

**THE INFLUENCE OF SHIP RATS (*RATTUS  
RATTUS*) ON THE HABITAT PREFERENCES  
OF THE HOUSE MOUSE (*MUS MUSCULUS*)**

By

Benjamin Hancock

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## Abstract

As methods and successes of *Rattus rattus* (ship rat) control progress, particularly in island environments, the importance of managing *Mus musculus* (house mouse) increases. *M. musculus* can negatively impact on a variety of native fauna and flora, potentially creating long term cascading effects. *M. musculus* populations benefit with the reduction in *R. rattus* abundance and recover sooner from pest control programs. This three-part study investigated the habitat utilisation of *M. musculus* and how their relationship with *R. rattus* influences their habitat preferences. Firstly, hypotheses about the habitat preferences of *M. musculus* were tested over a landscape scale to determine the features of the environment most important to their distribution. Then the direct effect of *R. rattus* presence on *M. musculus* habitat-use was investigated in arena trials. Lastly, in the same arenas, canopy cover was tested as an indirect cue for *M. musculus* to evaluate the presence of *R. rattus*. Across 32 sites, *M. musculus* were the most abundant in warm dry habitats. North facing slopes and rank grass cover were the features of the environment that had the strongest relationship with abundance. In arenas *M. musculus* foraging activity was 52% lower in patches of short grass when *R. rattus* scent was present but foraging in rank grass and bare ground was not altered, suggesting activity was suppressed not competitive displacement. There were no significant changes in *M. musculus* foraging behaviour between different canopy treatments. Although a trend of nocturnal foraging activity dropping 26% when high canopy cover was over short grass compared to short grass patches with lower or no canopy treatments may indicate a risky habitat. *M. musculus* use of dense ground cover was common theme in this study and in the literature. *R. rattus* do influence the habitat selection of *M. musculus* though this was with direct presence more than indirect cues.

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# **Chapter 1:**

## **Introduction**

Communities are complex networks of interacting species where even measuring and understanding the relationship between two species is a challenge to ecologists. Yet understanding how species interact and how those interactions mediate their individual relationships with the physical environment is key to advancing ecological science. Predator-prey and competitor relationships are known to modify the distribution and abundance of species (Nicholson 1933, Brand *et al.* 1976, Legendre and Fortin 1989, Lima 1998). Often these relationships are obvious but there are many other relationships that are too subtle and difficult to measure in natural systems.

New Zealand poses a unique opportunity to investigate vertebrate species interactions in a comparatively simple system because a limited number of exotic species were introduced during human colonisation. Ordinarily these species live in more biodiverse and complex communities (Schoener 1983, Blackwell and Linklater 2003, Blackwell 2005). As such, New Zealand provides a grand natural laboratory to investigate community dynamics in a way not available elsewhere. Furthermore, experiments with these invasive species are not as limited as work with native species, and the work has the practical application for improving invasive species management.

Invasive species are a global problem in ecosystems whether they are aquatic or terrestrial, island or continental (Dulloo *et al.* 2002, Andersen *et al.* 2004, Buckley 2008). Not only are native environments threatened but they have social and economic implications for human communities (Juliano and Philip Lounibos 2005, Pimentel *et al.* 2005). Approximately 6% of species on the IUCN Red List are known to be negatively impacted by naturalised exotic species, habitat loss is the main contributor (33%) to species decline, followed by exploitation (7.5%) (Gurevitch and Padilla 2004). Commensal rodents are particularly successful invasive species

(Atkinson 1996), their historical proximity with humans has meant that they have spread throughout the world and occur in every terrestrial region except polar regions (Ruscoe and Murphy 2005). Although, rodents have impacted on native species worldwide, they have been particularly damaging in island ecosystems (Towns *et al.* 2006).

New Zealand has been severely impacted by the arrival of rodents. Terrestrial mammals were absent from New Zealand prior to human arrival, except for three species of bats (Daniel 1990). The native species of New Zealand were vulnerable to introduced mammals because of the absence of mammalian predators and competitors in their evolutionary history (Holdaway 1989). Rodents contributed to and caused species decline, extinctions and habitat restrictions (Saunders and Norton 2001) and many native species became restricted to mammal-free offshore islands (Diamond and Veitch 1981, Towns and Daugherty 1994).

Four species of rodents became established in New Zealand, all from the Murid family. The first species, *Rattus exulans* (Polynesian rat, kiore, 60-80 g), arrived with Maori settlers as the first exotic mammal (Wilmshurst and Higham 2004), although the timing of this is debated (Holdaway and Beavan 1999, Wilmshurst and Higham 2004). McGlone (1989) proposes that predation by *R. exulans* was one of four main pre-European anthropogenic impacts on New Zealand's native species. With the arrival of Europeans three more species colonised New Zealand from approximately 1770 onwards (O'Donnell 1996): *R. norvegicus* (Norway rat, 200-300 g), *R. rattus* (ship rat, 120-160 g), and *Mus musculus* (house mouse, 15-20 g).

The house mouse in New Zealand was thought to be *M. musculus* (Ruscoe and Murphy 2005) but shares characteristics with *Mus domesticus* (Efford *et al.* 1988) and

this uncertainty has yet to be resolved (Ruscoe and Murphy 2005). *M. musculus* and *R. rattus* are the most widespread rodent species throughout New Zealand (Innes 2005b, Ruscoe and Murphy 2005). *R. norvegicus* distribution is more restricted being usually commensal or in proximity to bodies of water (Innes 2005a) and the range of *R. exulans* is probably restricted through competition with the other three rodent species (Taylor 1975).

The decline and extinction of some of New Zealand's flora and fauna is largely attributed to *R. rattus*. For example, in 1962 when *R. rattus* invaded Big South Cape Island off the coast of Stewart Island (Bell 1978) it caused the complete extinction of the *Xenicus longipes variabilis* (Stead's bush wren), *Coenocorypha aucklandica iredalei* (Stewart Island snipe), and *Mystacina robusta* (greater short-tailed bat). Additionally, four bird species and one bat species became locally extinct. *R. rattus* also eat invertebrates, birds, eggs and plant material, and destroy flowers and seeds (Ecroyd *et al.* 1995, Innes and Barker 1999). The direct and severe impact of *R. rattus* has meant that they have been a particular focus of pest management and eradication in New Zealand and globally (Murphy *et al.* 1998b, Basse *et al.* 2003, Towns *et al.* 2006), and over the last forty years the methods for controlling, eradicating and excluding *R. rattus* have improved (Towns and Broome 2003, Towns *et al.* 2006, Day and MacGibbon 2007).

*M. musculus* populations have repeatedly been shown to benefit from the removal of *R. rattus* (Innes *et al.* 1995, Miller and Miller 1995, Caut *et al.* 2007) because they rebound from control techniques sooner than other species due to their shorter life history (Innes *et al.* 1995, Ruscoe and Murphy 2005). *R. rattus* are generally considered not to be predators but dominant competitors of *M. musculus* (Brown *et al.* 1996, Yom-Tov *et al.* 1999, Sweetapple and Nugent 2005, Caut *et al.*

2007), they rarely occur in *R. rattus* diet even when *M. musculus* has been provided as food in captivity (Daniel 1973, Miller and Miller 1995). There is considerable overlap in the two species diets including seeds, invertebrates and plant matter (Miller and Miller 1995, Ruscoe 2001, Sweetapple and Nugent 2007) but an apparent habitat separation in New Zealand forests. *R. rattus* occupy arboreal habitats with continuous canopy and *M. musculus* are abundant in habitats with dense ground cover and broken canopy (Hooker and Innes 1995, King *et al.* 1996).

While there has been an emphasis on *R. rattus* control because of the damage they do, *M. musculus* are not innocuous. *M. musculus* are seed predators which can have large scale implications for ecosystems by limiting the recruitment of some plant species and altering the regeneration and succession dynamics of native forests (Wilson *et al.* 2007). Their competition for seed and depredation of native seed dispersers like *Hemidenina crassidens* (tree weta) may also limit dispersal of seeds (Duthie *et al.* 2006). *M. musculus* also impact on a variety of New Zealand's species, depredating and depressing lizard populations (Newman 1994, Lettink and Cree 2006), destroying bird eggs (Alterio *et al.* 1999), preying on invertebrates (Miller and Miller 1995, Fitzgerald *et al.* 1996) and the large *Paryphanta busbyi wattii* (kauri snail) (Stringer and Montefiore 2000), and even eat the eggs of *Galaxias maculatus* (inanga, whitebait) (Baker 2006).

*M. musculus* impacts can also be indirect. A common example is the increased predation of *Mohoua ochrocephala* (mohua, yellowhead) after mast seeding years in *Nothofagus* forest (King 1983, O'Donnell *et al.* 1996, O'Donnell and Phillipson 1996, White and King 2006). *Nothofagus* forests have heavy seeding years (mast years) with little seed production during the intervening years (Schauber *et al.* 2002). On *Nothofagus* mast years there are irruptions of *M. musculus* populations, although this

may not be directly due to seed predation but an abundance of *Tingena epimylia*, a litter feeding moth that features commonly in *M. musculus* diet (Fitzgerald *et al.* 1996). The *Mustela erminea* (stoat) population increases with the abundance of *M. musculus* for prey but after the mast seeding ends the *M. musculus* population declines rapidly (King 1983, King and White 2004). With the numerical increase of *M. erminea*, a greater portion of the threatened endemic *M. ochrocephala* population is affected causing a short-term, but catastrophic, decline in their survival and nesting success (King 1983, O'Donnell 1996, O'Donnell and Phillipson 1996).

Population increases of *M. musculus* with the reduction in *R. rattus*, coupled with the host of threats that *M. musculus* present, mean they should be considered a serious threat to native ecosystems. With the control of introduced mammals, particularly *R. rattus*, the implications throughout the exotic mammal community and flow-on effects from manipulating these species need to be considered (Zavaleta *et al.* 2001). The dynamics between *M. musculus* and *R. rattus* need to be investigated further (Innes *et al.* 1995, Brown *et al.* 1996, King *et al.* 1996, Sweetapple and Nugent 2005, Caut *et al.* 2007) to clarify whether habitat-use by *M. musculus* is altered by *R. rattus* direct displacement, or if *M. musculus* take indirect cues from features of the habitat to avoid encounters with *R. rattus* (Orrock *et al.* 2004). The investigation of habitat selection cues by rodents has often been related to predators (Kotler *et al.* 1988, Brown 1992, Dickman 1992, Arthur *et al.* 2004) not competitors (Schoener 1983, Abramsky *et al.* 2001, Jones *et al.* 2001, Kotler *et al.* 2001).

To further our knowledge of the competitive dynamics between *R. rattus* and *M. musculus* a three part study was undertaken to; 1) establish the habitat preferences of *M. musculus* on a landscape scale across a variety of habitat types in a natural setting, 2) observe how the presence of direct *R. rattus* cues affect the habitat

preferences of *M. musculus*, and 3) whether *M. musculus* mediate interactions with *R. rattus* by using features of their environment, particularly the canopy, as an indirect cue of *R. rattus* presence.

In Chapter 2 *M. musculus* habitat selection was investigated. I set out survey sites across the South Wairarapa District in a variety of exotic and native habitats. I used covered and uncovered feed trays to measure giving up densities (GUDs) (Brown 1988) at each site. Trapping was used to index *M. musculus* abundance at each site and features of the habitat measured so that preferences could be related to aspects of their ecology and their surrounding environment. I used an information theoretic approach to test hypotheses about the habitat preferences of *M. musculus*.

