive Species Specialist Group. Pp. 413.

Stenseth NC, Leirs H, Skonhoft A, Davis SA, Pech RP, Andreassen HP, Singleton GR, Lima M, Machang'u RS, Makundi RH and others 2003. Mice, rats, and people: the bio-economics of agricultural rodent pests. Frontiers in Ecology and the Environment 1(7): 367-375.

Sutherland WJ 1998. The importance of behavioural studies in conservation biology. Animal Behaviour 56: 801-809.

Taylor D, Katahira L 1988. Radio telemetry as an aid in eradicating remnant feral goats. Wildlife Society Bulletin 16(3): 297-299.

Thom MD, Hurst JL 2004. Individual recognition by scent. Annales Zoologici Fennici 41(6): 765-787.

Tidemann C 2005. Indian mynas - can the problem be controlled? 15th Urban Animal Management Conference. Australian Veterinary Association, Canbara. Pp. 55-57.

Towns DR, Broome KG 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. New Zealand Journal of Zoology 30(4): 377-398.

Tsachalidis EP, Sokos CK, Birtsas PK, Patsikas NK 2006. The Australian crow trap and the Larsen trap: their capture success in Greece. In: Manolas EI ed. Proceedings of the 2006 Naxos International Conference on Sustainable Management and Development of Mountainous and Island Areas. Pp. 325-329.

Ulfstrand S 1996. Behavioural ecology and conservation biology. Oikos 77: 183.

Volfova R, Stejskal V, Aulicky R, Frynta D 2011. Presence of conspecific odours enhances responses of commensal house mice (*Mus musculus*) to bait stations. International Journal of Pest Management 57(1): 35-40.

Wace NM 1986. The rat problem on oceanic islands - research is needed. Oryx 20: 79-86.

Ward MP, Schlossberg S 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18(2): 519-525.

Webb JK, Pike DA, Shine R 2010. Olfactory recognition of predators by nocturnal lizards: safety outweighs thermal benefits. Behavioral Ecology 21(1): 72-77.

Wiggins D 1990. Moral cognitivism, moral relativism and motivating moral beliefs. Proceedings of the Aristotelian Society 91: 61-85.

APPENDICES

Appendix 1

Shapira I, Shanas U, Raubenheimer D, Brunton D 2013a. **Laboratory rats as trap lures for invasive Norway rats: field trial and recommendations**. New Zealand Journal of Ecology 37: 240-245.

Abstract The Norway rat (*Rattus norvegicus*) is a highly destructive invasive species but while rat eradications on islands are effective, detection of survivors or reinvasions is challenging. We tested whether laboratory rats can act as lures for wild rats. We live trapped rats first by using food baits, followed by live trapping using male and female lure rats vs controls (i.e. the same trapping device but without the lure animal). Norway rats were more frequently attracted to lure rats compared with controls. There was no sex bias in the trapped animals. Numbers of Norway rats caught with food baits compared with lure rats did not differ, but trapping rates were higher when using lure rats. Rat activity was detected only around lure rats. Ship rats (*Rattus rattus*) were not caught with Norway lure rats. We demonstrate the potential for detecting invasive Norway rats using conspecific rats as lures. Further research looking at conspecific attraction in other situations and in direct comparison with food-baited traps is needed to determine the efficacy of this method as a control measure.

Appendix 2

Shapira I, Shanas U, Raubenheimer D, Knapp C, Alberts S, Brunton D 2013d. **Laboratory rats as conspecific biocontrol agents for invasive Norway rats *Rattus norvegicus***. Biological Control 66: 83-91.

Abstract We tested whether conspecific attraction can be more efficient than food bait for the detection and capture of an invasive, social species, the Norway rat *Rattus norvegicus*. I compared trapping rates between male and female laboratory rats and food baited controls at four mainland sites with low rat population densities, three recreational sites (Zoos) with abundant of food in the environment, and in manipulated island rat incursions. Live lures were more efficient than food baits at both the mainland and recreational sites. There were no differences between the attractiveness of lure animals based on gender either of the lure or of the captured animals. In the manipulated rat incursions, where radio collared male rats were released on a rat free island, two animals were caught with female lures, and the third lost its collar and evaded detection. In the current study we advocate that animal behaviour can help inform and guide innovative tools in the control and management of invasive species. We show that laboratory rats might be efficient as lures for their wild counterparts. Furthermore, our results emphasize the need for a flexible and varied rat control toolbox. We suggest that the use of laboratory rats should be considered in future control management plans for invasive Norway rats.

Appendix 3

Shapira I, Shanas U, Raubenheimer D, Brunton D 2013b. **Conspecific attraction in invasive wild house mice: effects of strain, sex and diet**. Applied Animal Behaviour Science 147: 186-193.

Abstract Invasive rodents pose major concerns for human health, agriculture and conservation. House mice *Mus musculus* are one of the most formidable invasive rodents, and require intensive efforts for their control. Control measures rely largely on food baits but difficulties in the eradication of mouse populations necessitates the development of alternative pest control methods. Conspecific attraction is used as a luring method for invasive species control and can be used to attract wild mice into traps. The proximate cause of the live lure attraction might be primarily scent or a more complex array of stimuli emanating from a live animal. We used a Y maze apparatus to test the effect of urine from mice fed high vs. low protein diets on the attraction of male and female conspecific wild mice (focal animals), and tested whether the protein content of the diet of focal animals affected their response. We further compared the strength of attraction of wild mice toward wild and laboratory (Swiss Webster) live lure conspecifics of the opposite sex. Both males and females were marginally more attracted to conspecific scent originating from lure animals previously on high protein diets, regardless of the focal animal's diet. Wild mice were equally attracted to laboratory mice of the Swiss Webster strain and wild mice. However, preference for one side of the maze was significant. Males were more attracted to female lures than females were to male lures. Activity of both sexes near conspecifics was significantly reduced over exposure time. We discuss the implications of these findings for the control of invasive mice.

Appendix 4

Shapira I, Walker E, Brunton D, Raubenheimer D 2013c. **Responses to direct versus indirect cues of predation and competition in naïve invasive mice: implications for management**. New Zealand Journal of Ecology 37: 33-40.

Abstract Many populations of invasive mice *Mus musculus* in New Zealand have experienced the removal of mammalian predators and competitors, with the consequence of mouse population irruptions. The effects of these removals on mouse foraging are largely unknown, yet this information is essential for developing and implementing better mouse control. We investigated the effects of direct and indirect predatory cues on foraging of free-ranging mice at a site where mammalian predators were eradicated 5 years previously. We used 17 stations, each containing four trays of millet seeds mixed thoroughly in sand, with three unfamiliar mammalian (a predator, a competitor, and a herbivore) odour treatments and a control (water), during the four phases of the moon. We measured mouse selectivity for treatment/control trays, giving-up densities (GUDs, a measure of food consumption), and tray encounter rates. Foraging by mice was not affected by odour cues from any of the unfamiliar mammals. Moonlight intensity, however, affected mouse foraging, with higher GUDs being recorded on brighter moon phases (full and waxing > new and waning) during the first night of the trials. This effect was less pronounced during the second night. Resource encounter rates were also affected, with the proportion of trays foraged lower during the brighter phases of the moon on both the first and second nights. We suggest that coordinating management efforts according to the phases of the moon has the potential to improve mouse control and reduce bait wastage.