In Chapter 3 the influence of *R. rattus* scent on *M. musculus* habitat-use was examined in large outdoor arenas. Six arenas were built to house a single mouse each with three even sized patches of different ground cover within them: long rank grass, short trimmed grass, and bare ground. Quitting harvest rates (QHR) were used to gauge changes in foraging activity in each habitat patch with and without *R. rattus* scent.

In Chapter 4 the same six arenas were used to investigate the use of indirect cues by *M. musculus* to evaluate *R. rattus* presence. The *R. rattus* scent was removed and varying heights of canopy treatments placed over arenas: high canopy (2 m approx.), low cover (1 m approx.), and no canopy cover. QHRs were used to test whether *M. musculus* used canopy cover as an indirect cue for evaluating *R. rattus* presence.

My overall hypothesis is that the direct presence of *R. rattus* will alter *M. musculus* habitat-use and that to a lesser degree *M. musculus* will use high canopy as an indicator of *R. rattus* presence. *R. rattus* influence *M. musculus* populations (Innes *et*

*al.* 1995, Miller and Miller 1995, Caut *et al.* 2007) so it would seem highly likely that the presence of *R. rattus* would alter their behaviour. Although Dickman (1992) stated that *M. domesticus* did not value vegetation over 1 m, *R. rattus* are aboreal (Hooker and Innes 1995) and play an important role in *M. musculus* ecology so it could be beneficial for *M. musculus* to consider canopy cover as an indicator of *R. rattus* occurrence.



**Chapter 2:**  
**Landscape habitat preferences of house mice**  
**(*Mus musculus*)**

## Abstract

Knowledge of the relationships within a community is useful when managing a species, whether for improving, maintaining or removing a population. *Mus musculus* (house mouse) is an introduced rodent that detrimentally affects New Zealand's native flora and fauna. Management of *M. musculus* can improve with further understanding how they use their surrounding environment. The giving up density (GUD) method was used to give values relative to predation risk and food availability in the surrounding environment. GUDs, *M. musculus* abundance, and physical features habitat of the habitat were measured at 32 sites across the South Wairarapa District. Unfortunately, GUD values were found not to be representative of *M. musculus* activity. Using Akaike's information criterion (AIC), the strength of hypothetical models of *M. musculus* ecology for explaining the abundance patterns of *M. musculus* were compared. The use of rank grass model was the strongest accounting for almost 60% of the support of the models. The next two strongest models were the suitable breeding habitat and topography models (12.5% and 12.1% of the support respectively). Models of low and high ground cover were the next models. No single model clearly explained *M. musculus* abundance variation but rank grass cover and slope aspect both featured strongly in the four strongest models. Rank grass ground cover at 0.25m and north facing slopes were positively correlated with abundance and sites facing northeast around to the west were negatively correlated. This is likely due to more exposure to the sun and the warm dry north-west wind. This study presents rank grass cover and north facing slopes as the strongest predictors of *M. musculus* abundance from the parameters examined. Further work is required on how other species affect *M. musculus* distribution and behaviour.

## Introduction

How species are influenced by their environment is a key question in ecology. Biotic and abiotic factors modify population dynamics, predator-prey relationships, interspecific competition, and even the physical habitat itself (Ricklefs and Miller 1999). Understanding the relationships of a single species to its environment contributes to the overall knowledge of a community and benefits species management, whether for conserving, harvesting or eradication.

Invasive pests are a global problem but especially in island ecosystems (Towns *et al.* 2006). Rodents are adept at colonising new ecosystems and New Zealand is a prime example of this (Atkinson 1996). Management of exotic mammals is an ongoing and costly process (Innes and Barker 1999, Brown and Ulrich 2005) with labour costs making up a large portion of pest control programs (Innes *et al.* 1995, Brown and Ulrich 2005). Increasing the efficiency and scope of pest animal management could be achieved with improved understanding of the target species to enhance the implementation of tools such as poisoning and trapping.

*Rattus rattus* (ship rats) and *Mus musculus* (house mice) both negatively impact on New Zealand's native flora and fauna through predation and competition (King 1983, Newman 1994, Fitzgerald *et al.* 1996, Baker 2006), although more pest management effort is targeted at *R. rattus* (Towns *et al.* 2006). *M. musculus* populations have been reported to increase after *R. rattus* control in New Zealand forests (Innes *et al.* 1995, Ruscoe 2001, Sweetapple and Nugent 2005, Caut *et al.* 2007, Sweetapple and Nugent 2007). As the management of *R. rattus* improves, the importance of effective *M. musculus* control increases (Towns and Broome 2003, Caut *et al.* 2007). To increase the efficiency of *M. musculus* control programs, their habitat preferences and population success in different habitats should be understood.

The giving up density (hereafter GUD) method (Brown 1988) can be used to compare the habitat preferences of *M. musculus*. Trays are filled with a substrate with food mixed through. As the forager depletes the food resource greater search effort is required to find the same quantity of food. The method assumes that an individual will no longer feed from the tray when the food reward does not justify the effort or risk of further searching compared to foraging in the surrounding environment (Charnov 1976, Brown 1988). The GUD is the level at which the harvester quits searching in the tray, in this way the GUD reflects the habitat preferences of *M. musculus* because in better quality or higher risk habitat the GUD will be higher.

Linking the observed patterns of *M. musculus* abundance, perceived predator risk and food availability to particular features of the environment improves our understanding about which elements of their environment play important roles in their habitat-use behaviour. Hypothetical models can be made from the habitat features that pertain to a certain aspect of *M. musculus* ecology. Parameters within the hypothetical models (predictors) that are strongly supported by the observation data may become apparent as habitat preferences.

It would be useful to know the habitat preferences of *M. musculus* when eradicating *M. musculus*. For example, assume dense rank grass was positively related to *M. musculus* abundance and negatively to predation risk, then management plans could then focus on habitats with high grass cover because they could be reservoirs of *M. musculus* and sources of immigrants during population expansion.

I expect that sites with plentiful ground cover will have higher numbers of *M. musculus*, lower perceived predation risk (Dickman *et al.* 1991, Dickman 1992, King *et al.* 1996, Arthur *et al.* 2004), and potentially high food availability because the cover provides a substrate to accommodate invertebrates (Miller and Miller 1995,

Fitzgerald *et al.* 1996). Variations in this association are expected to be caused by the presence of mature fruiting trees that provide food and aerial cover that would also restrict avian predators, and features that provide a less severe micro-climate and lower rates of habitat disturbance.

## Methods

### Study Area

The South Wairarapa District in the south eastern corner of North Island, New Zealand (Figure 2.1) has a seasonally mild, temperate climate with an average annual rainfall of 979 mm and 1915 sunshine hours. In spring and summer Wairarapa weather is dominated by winds from mountain ranges to the north-west and west that are warm and dry. During the autumn and winter cool and wet weather arrives from the south and east. Average January and July temperatures are 17.8 °C and 7.5 °C respectively (Tait *et al.* 2002, National Climate Database, National Institute of Water and Atmospheric Research Ltd (NIWA)).

The South Wairarapa has three distinct areas; mountain ranges to the west with peaks reaching to 1571 m above sea level (Mitre peak) in the Tararua Forest Park, an eastern hill range which reaches 983 m above sea level (Mt Ross) in the Aorangi Forest Park, and the central Wairarapa Valley running between the two ranges (Marra 2003). The Rimutaka and Tararua Forest Parks comprise the western boundary. These are forested by mixed podocarp-broadleaf species with areas of *Nothofagus* species (Moffat and Minot 1994, Rogers and McGlone 1994). Catchments on the Wairarapa side of these ranges drain east into the main Wairarapa

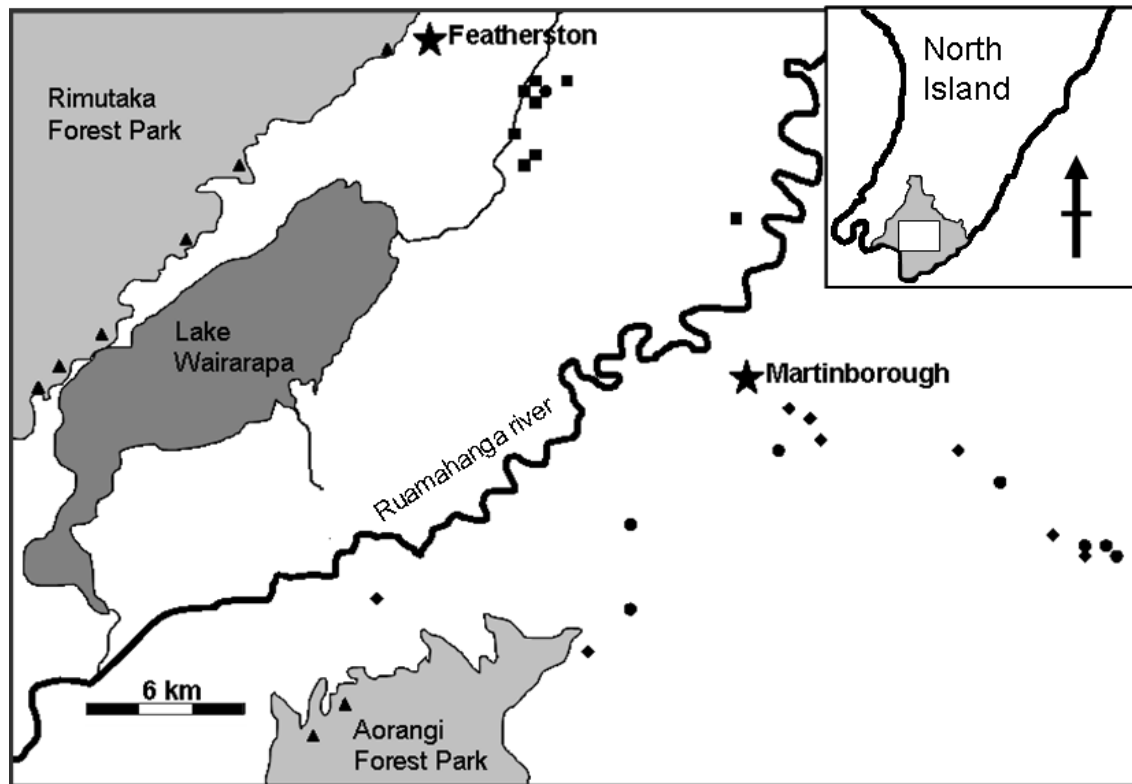


Figure 2.1 Distribution of survey sites across the South Wairarapa District (location in North Island, New Zealand, shown in top-right insert). Rimutaka Forest Park is in the north-western corner with Lake Wairarapa below. The Ruamahanga runs from north-east to south-west. The Aorangi Forest Park is bottom centre and Martinborough is east of centre. Exotic pine forest (◆), farm shelter belt (●), native forest fragment (■), and continuous native forest (▲) sites are indicated.

Valley to contribute to the Ruamahanga River and Lake Wairarapa. The eastern hills range from the edge of the main valley to the eastern coastline of the province, gradually building from gentler foothills in the west to higher and steeper hills on the coast. Dry stock farming is the dominant land use in the eastern hills with a scrub belt running along the coastal edge of the range. The Ruamahanga River is the main river that flows the length of the valley and is chiefly fed by tributary rivers from the western mountain ranges. The Wairarapa Valley is low lying area made up of remnant river terraces, fans and drained floodplains and is principally modified for agriculture and horticulture.

### **Habitat types and survey sites**

Two exotic and two native vegetative community types varying in history, conditions and size were used for the study. These types were; (1) exotic pine forest, (2) farm shelter belts, (3) native forest fragments, and (4) continuous native forest (Figure 2.1).

Exotic pine forests were defined as uniform man-made forests of conifers exotic to New Zealand. *Pinus radiata* was the most prevalent species used in the Wairarapa and all of the exotic pine forest survey sites used occurred in forests of this species. Sites were chosen in pine plantations greater than 100 m wide so that sites were representative of the habitat and influence from neighbouring habitats was reduced (Young and Mitchell 1994, Herbst *et al.* 2007). These forests are generally in the eastern hills and sparse in the main valley or western ranges. Pine forests were often fenced to exclude livestock though some were grazed sporadically. The trees were planted in large cohorts and then thinned and pruned such that under more established forests there was often debris from branches and surplus trees.

Farm shelter belts were plantings a few metres wide of hardy exotic and some native species along pasture boundaries between fields. Sites selected were uniform in

width and livestock were excluded with fences. Shelter belts were planted from the eastern hills to the western side of the main valley on arable land and widely used to protect agricultural and horticultural land from strong winds and to provide shelter for livestock.

Native forest fragments were areas with a minimum radius of 50 m that were predominantly podocarp-broadleaf native bush surrounded by modified land. Fifty metres was considered to be a sufficient distance to reduce the influence of neighbouring habitats (Young and Mitchell 1994, Herbst *et al.* 2007). All of these areas were fenced to exclude livestock. A majority of the native forest fragments used are designated “key native ecosystems” by the Greater Wellington Regional Council as part of a program managing remnant native habitats on privately owned land. All of these fragments occur in the central Wairarapa Valley. The number and distribution of remnants were limited because of the low number of remnants that remained and access across private land was not always granted.

Continuous native forests were defined as predominantly native forest that was part of, or continuous, with the Rimutaka Forest or Aorangi Forest Parks. These sites were usually *Nothofagus* sp. forest but not exclusively. Some sites were broadleaf forest and earlier successional forest.

Thirty-two survey sites were distributed amongst the four different habitat types throughout the South Wairarapa District (Figure 2.1). For each of these habitat types, eight survey sites were spread as much as possible across the landscape such that all could be sampled within a day to reduce the weather variation within sampling events. In a pilot trial, 10 sites for each habitat type were initially selected but it was not possible to sample each of these sites in one day so eight sites were selected for each habitat type. No survey sites were located in the same forest remnant, plantation or



shelter belt. It was not possible to use separate unconnected habitat patches for the continuous native forest survey sites. Nevertheless, 1 km was used as a minimum distance between each site as mice are unlikely to travel this distance and use more than one survey site in a night such that sample sites are independent (Fitzgerald *et al.* 1981, Krebs *et al.* 1995). Once a suitable forest, remnant, plantation or shelter belt was selected the survey site was identified by using random compass bearings and numbers for short distances to locate a site at least 50 m from the habitat edge.

### **Survey site layout**

At each survey site two round trays were placed 10 m apart (Hughes and Ward 1993, Kotler *et al.* 2001). The distance between trays ensured that an individual mouse would assess and feed from each individually but close enough so that the mouse could visit both trays over the period of a trial. Feed trays were cut from 200 mm diameter dark green plastic buckets at approximately 35 mm depth so the volume of trays was slightly larger than 1 litre.

If the survey site was on sloping ground then the trays were placed laterally across the slope. On negligible slopes the trays were organised parallel to the nearest habitat edge. Each tray was dug into the ground so that its upper edge was level with the ground surface and so the tray provided no additional cover, thus removing the possibility that the tray provided an unintended refuge for mice (Gray *et al.* 2000). On sloping ground, the tray was dug down until tray was level with the ground down slope. The soil was removed upslope of the tray so that animals could approach from all sides.

One tray was left open while the other was covered. The covered tray was randomly selected then covered with an approximately 400 mm branch of dry *Kunzea ericoides* (kanuka) and six 300 mm fronds of *Pteridium esculentum* (bracken). The

stalk of the kanuka branch was wedged into the ground so that its foliage overhung the tray and supported the sprigs of bracken. This created a gap >30 mm between the cover and tray substrate so that mice could manoeuvre once under the cover (Kotler *et al.* 1991).

Three Victor® professional mouse traps were placed at each survey site (Wiener and Smith 1972). One trap was placed centrally between the feed trays and the other two within 1 m of each feed tray. Each mouse trap was wired onto a piece of untreated kiln dried timber. A 105 x 70 x 50 mm cage made of fine aluminium 12.5 x 12.5 mm mesh was placed over each trap. A 35 x 25 mm opening in the cage at the trigger-pedal end of the trap (King *et al.* 1996, Choquenot and Ruscoe 2000) was made so that the mice could only enter the trap from the trigger end. The cage prevented non-target animals getting caught in the trap. The traps were baited with quarter of a button of Nestle® chocolate melts fixed onto the pedal of the trap, and then the trigger pin was set to sensitive on the trigger pedal. All pieces of equipment were placed unset at least five days prior to the trials beginning to allow rodents to habituate to them (Brown *et al.* 1996).

## **Feed trial protocol**

*M. musculus* GUDs were used to gauge *M. musculus* perception of predation risk and the food availability of the surrounding habitat (Brown 1988). Trays were filled with a mix of substrate and a known amount of particulate food. Substrate limits the rate at which *M. musculus* find and harvest the food. As the ratio of food to substrate decreases, the rate of harvesting decreases exponentially to an asymptote. The final amount of seed that was left in the substrate was the density of seeds at which *M. musculus* quit searching the trays, i.e. the giving up density. The GUD for individual trays was influenced by the value and risk of the surrounding environment. The

method assumes that if a habitat patch has low predation risk then individuals will be inclined to remain there longer and deplete the food resource further. Conversely, if the surrounding environment has high food availability then individuals will deplete the tray less because of the other feeding opportunities available. Both scenarios are preferable situations though they would create opposing GUDs.

By pairing trays at the site and reducing predation risk with added cover at one of the trays the influence of perceived predation risk on foraging behaviour can be investigated. At trays where there was no added cover, mice are prone to the inherent predation risk of the surrounding environment. Predation risk can be inferred from the difference in GUDs between uncovered and covered trays, and food availability from GUDs of covered trays where predation risk is reduced.

Feed trays were filled with 1 litre of Hudson® attapulgate pet litter, mixed with 5 g of Sharpes® feed wheat. The pet litter was used because it limited the feed tray filling with water and was easier to sort through when wet compared to other substrates like sand. Care was taken to disturb the surrounding area as little as possible when approaching and leaving the trays. All feed trays were stocked on the same day and left for five consecutive nights in each trial. The wheat was sifted out of every tray on the day after the fifth night and seeds put into an individual ziplock® bag labelled with the trays identity number and date. The litter was returned to the tray. Trials lasting five nights were used to give ample opportunity for the feed trays to be depleted to the GUD.

### **Preliminary trial**

A preliminary trial was conducted for three nights from 13 September 2008 to test how many survey sites could be sampled in a day and whether there would be any activity at the feed trays at each site. The methods previously described were followed

except the wheat was not mixed through the litter but 10 seeds instead placed on top of the litter. In this preliminary trial ten survey sites were placed in each of the four habitat types. It proved not possible to visit all 40 survey sites in one day. Five survey sites that took too much time to access were removed and three were randomly selected for removal to reduce the total number of survey sites to 32. Twenty-eight of the 32 sites had some activity with at least a few of the seeds removed.

## **Timeline**

Trials were conducted during September and October 2007. Feed trays were stocked on 16 September for the first trial and remaining seeds collected on 21 September. A second trial was conducted immediately after the first trial, with each tray being re-stocked. The second trial was completed on 26 September. Three nights of mouse trapping began after the second trial on the night of 27 September. Seeds that were removed during each of the three trials were dried in an oven at 60 °C for seven hours and weighed to the nearest 0.01 g (Orrock *et al.* 2004).

## **Habitat surveys**

A range of micro-habitat features were measured (King *et al.* 1996) at each of the 32 survey sites to determine the habitat preferences of *M. musculus*. Surveys were done using a modified reconnaissance plot of 15 m diameter (King *et al.* 1996). Surveys of shelter belt sites were truncated where they met the habitat's edge. Canopy height, canopy cover, altitude, slope aspect, slope gradient, the percentage and type of ground cover, and distance from survey site to the nearest change in ecotype were the features measured.

Average canopy height was initially measured by using a clinometer to the nearest metre. The canopy height was gained by walking away from the tree forming

part of the canopy until the sighting angle through the clinometer was  $45^\circ$ . The measured distance from the base of the tree plus the height of the observer was equal to the height of the canopy.

Canopy density was measured with a convex densiometer by recording the percentage of open sky blocked by vegetation at 1.35 m above the ground. A random bearing was taken by throwing a pen in the air and following which direction it pointed. From this direction another three readings were taken at  $90^\circ$  from each other at the same spot. Twenty-four even squares were etched into the face of the densiometer. Four equally spaced points were visualised in each square and every point that was covered by vegetation was counted. The count was averaged over the four readings and then multiplied by 1.04 to give percent canopy cover.

Altitude in metres above sea level was recorded from the handheld Global Positioning System (GPS) (Garmin *etrex*) and confirmed against a topographical map.

Slope aspect was gauged by estimating the general direction of the slope by eye and then taking a compass bearing to the nearest whole degree.

Slope gradient was taken on the same bearing as the aspect of the slope using a clinometer. Measurement was taken by standing 2.5 m up the slope from the centre of the survey site and looking through the clinometer at a reference point at eye level 2.5 m downhill of the survey site. If no reference point was available, then a stick that reached eye level was anchored in the ground as a guide.

Percentage ground cover was estimated at 0.25 m and 1 m heights for; vascular plants, rank grasses ( $>150$  mm), short grasses ( $<150$  mm), leaf litter, and exposed rock or soil.

Distance to the next ecotype was measured from the centre of the survey site to the nearest boundary of the next ecotype with the handheld GPS. Half the width of a shelter belt was measured in place of the distance to nearest ecotype.

## Analysis

### Giving up densities

The use of GUDs as measure of perceived predation risk and food availability for *M. musculus* was checked by conducting Student's t-tests in Microsoft Excel®.

Comparing the GUDs of covered with uncovered trays and sites with and without *M. musculus* would clarify if the GUDs were representative of *M. musculus* foraging activity and if the additional cover reduced predation risk. The second GUD trial was discarded because some trays were disturbed so the sample set was not complete.

### Mouse abundance

An index of abundance (IA) was used to gain a value of mouse abundance at each site (Cunningham and Moors 1993). Based on the percentage of mice caught per possible trapping effort, a measure of relative abundance was obtained.

Trapping effort and rodents caught per 100 trapping nights is calculated by:

$$\text{Index of abundance (IA)} = \frac{\text{Captures} \times 100}{\text{Corrected trap nights}}$$

$$\text{Total trap nights} = \text{No\# traps set} \times \text{No\# of nights}$$

$$\text{Trap nights lost} = \frac{(\text{Captures} + \text{Sprung, empty traps})}{2}$$

$$\text{Corrected trap nights} = \text{Total trap nights} - \text{Trap nights lost}$$

## Habitat models

Eight *a priori* candidate models were developed from hypotheses using combinations of habitat features as predictors of *M. musculus* habitat preferences. These models were then ranked in order based on the predicted importance of the model in *M. musculus* habitat selection. The eight hypotheses were;

1. Rank grass use. This hypothesis only included rank grass cover at 0.25 m as a predictor of dense ground cover which has been ascribed as being important for providing cover from predation (Dickman *et al.* 1991, Dickman 1992) and correlated with *M. musculus* abundance (King *et al.* 1996).

2. High ground cover. This hypothesis included the percentage of ground covered at 1 m by short grass, rank grass and vascular foliage as predictors. The model provides the benefits of ground cover as well as immediate aerial cover from predators of *M. musculus*.

3. Food availability. This hypothesis included habitat type, canopy height, and leaf litter cover and rank grass cover measured at 0.25 m as predictors in the model. The type of habitat and age of forest could influence the type and amounts of foods available and the seed bank can be affected by the age and stage of succession of the site (Bossuyt *et al.* 2002). Leaf litter provides a substrate for *M. musculus* to forage for invertebrates and rank grass is another source of seeds. Both seeds and invertebrates have been shown to be large components of *M. musculus* diet (Fitzgerald *et al.* 1996). With more food available, a denser population would be able to be sustained within the habitat.

4. Low ground cover. The hypothesis included percentage of ground covered at 0.25 m by short grass, rank grass and vascular foliage as predictors. These three habitat features measure cover from predators and competitors on the ground that a

mouse could move through. This is a similar model to the high ground cover model but without the low aerial cover and includes information on more types of ground cover than the rank grass model.

5. Cover from aerial predators. This hypothesis included vascular ground cover at 1m, canopy height, canopy density, and habitat type as predictors. These variables would provide some protection from aerial predators except for habitat type. Shelter belts may have had dense canopy cover directly above but little cover would be provided from the edges because they were often narrow strips so habitat type was included in the model.

6. Suitable breeding habitat. This hypothesis included slope gradient, slope aspect, percentage of ground cover at 250 mm by rank grass and woody debris as estimable variables. These factors included aspects that contribute to a warm, dry and stable habitat. A moderate gradient would offer drainage and stability, and north facing sites would receive more sunlight, creating a location where nests could be warmer, dryer and remain intact until the young leave.

7. Topographical features. This hypothesis included the aspect of the slope, slope gradient, and altitude as predictors. Aspect is used as gauge for exposure to different prevailing weather conditions with dry warmer air arriving from the northwest and colder wet weather from the south (Tait *et al.* 2002). The slope gradient gives information of the sites drainage ability which may have been important for a small ground dwelling mammal.

8. Habitat heterogeneity. This hypothesis included the distance to eco-tone, next eco-type, percentage of canopy made up by the dominant species, canopy density, and number of species present in the canopy as predictors. These habitat



features contributed to the physical variability and biodiversity of the site which may promote mouse abundance with a more complex habitat structure and composition.

### Information theoretic analysis

An information theoretic analysis was used to find the candidate model that best explains abundance of *M. musculus* or habitat preference with the information available (Burnham and Anderson 2002). Each survey site was treated as a single replicate. GUDs were used as a measure of *M. musculus* habitat preference and IA as a measure of *M. musculus* abundance at each survey site. A general linear model (GLM) was conducted using R 2.7.2 (R Foundation for Statistical Computing, Vienna, Austria) for each hypothesis to acquire an Akaike's information criterion (AIC) for each candidate model.

Due to the small sample size of the candidate models ( $n = 32$ ) a second order Akaike's information criterion ( $AIC_c$ ) was used because  $n/K < 40$  (range  $1 < K < 11$ ) (Burnham and Anderson 2002). Each model was then ranked using the lowest difference in  $AIC_c$  ( $\Delta AIC_c$ ) from the model with the smallest  $AIC_c$ . The lower the  $\Delta AIC_c$  value the more comparative strength the model has. Where  $\Delta AIC_c \leq 2$  models have convincing support from the data (Burnham and Anderson 2002). The Akaike weight ( $w_i$ ) is the relative support for each of the models and conveys the likelihood of the model explaining variation in *M. musculus* abundance between the survey sites (Burnham and Anderson 2002).

The IA and GUDs were entered as scale dependent variables. The habitat features that were used in the model were treated as scale data, except for the data from the "next eco-type" and "habitat type" measurements that were treated as categorical. The raw bearing measurements for the aspect of a slope were transformed into categorical data because of the nonlinear nature of compass bearings. Slope

aspect bearings were placed into eight categories of 45°; north (338-022°), northeast (023-067°), east (068-112°), southeast (113-157°), south (158-202°), southwest (203-247°), west (248-292°), northwest (293-337°). Each category of data counted as an explanatory variable for the models they were used in. Slope aspect was not treated as 1 explanatory variable but 8 for each of the data categories.

## Results

GUDs were not different between covered and uncovered trays in the presence or absence of *M. musculus* (paired two sample for means Student's *t*-test, mice present  $P = 0.413$ , no mice present  $P = 0.370$ ). There was also no significant difference in GUDs between the sites with and without *M. musculus* (one tailed two sample assuming unequal variances Student's *t*-test,  $P = 0.179$ ) (Figure 2.2). Thus, GUD values are not conclusively representative of *M. musculus* foraging and could not be used as an indicator of mice habitat preference.

All models had some degree of support from the mouse abundance data except the aerial cover and food availability models ( $\Delta AIC_c > 10$ ). Rank grass use was the strongest model, accounting for over half of Akaike weight ( $w_i = 0.580$ ) though not clearly dominant compared to the other models ( $w_i < 0.9$ ). The next two

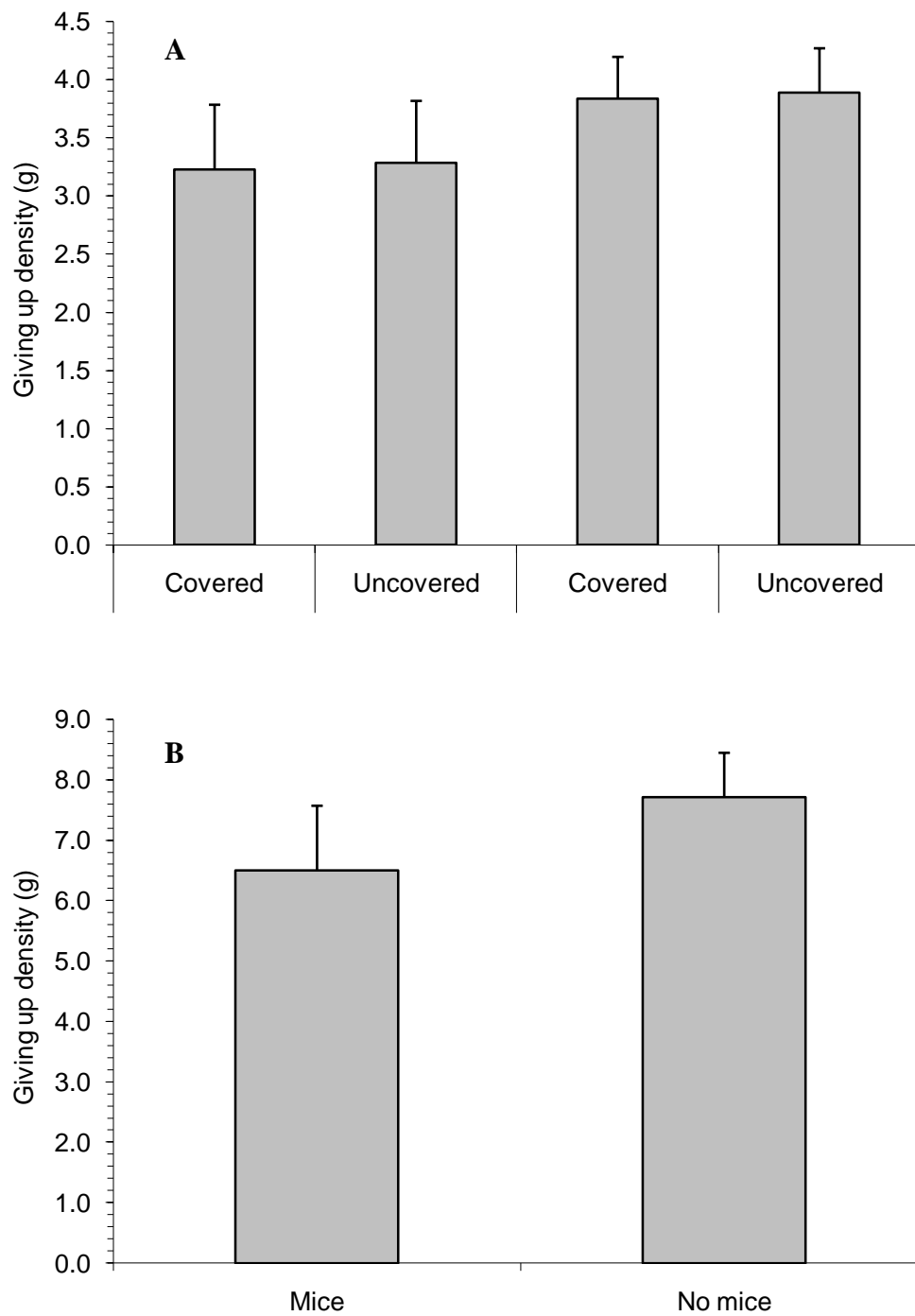


Figure 2.2. Giving up densities (GUD) across the South Wairarapa District of paired trays at 32 sites. A) The effect of additional cover over the tray at sites with *M. musculus* present and sites without *M. musculus* present. B) Combined covered and uncovered GUDs between sites with and without *M. musculus* present.

Table 2.1. Predicted rankings of candidate models against the actual ranking from lowest second order Akaike's information criterion ( $AIC_c$ ) values. Models with lower  $AIC_c$  values were supported more by the *M. musculus* abundance data. The models are not absolute explanations of habitat features or aspects of *M. musculus* ecology that are conducive to *M. musculus* abundance, they are the best explanation from the information gathered and hypothesis constructed.

Predicted ranking	Candidate models	K <sup>a</sup>	$AIC_c$	$\Delta AIC_c$	$w_i$
1	Rank grass	1	250.333	0.000	0.580
6	Breeding habitat	11	253.400	3.067	0.125
7	Topographical features	10	253.476	3.143	0.121
4	Low ground cover	3	254.057	3.724	0.090
2	Higher ground cover	3	254.557	4.224	0.070
8	Habitat heterogeneity	6	258.460	8.127	0.010
5	Aerial cover	7	261.366	11.033	0.002
3	Food availability	7	262.466	12.133	0.001

Notes:  $\Delta AIC_c$  is the difference between the smallest  $AIC_c$  and the models  $AIC_c$

$w_i$  is Akaike weight or relative probability that the model was the best for predicting *M. musculus* abundance

<sup>a</sup> the number of explanatory variables in the candidate model.

If categorical data was used then each data category was counted as an explanatory variable.

Table 2.2. Second order Akaike's information criterion ( $AIC_c$ ) of the common estimable parameters of the breeding habitat and topographical features models.

Estimable parameter	K <sup>a</sup>	$AIC_c$	$\Delta AIC_c$
Aspect <sup>b</sup>	8	240.563	0.000
Slope <sup>c</sup>	1	255.943	9.252

Notes: <sup>a</sup> the number of explanatory variables in the candidate model

<sup>b</sup> 45° categories of aspect for the slope

<sup>c</sup> gradient of the slope.

models best fitted to the data were suitable breeding habitat ( $\Delta AIC_c = 3.067$ ,  $w_i = 0.125$ ) and topographical features ( $\Delta AIC_c = 3.143$ ,  $w_i = 0.121$ ), with similar support from the data. Suitable breeding habitat and topographical features had a similar number of explanatory variables (Table 2.1) and share 9 parameters (8 were categories of slope aspect). Low and high ground cover models followed next ( $\Delta AIC_c = 3.724$ ,  $w_i = 0.090$  and  $\Delta AIC_c = 4.224$ ,  $w_i = 0.070$  respectively). Both models shared the same habitat features though were measured at different heights from the ground. The order of strength of these two models was reversed from what was predicted (Table 1), with low ground cover only having 2% higher weight of support. The data partially supported the habitat heterogeneity model as well ( $2 \leq \Delta AIC_c < 10$ ).

Rank grass was clearly the strongest single parameter for predicting *M. musculus* abundance (Table 2.1). It is probable that the explanatory strength for low and high ground cover models comes from their respective rank grass measures. The rank grass use model only featured the estimable variable for percentage of rank grass from 0.25 m and had 58% of the estimated explanatory power. Aspect of the slope and slope gradient were the common variables in the next two strongest models. A linear regression was conducted for both variables in R 2.7.2 (R Foundation for Statistical Computing, Vienna, Austria) to determine which or if indeed both parameters provided support to the two models. The large  $\Delta AIC_c$  of the slope gradient ( $\Delta AIC_c = 9.252$ ) asserts that slope aspect lends greater support to the topographical and breeding habitat models (Table 2.2), despite slope aspect having a larger number parameters ( $K = 8$ ). From the regression, north facing slopes were positively correlated with *M. musculus* abundance and the six slopes facing northeast around to west were all negatively correlated ( $P < 0.01$ ).

The four models best supported by the data were predominantly driven by the inclusion of slope aspect and rank grass cover as predictors. The cumulative Akaike weights of these four models was above the 0.9 ( $\Sigma w_i = 0.916$ ) threshold for explaining the majority of the variation in the data. While the cumulative weights was not as sound as model averaging (Burnham and Anderson 2002) this does indicate that the combination of slope aspect and rank grass cover from 0.25 m are the best estimable parameters of *M. musculus* abundance data.

## Discussion

The hypothesis most supported was the model of rank grass that only estimated rank grass cover at 0.25 m. The four models best supported by the data had a cumulative Akaike weight that would be sufficient to be a clear expression of *M. musculus* abundance. Each of those four models was largely contributed to by either the percentage of rank grass cover at 0.25 m or aspect of the slope at the survey sites. Only two of the candidate models, aerial cover and food availability, were not supported by the data to some extent ( $\Delta AICc > 10$ ) (Burnham and Anderson 2002).

Because slope aspect data was entered as 8 categories of data, each category was treated as a separate explanatory variable in the models. The only category of slope aspect not significantly correlated with *M. musculus* abundance was northwest facing sites. The north facing slopes were the only significant categories with positive correlations, likely due to these slopes being warmer and dryer. These conditions would not just be produced by higher exposure to the sunlight but the frequent dry northwest wind, particularly in October (Tait *et al.* 2002) when the trials were conducted. The other six significant aspect categories had negative correlations. The

lack of exposure to the sun and northwest wind would have made the environment colder and damper on these slope aspects.

*R. rattus* have been shown to be abundant on warmer steeper slopes (King *et al.* 1996). An overlap in use of warm, dry habitats by *M. musculus* and *R. rattus* could be mediated in two ways. King *et al.* (1996) established that in Pureora Forest Park, *M. musculus* and *R. rattus* used separate habitats: broken canopy and dense ground cover for *M. musculus* and continuous canopy for *R. rattus*. *M. musculus* were not found to be abundant on the warm dry slopes in King *et al.* (1996). This may have been caused by competitive exclusion by *R. rattus* (Brown *et al.* 1996, Caut *et al.* 2007) or *M. musculus* selecting micro-habitats that would limit direct interactions where their ranges overlapped with *R. rattus* (Dickman 1992, Orrock *et al.* 2004). The use of dense cover by *M. musculus* and other rodent species is widely documented (Dickman *et al.* 1991, Dickman 1992, King *et al.* 1996, Mandelik *et al.* 2003, Arthur *et al.* 2004).

The possible competition of these two species for warm and dry locations may have serious implications for native plants and animals adapted to these warmer dryer slopes (Holland and Steyn 1975, Wilson *et al.* 2007). The impacts of *M. musculus* on native species may have been under-estimated previously because *M. musculus* were competitively excluded by *R. rattus* (Caut *et al.* 2007). Removal of *R. rattus* from these warm dry locations may not provide relief for the native species communities because *M. musculus* could replace the *R. rattus*. Previously unregistered negative impacts of *M. musculus* may become prominent if activity in these areas increases after *R. rattus* eradication.

The suitable breeding habitat model may not have necessarily been a model exclusively explaining breeding habitat. The two significant estimable parameters of

the model could relate to fitness of the individual as well, particularly if one considers the timing of the study. The positive correlation with the warm dryer slopes may relate to the survival of individuals and the population during the colder period of the year (Hamilton 1942). The similarity between the suitable breeding habitat and topographical models is understandable considering the breeding habitat model contained 9 of the 10 explanatory variables of the topography model. The combination of amiable climate and refuge in rank grass provided the model with the second strongest correlation with *M. musculus* abundance. It was predicted that including features of ground cover and disturbance rates into a model with topography would create a model with more support than the topography model, though this increase was minimal.

Comparing both models that focussed on degrees of ground cover at different heights (0.25 m and 1m) showed that *M. musculus* abundance had a stronger correlation with lower patterns of ground cover. In Dickman (1992), vegetative cover above 1 m high did to provide cover for mice. The support from the mouse abundance data for the low ground cover model over higher ground cover supports Dickman (1992). Measurements for ground cover percentages mainly differed by more vascular cover being included at 1 m high. This was initially thought to have provided supplementary cover over the grass cover. If the vascular cover was not associated with *M. musculus* abundance and grass cover was (Table 2.1), then vascular cover over the grass would reduce the strength of the model by lowering the amount of grass represented.

Food availability and aerial cover were two models that were predicted to be strongly related to *M. musculus* occurrence (predicted rank: 3 and 5 respectively), but were the least supported by the abundance data (actual rank: 8 and 7 respectively).



Perhaps more direct measurements of food sources like invertebrate and seed densities were needed than inferences from indirect elements of habitat. Seed fall traps and invertebrate traps would involve more effort as tools for estimating *M. musculus* abundance than gauging aspects of the habitat, making them less practical as tools for pest managers. It is understandable that the aerial cover model did not correlate with *M. musculus* abundance considering high ground cover was supported less than low ground cover, providing more support for that cover over 1 m is not valued by *M. musculus* (Dickman 1992). Though the positive relationship of lower direct cover was important there was still scope for a negative correlation with aerial cover. As the canopy or sub-canopy became more continuous less light would be available in the undergrowth, thus limiting the extent of low ground cover growth. However, I found no evidence that canopy cover played a role in this study.

Inferences could not be made on the habitat preferences of *M. musculus* because GUD values that would have given insight to predation risk and food availability at each site were not different at sites with or without *M. musculus*. The trapping index gives an indication of *M. musculus* abundance across habitats but no insight to the mechanisms and behaviours that produce the resulting pattern. It may be possible for certain habitat conditions to produce a situation where a habitat is preferred by *M. musculus* but the species is numerically lower than in another habitat, i.e. lower predation risk but lower food availability creating a safe but low carrying capacity habitat. This would be akin to source-sink population dynamics, where a stable population with positive population growth (source) is connected to and maintains a population that is not self-sustaining (sink) (Pulliam 1988), creating a net flow of individuals from the source population to the sink population. Dickman *et al.*

(1991) displayed a possible example of this with *Mus domesticus* on Boullanger Island, Western Australia.

The likely explanation for the feed trays not being representative of GUDs was activity from other species of rodents and the avifauna. *R. rattus* have been shown to prohibit *M. musculus* access to resources (Brown *et al.* 1996) and it would be expected that birds such as *Turdus merula* (common blackbirds) and *Turdus philomelos* (song thrushes) (*pers. obs.*) would not be excluded by *M. musculus* due to their larger size. It was assumed from similar studies (Brown 1988, Kotler *et al.* 2001) that smaller species would have had lower GUDs but this did not appear to be correct.

Another possible explanation to the lack of difference for GUDs between covered and uncovered trays at sites with *M. musculus* present could be that a dominant mouse was excluding other con-specifics which may have forced them to use the riskier tray, therefore removing the difference between covered and uncovered trays. This is unlikely, however, because it has not occurred in other similar studies of rodents using GUDs that were available to multiple individuals (Brown 1988, Abramsky *et al.* 2001, Ylönen *et al.* 2002, Arthur *et al.* 2004). Brown (1988) explained that the GUD will be representative of the individual with the lowest GUD, which is relative to environment not the number of individuals. If an individual reaches a tray that has already been depleted, they are not going to take the same amount of food from the tray as the prior visitor. The individual will search for the food until it is depleted to a level where the effort and risk of foraging in that patch outweighs the return.

A potential limitation for using the trapping index as a measure of *M. musculus* abundance was the potential decrease in trapping efficiency when *M. musculus* are in preferable conditions (Weihong *et al.* 1999). If food was plentiful or

competition for resources was minimal then individuals may be less inclined to visit the traps, though generally this has not been the case (Innes *et al.* 1995, Fitzgerald *et al.* 1996, Choquenot and Ruscoe 2000, Ruscoe *et al.* 2001).

From this investigation, two features of the habitat were shown to positively relate to *M. musculus* abundance: north facing slopes and higher amounts of rank grass cover. These two features provide practical tools for estimating *M. musculus* abundance for they can be gauged quickly and easily. This does not suggest that these were the best possible estimable parameters, but the best of those measured in this study.

If a correlation between suitable breeding habitat and habitat preferences of *M. musculus* was made, then their population dynamics may be consistent with source-sink dynamics. It may be possible that the strongest two estimable parameters could indicate potential source populations of *M. musculus*, making ongoing management of *M. musculus* logistically simpler. Studies of the occurrence of source-sink dynamics between *M. musculus* populations could have beneficial outcomes for managing this pest.

Understanding *M. musculus* habitat selection would give important insight to management of this pest species. Investigation into whether the apparent habitat segregation was due to *M. musculus* selection or *R. rattus* interference forcing *M. musculus* away would improve the knowledge of this small mammal community. Higher vegetation may play some degree in *M. musculus* habitat selection if other aspects of the habitat are equal. It would be expected that higher vegetation would likely play a minor role compared to the levels of ground cover.

### **Chapter 3:**

**Change in house mouse (*Mus musculus*) habitat preferences and foraging behaviour with the removal of ship rat (*Rattus rattus*)**

## Abstract

*Rattus rattus* (ship rats) play a major role in *Mus musculus* (house mouse) ecology as a dominant competitor affecting their distribution and population dynamics, so mechanisms of this relationship are examined here. The scent of *R. rattus* was used in a series of arena trials investigating how the presence of a direct cue of *R. rattus* affected *M. musculus* habitat preferences and foraging behaviour. Quitting harvest rates (QHR) were used to measure changes in *M. musculus* activity in the arenas. Regardless of scent treatment, nocturnal foraging was 78% higher than diurnal foraging. In the absence of the rat scent, *M. musculus* clearly preferred dense cover over the intermediate short grass cover by 47% and used a bare ground the least. The short grass cover became preferred the least in the presence of the *R. rattus* cue dropping 52% with little change in the other two ground cover treatments. The preference of bare ground over the intermediate cover in the presence of *R. rattus* scent was an unexpected result. This pattern was likely due to improved vigilance and swifter movement in the bare ground patch. Foraging behaviour was suppressed in the intermediate cover without a shift to harvesting more food in other habitats. Suppression of *M. musculus* activity supports some of the literature and has implications for the success and distribution of their populations. The findings improve the understanding of rodent community interactions and imply how they may help with pest management, although further investigations are needed of interactions of the relationship of these species and the small mammal communities they occupy.

## Introduction

Inter-specific competition can reduce a subordinate species survival (Valone and Brown 1995) and fecundity (Arthur *et al.* 2004), and a populations range (Abramsky *et al.* 2001) through its impacts on the fitness of individuals (Dickman *et al.* 1991, Dickman 1992, Orrock *et al.* 2004). A dominant competitor can impact subordinate species similarly to a predator (Valone and Brown 1995). By removing a dominant species from an eco-system a subordinate species experiences the benefits of competitive release (Yeaton and Cody 1974, Heske *et al.* 1994).

Direct cues are signs of a species presence like calls, scent markings or visual territory markings. Usually a direct cue would only be present if the species was actually there. Subordinate species can use the direct cues of a dominant species as a proxy to avoid competition (Orrock *et al.* 2004, Nunes 2007). If the dominant species was removed then there would be a response from the subordinate species because the former's cue was also removed. An indirect cue is unlike a direct cue because it is not created by the dominant species, but indicators that the subordinate associated with increased vulnerability or coincidence with the dominant species such as brighter moonlight, lack of refuge, or at locations preferred by the other species (Dickman 1992, Abramsky *et al.* 2001, Orrock *et al.* 2004). Moreover, responses to indirect cues still occur even if the dominant species is absent. Brown *et al.* (1999) stated that predators change how prey use habitat by altering the time they spend in low versus high risk habitats or increasing time individuals spend vigilant at the expense of other behaviours. It is possible that this may also be true of an individual's response to a competitor (Valone and Brown 1995).

*Rattus rattus* (ship rats) and *Mus musculus* (house mouse) are the most widespread invasive rodents in New Zealand (Innes 2001, Ruscoe and Murphy 2005), competitors divergent in their use of habitat. *M. musculus* are more abundant in habitat with broken canopy and dense ground cover while *R. rattus* are more prevalent in forest with continuous canopy (Hooker and Innes 1995, King *et al.* 1996). *R. rattus* are often the focus of pest control programs which has lead to cases of *M. musculus* populations responding positively after the removal of *R. rattus* (Innes *et al.* 1995, Miller and Miller 1995, Sweetapple and Nugent 2005, Caut *et al.* 2007). The two species relationship has not been intensely investigated (Caut *et al.* 2007), and the need to examine this relationship has been repeatedly highlighted (Innes *et al.* 1995, Brown *et al.* 1996, Sweetapple and Nugent 2005, 2007). The response of *M. musculus* to the removal of *R. rattus* may depend on the type of cues which *M. musculus* use to evaluate the presence. If the interactions between these two species are reliant on direct cues and *R. rattus* was removed then the flow on effects of removing a competitor would reach their full extent more immediately. Managers may be able to incorporate this into the management of other pest species or predict further long-term distribution and population patterns.

If the presence of *R. rattus* displaced *M. musculus* then a shift in temporal activity or allocation of foraging activity from one habitat to a safer habitat would be observed. It would be expected that foraging activity would decrease without increased activity in alternative times or habitats if *M. musculus* were changing their behaviour, by expending more effort into other activities, like vigilance, and reducing the time spent foraging (Brown 1988, Abramsky *et al.* 2002).

I conducted simultaneous arena trials with *M. musculus* in the presence of *R. rattus* scent as a direct cue treatment to test if *M. musculus* use direct cues to avoid *R.*

*rattus* and to clarify how *R. rattus* displace *M. musculus* temporally or spatially, or alter their investment in foraging behaviours. I would expect that in the presence of *R. rattus* scent *M. musculus* would decrease foraging activity in habitat patches that provide less cover and increase in those that provide more cover. The cover would act as refuge and reduce the conspicuousness of *M. musculus*. Nocturnal foraging would increase for the same reason. There may be a slight depression in the amounts of food taken as the patches that are utilised more become more depleted and harvesting efficiency decreases.

## Methods

### Arena location, construction and dimensions

Six 23.4 m<sup>2</sup> arenas were built amongst rank grass within a fenced area on the brow of a low-lying flat topped ridge (41°14'42.13"S, 175°29'2.91"E) between pastoral fields near Martinborough (Figure 3.1). Vegetation within the fenced area was dominated by *Chamaecytisus palmensis* (Leguminosae) (tree lucerne) and rank pastoral grasses but also consisted of a variety of native and exotic trees, shrubs and flaxes. Livestock pasture surrounded this site with shelter belts nearby (Figure 3.1).

Hexagon shaped arenas were built because of the simplicity of construction and because they could be divided into equal diamond shaped thirds for different internal treatments. Sheets of plywood (3 x 0.65 x 0.025 m) were fixed in a hexagon shape and placed into a narrow trench approximately 50 mm deep. The loosened sod along the trench was pressed down by foot on the interior side of the wall and compressed down on the exterior side by a hand soil compactor. The entire wall was approximately 50 mm underground to prevent mice from digging under the wall. The height of the wooden wall was approximately 0.6 metres similar to other arena trials



(Kotler *et al.* 1988, Arthur *et al.* 2004). Strips of corflute plastic 250 mm wide were nailed to the top of the plywood sheets to prevent mice from climbing over the fence. Joins between corflute sheets were taped together so there were no edges that mice might use to climb the wall. The corflute plastic increased the height of the arena walls to just over 0.8 m. Grass around the internal perimeter was cut to 250 mm and stalks of seed heads throughout the arena were cut to approximately 500 mm to prevent mice using the grass to climb over the fence.

### **Ground cover treatments**

Each third of the arena was randomly assigned a different height of ground cover. The three heights of ground cover used were bare ground, short grass (80-130 mm), and rank grass (max. 500 mm) (Arthur *et al.* 2004). To create bare ground, the grass was cut as close as possible to the soil surface (Figure 3.2 and 3.3). An edge-trimmer with a whipping nylon cord was used to cut the grass because it would not dig up the soil or damage the arena walls. Between each trial the grass was trimmed to the appropriate height and any clippings raked and removed from the arena.

One feed tray filled with a litre of sand was placed in the middle of each ground cover treatment. Holes were dug for the 200mm round x 40mm deep trays so the upper edge was flush with ground level. The shortest distance from the tray to the adjacent ground cover type was 1.299m. This distance prevents the neighbouring patch providing cover. From 1m to 1.5m has been used previously to separate covered and open foraging patches or as a minimum distance to a refuge (Kotler *et al.* 1991, Kotler *et al.* 2001, Orrock *et al.* 2004).



Figure 3.1. Arenas situated in area fenced from livestock and surrounded by trees and rank grass facing west. Inset in the top-right corner displays the location of Martinborough in New Zealand, Martinborough is located beyond the fields in the background. This photo depicts the canopy treatments of chapter 4 that were not part of this chapter's treatment.

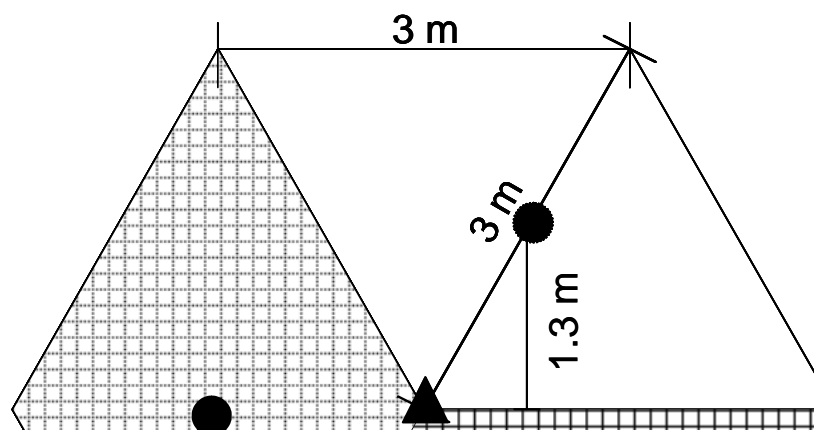


Figure 3.2. Dimensions of hexagon shaped arena with 3 m sides and 3 ground cover treatments: bare ground = no cover, short grass = 80-130 mm, rank grass < 500 mm within the arena that *M. musculus* could move between. In the centre of each ground cover patch is a feed tray.



Figure 3.3. Three levels of ground cover as treatments with a feed tray in the foreground within an arena. The scent container was the centre of the arena at the junction of the three ground cover treatments. The three ground cover treatments were: bare ground = no cover, short grass = 80-130 mm, rank grass < 500 mm.

## **Dominant competitor treatment**

In the centre of each arena, where the three ground cover treatments converge, a 0.5 litre plastic container was placed. The containers had three evenly spaced 25 x 25 mm holes cut around their wall near the top so that the lid still remained in place. Sawdust litter from caged *R. rattus* was collected the day before the trial and stored away from the arenas in an air-tight plastic bucket. On the day the trial began three of the arenas were randomly selected and their central container half filled with the scent impregnated sawdust and placed back in the centre of their respective arena. The empty containers remained in the other arenas. Before the containers were put in place, wine vinegar was sprayed in the immediate spot to neutralise any prior odours (*pers. comms.* Hancock, E. A. Veterinarian). This was important for consecutive trials when the treatments would be swapped between arenas so lingering rat odour would be removed.

The rat scented sawdust in the central containers was refreshed from the stored sawdust every occasion the feed trays were renewed during a trial (see “Quitting harvest rate protocol” below) (Orrock *et al.* 2004). Refreshing the sawdust after renewing the food prevented the feed trays becoming contaminated with rat odour.

## **Quitting harvest rate trial protocol**

A method of measuring the quitting harvest rate (QHR) (Schmidt and Ostfeld 2003) was used to examine the habitat preferences of *M. musculus* (Brown 1988, Brown 1992). A giving up density (GUD) gives more absolute values of habitat quality while QHR gives relative rates of harvesting between the habitats. Trays were filled with a substrate and a designated amount of granule food mixed through it. The rate at which that food was harvested was at a rate relative to the perceived risk and harvesting

opportunities in surrounding habitats. The rate of harvest decreases as the individual spends more time depleting the food tray. The amount of food remaining gives a value of the minimum harvest rate of an individual for that time period relative to the other available patches. Different harvest rates between different habitats indicate habitat preference. In this study, the food in each tray was limited so that an individual could not be satiated by feeding in only one habitat type. Thus, mice have to select between multiple ground cover types when foraging to meet their metabolic requirements. Nevertheless, food trays were adequately stocked with food such that a mouse would not exhaust itself searching through trays trying to meet its needs. The QHRs taken from trays were relative to harvest rate and perceived risk of the other habitat patches available to the individual over a twelve hour period. The conventional GUD method (Brown 1988) repeatedly leaves trays until they are depleted to a level relative to the surrounding environment, then the amount of food at which the species quits foraging in the patch was averaged.

A preliminary trial was conducted to ensure that an adequate amount of food for the mice to meet their metabolic demands for a twelve hour period was placed in each arena while still requiring the mouse to search between the habitat patches. *M. musculus* require approximately 3 g of dry matter per day (Crowcroft 1966). One gram mixed through 1 litre of sand in each of the three trays of the arena every 12 hours was therefore thought sufficient and most likely for selective consumption from trays to reflect the influence of treatments. The preliminary trial also created a presence of prior activity in each of the arenas for the first round of trials that were sampled thus creating similar conditions for each of the sampled trials that followed. Sampling every twelve hours would identify any diurnal or nocturnal changes in *M. musculus* foraging activity.

Every feed tray was stocked from the first morning between 7-7:30am with 1 g of Sharpes® feed wheat mixed through a litre of sand in each tray. The sand and wheat were mixed in a twenty litre bucket and poured into the feed tray. The tray was gently shaken so that the sand levelled to a smooth surface so that *M. musculus* tracks and foraging activity on its surface could be detected. Trays were replenished with wheat every twelve hours for three days and all at the same time to reduce human activity in the vicinity and within the arenas. Before removing a tray for replenishment they were examined for evidence of track and sign according with previous studies (Arthur *et al.* 2004, Orrock *et al.* 2004). Those trays with mice sign were sieved into a twenty litre bucket and any seeds that remained removed and placed into a small labelled paper envelope. Envelopes were labelled detailing; the trial number, arena number, sample period, and ground cover type from which the sample was taken. Seeds from samples were dried in a oven at 60°C for seven hours and weighed to the nearest 0.01g (Orrock *et al.* 2004). If sand had been lost from the tray it was replaced so the volume was returned to 1 litre and the next 1g of seed mixed through it. Trays that did not have any sign of mice were re-mixed and deposited back into the tray. Trays were put randomly back into the holes in the arenas for another twelve hours. QHRs from the first 24 hours that the mice were in the arena were discarded as habituation time, giving 48 hours of sampling.

### **Study specimens**

Wild *M. musculus* from the surrounding farm environment were used in arena trials because they were likely to have been exposed to the local potential predators and competitors. *Circus approximans* (harrier hawk), *Ninox novaeseelandiae* (morepork), *Mustela erminea* (stoat), *Mustela nivalis* (weasel), *Felis catus* (feral cat), *Canis familiaris* (domestic dog) and *R. rattus* all occurred on the surrounding farmland



(*pers. obs.*). The responses of wild *M. musculus* were more likely to reflect behaviour in a natural setting than the behaviour naïve or commensal mice. *M. musculus* have been shown to retain anti-predator behaviour when moved to an environment in which predators were absent (Dickman 1992).

Up to seventeen Longworth® live mouse traps were used on the surrounding farmland to catch six mice in one night. Traps were baited with a half teaspoon of Sanitarium® peanut butter and with Nestle® chocolate melt buttons. The traps were placed around shelterbelts, unused timber and stacked debris on the farm and in shade where direct sunlight would not heat the traps. Two nights prior to the night of actual trapping, the traps were baited and placed with the trap door locked open so mice became acclimatised to the traps and feeding from them. About an hour prior to dusk on the day before mice were required, the traps were re-baited and the doors set. All traps were checked the following morning and the mice caught released into the arenas between 7-7:30 am. Only one mouse was released into each arena to prevent dominant-subordinate mouse interactions confounding habitat-use preferences (Dickman *et al.* 1991). Any surplus mice were released where they were caught. If less than six mice were caught in a single night, the trial would be delayed and trapping continued until six had been caught in a single night so that every arena could be occupied over the same period.

Mice of previous trials were removed from arenas by placing a baited and set live trap while the feed trays from the previous night were sieved. If a mouse was not caught in the arena by the time the new mice were ready to be released, the new mouse was placed in the shade near the assigned arena until the old mouse was caught.

## Analysis

Data was analysed with SPSS 16.0 (SPSS, Inc., Chicago, IL) general linear models procedure. I used an analysis of variance (ANOVA) with repeated measures to test for the influence of the two *R.rattus* scent treatments (between subjects factor) on the two levels of diurnal foraging behaviour and three levels ground cover usage (within subject factors). This analysis is generally done for repeated measures over time (Gotelli and Ellison 2004). A repeated measures ANOVA was used because the diurnal and grass cover factors occurred within each of the canopy treatments. Data from both days were pooled for each arena to remove issues of pseudo-replication when sampling was done from the same enclosures with the same mouse and treatment. Pallai's Trace test was used to identify significant treatment effects and interaction after Mauchly's test of sphericity showed that the assumption of sphericity was met.

## Results

Foraging activity in arenas differed significantly temporally and between ground cover treatments. *M. musculus* foraged 78% more at night (Pillai's Trace,  $F_{1, 10} = 131.5$ ,  $P = 0.000$ ) and at least 60% more in the rank grass ground cover than the other ground cover patches (Pillai's Trace,  $F_{2, 9} = 79.509$ ,  $P < 0.001$ ). The presence of *R. rattus* scent in arenas did not alter the amount of day time activity by *M. musculus*, but nocturnal feeding was reduced by 24%, although the reduction was only approaching significance (Pillai's Trace,  $F_{1, 10} = 4.297$ ,  $P = 0.065$ ) (Figure 3.4).

The presence of *R. rattus* scent significantly altered *M. musculus* habitat preferences (Pillai's Trace,  $F_{2, 9} = 8.692$ ,  $P = 0.008$ ). Rank grass was still the preferred

ground cover but the order of preference for short grass and bare ground had reversed due to foraging activity in the short grass patches dropping by 52% (Figure 3.5).

A three way interaction between the factors temporal activity, ground cover type and rat scent was significant (Pillai's Trace,  $F_{2,9} = 6.236$ ,  $P = 0.020$ ) (Figure 3.6). Rank grass was still preferred over the two other types of ground cover during the day time. However, the presence of *R. rattus* depressed foraging at night at all ground cover types although this difference was largest between the two short grass treatments.

## Discussion

The scent of *R. rattus*, a direct cue from a dominant competitor, modified *M. musculus* foraging activity and habitat use. The introduction of a competitor's direct cue reduced feeding by *M. musculus* at night and foraging activity in patches with short grass ground cover. Rat presence did not affect the amount of food removed during diurnal foraging.

The lack of change in diurnal foraging with the addition of *R. rattus* scent was possibly due to *M. musculus* and *R. rattus* being predominantly nocturnal so a change in *M. musculus* behaviour might be more apparent when they are both more

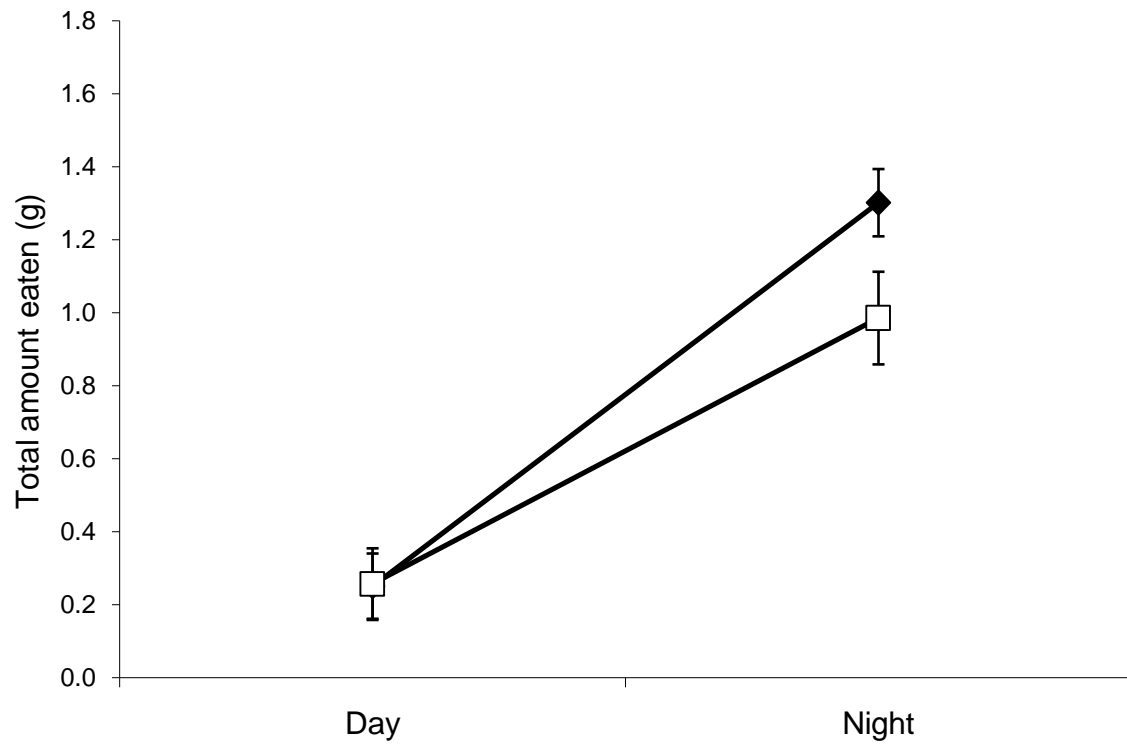


Figure 3.4. Total amount eaten (g) in control ◆ and rat presence □ treatments, displaying the influence of the perceived presence of *R. rattus* on temporal *M. musculus* foraging activity ( $F_{1,10} = 4.297$ ,  $P = 0.065$ ) ( $n = 18$ )

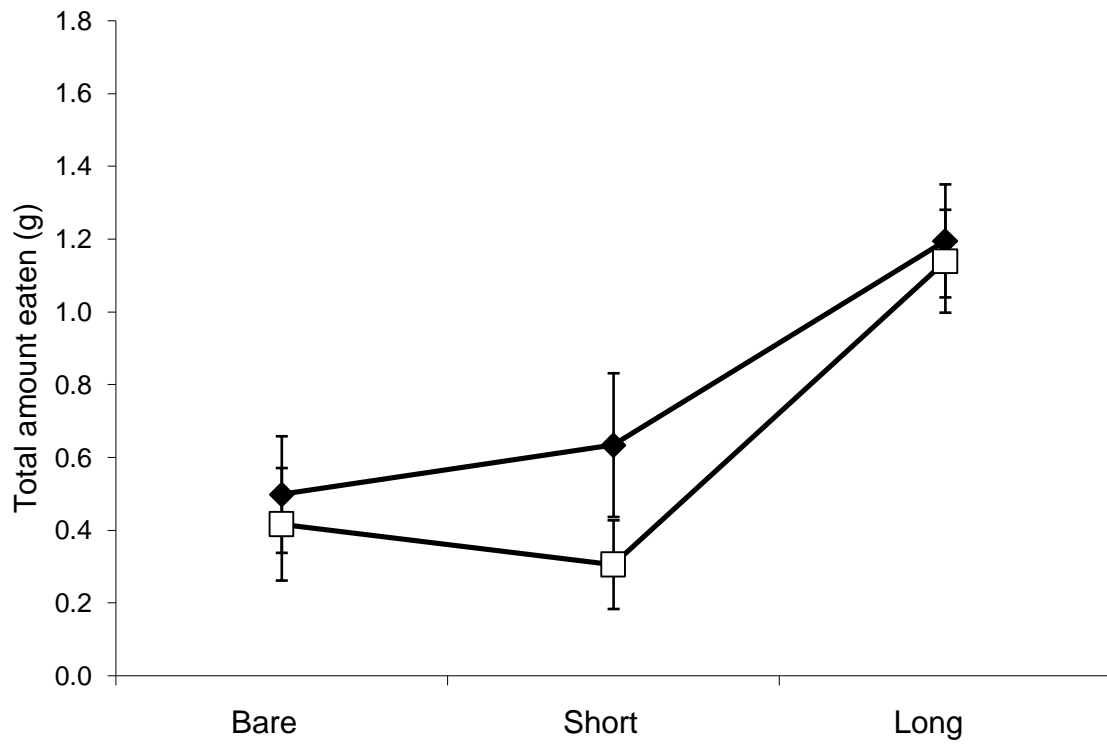


Figure 3.5. Total amount eaten (g) in control  $\blacklozenge$  and rat presence  $\square$  treatments, displaying the influence of the perceived presence of *R. rattus* on *M. musculus* use of ground cover while foraging ( $F_{2,9} = 8.692$ ,  $P = 0.008$ ) ( $n = 24$ ).

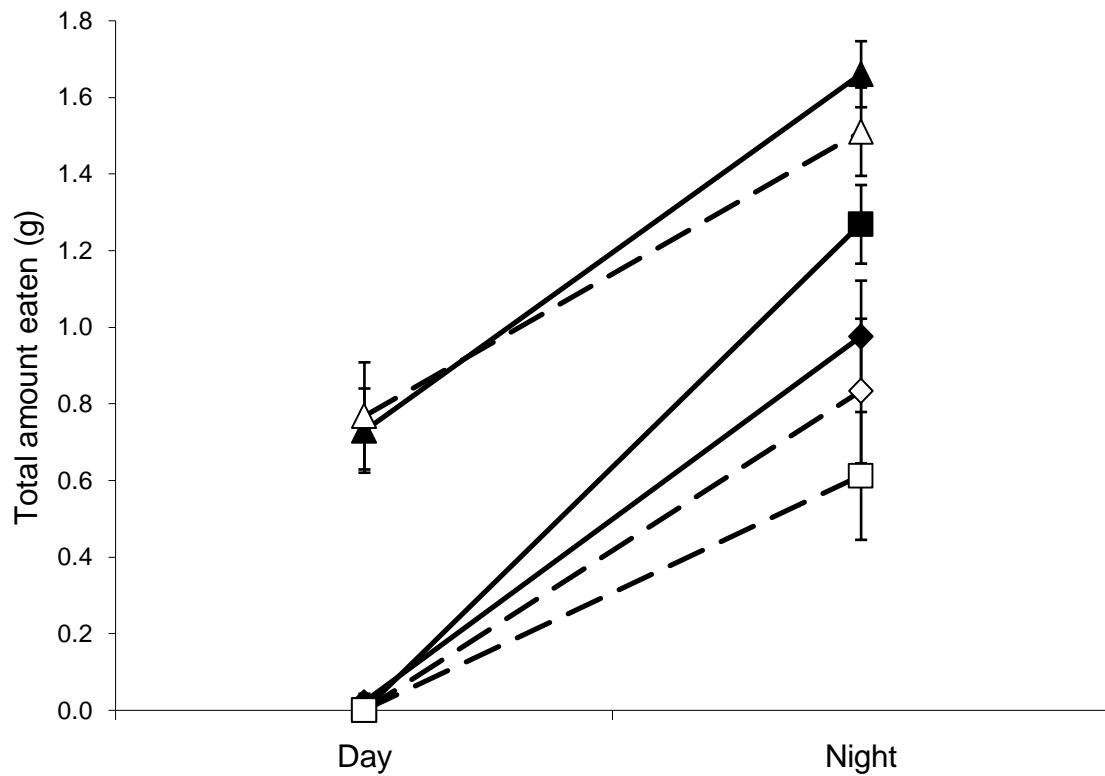


Figure 3.6 Total amount eaten (g) in control-no ground cover ◆, rat presence-no ground cover ◇, control-short grass cover ■, rat presence-short grass cover □, control-rank grass cover ▲, and rat presence-rank grass △ treatments, displaying the influence of the perceived presence of *R. rattus* on *M. musculus* temporal foraging activity and ground cover selection ( $F_{2,9} = 6.236$ ,  $P = 0.020$ ) ( $n = 6$ )

active (Hooker and Innes 1995) and likely to come into contact with each other. Alternatively, *M. musculus* may already take a minimum amount of food over the diurnal period in the absence of the scent cue so it could not be lowered without the individual perishing. If *M. musculus* were restricting themselves during the day to the minimum amount of food required to subsist on throughout the day when they are less active (Mackintosh 1981), then the level of food harvested would not have been reducible. This would have meant that *R. rattus* presence could not reduce the amount of food harvested from control arenas unless the individual mouse perished due to the necessary metabolic requirements not being met.

A similar depression of foraging activity was demonstrated in the interaction between *R. rattus* scent and ground cover treatments. Foraging activity in the bare ground and rank grass ground cover patches did not differ significantly between the *R. rattus* scent treatment and control arenas. But foraging activity in the short grass ground cover went from being lower than bare ground in the presence of *R. rattus* scent to being higher than the bare ground cover patches in arenas without *R. rattus* scent. The decrease of foraging activity in a time period or habitat patch without an increase in an alternative time or patch was predicted if individuals were required to allocate time to activities other than foraging. Increased vigilance was a probable explanation for the decrease in foraging at night or in short grass (Brown *et al.* 1999, Abramsky *et al.* 2002), because the introduction of a dominant competitor cue was the only change in the series of balanced trials. There was no direct exclusion from the trays in the short grass patches so the decrease in food is not an analogous situation to Abramsky *et al.* (2001) where a subordinate competitor, *Gerbillus allenbyi* (Allenby's gerbil) was physically excluded by a dominant rodent species, *G. pyramidum* (Egyptian sand gerbil). The situation is more comparable to Abramsky *et al.* (2002)

where under increased predation risk, *G. allenbyi* foraging was reduced and vigilance behaviour increased. The likelihood of *M. musculus* partaking in other activities was limited because the mice were alone and unable to interact socially and the mice of both treatments were given equal time to acclimatise to the enclosures.

The three-way interaction between *R. rattus* scent treatments, temporal foraging activity, and ground cover patches displayed the small increase of nocturnal *M. musculus* foraging activity in the short grass when the *R. rattus* scent was introduced. Short grass was originally designed to be an intermediate habitat and the other two habitat patches as extremes, this held true when foraging activity was considered in the absence of *R. rattus* scent. In the presence of *R. rattus* scent, short grass became a patch that *M. musculus* became vulnerable because detection of *R. rattus* was limited without providing refuge and restricted their ability to evade, a combination of the negatives of the other two ground cover types with none of the benefits.

In patches of bare ground there are no visual obstructions so detection of *R. rattus* would be sooner and escape quicker. The short grass may have restricted *M. musculus* line of sight and their ability to detect *R. rattus* which would decrease their flight distance from *R. rattus*. When individuals were released into the arena mice would occasionally run across the bare ground quickly in a fluid motion compared to individuals that initially ran into the short grass patches that had to hop incrementally over the short grass (*pers. obs.*). While the short grass probably did provide some cover, suggested by the higher foraging activity in the absence of *R. rattus* scent, it may not have been sufficient refuge to elude the dominant competitor. Vigilance and escape methods are important to successfully reach refuge and avoid confrontation



with *R. rattus*. Foraging and escape substrate have been shown to be important to species and community assemblage (Lima 1998, Kotler *et al.* 2001).

An alternative explanation to the reduced foraging activity in the short grass ground cover in the presence of *R. rattus* was that *M. musculus* spent less time in the patch. That would have meant that individuals would have had to spend more time in other patches. If this was occurring then it would have been expected that more food was taken from the other patches, which did not happen.

*M. musculus* could be flexible in their foraging behaviour by shifting their temporal or spatial activity (Dell'Omo *et al.* 2000). There was no increase in foraging in any habitat patch or time period in the presence of a competitors cue, despite the nocturnal foraging activity in short grass patches being decreased. This may have been due to another cause that had a stronger influence than the potential competitive interference from *R. rattus*. The threat of predation by a diurnal species could explain the lack of shift to daytime foraging when nocturnal foraging was reduced. *Circus approximans* (harrier hawk) is a diurnal predator of *M. musculus* that visually detects prey and was present in the area (Baker-Gabb 1981a, b). The lack of diurnal foraging activity in the two habitat patch types with reduced cover and higher conspicuousness provides support for this hypothesis. A shift in activity spatially may not have been possible if *M. musculus* were already harvesting as much food as they were prepared to take from a habitat patch or the tray was depleted so it was not energetically viable to harvest more.

The response of *M. musculus* would indicate that in short grass they expect to encounter *R. rattus* or are more vulnerable to *R. rattus* than in the other two patch types. *M. musculus* appeared to treat the rank grass patches as refuge because of the higher amount of activity at all times, fitting with other arena trials involving rodents

(Kotler *et al.* 2001, Arthur *et al.* 2004) and observations of mice retreating there when they were introduced into arenas (*pers. obs.*).

A different hypothesis for the result is that *R. rattus* act as an indirect cue for higher predation risk from rodent predators. Increased vulnerability may only alter behaviour in short grass where *M. musculus* decrease foraging because *R. rattus* are more likely to occur there and therefore attract predators to the habitat. It could be postulated that *R. rattus* would prefer the short grass habitat. In Kotler (1991) the larger *G. pyramldurn* (39 g) was hindered by dense cover more than the smaller *G. allenbyi* (25 g). It would fit that *R. rattus* would also be encumbered by the dense cover of the rank grass habitat patches due to their size. *R. rattus* would be conspicuous in open areas because of their size thus attracting predators. Their increased mass may help them move through the short grass habitat by pushing through the blades of grass. King *et al.* (1996) found *M. musculus* and *M. nivalis* (weasel) occurred in similar habitats, as did *R. rattus* and *M. erminea* (stoat). *M. nivalis* are not as common in New Zealand as *M. erminea* (Murphy *et al.* 1998b, King *et al.* 2001), and *R. rattus* can make up a large portion of *M. erminea* diet (Murphy and Bradfield 1992, Murphy *et al.* 1998b). It is plausible that *R. rattus* could attract *M. erminea* and increase the predation risk for *M. musculus*. Consequently, direct cues of *R. rattus* could be used by *M. musculus* as an indirect cue of *M. erminea*, and modify their foraging behaviour as observed in the trials.

The direct effect of *R. rattus* suppressing *M. musculus* foraging behaviour in the short grass habitat patches could have flow on indirect negative effects on *M. musculus* individual growth rates, population breeding success and population density (Arthur *et al.* 2004). Population viability of *M. musculus* might increase without the direct presence of *R. rattus* in habitats that would otherwise be marginal, potentially

more than in habitats already inhabited. This prediction would imply that the removal of *R. rattus* would benefit *M. musculus* by increasing fitness in a wider range of habitats. In instances where both species have been removed *R. rattus* have been shown to lag behind *M. musculus* when recovering from pest control operations (Innes *et al.* 1995, Blackwell *et al.* 2003, Tompkins and Veltman 2006). This may be because *M. musculus* are able to utilise more habitats in the absence of *R. rattus* in addition to their shorter life history and compensating recruitment (Bronson 1979, Innes *et al.* 1995). These predictions fit with previous observations involving removal of *R. rattus* across landscapes (Clout *et al.* 1995, Innes *et al.* 1995, Gillies and Pierce 1999, Murphy *et al.* 1999).

The change of order in preference for different habitat patches could be a concern for pest control managers. Not only was the short grass ground cover used more in the absence of a *R. rattus* cue but it was preferred more than the bare ground patch (Figure 3.5). This could imply that not only does *M. musculus* fitness improve in a wider range of habitats but that they may be more successful than in some of their previous range.

The differing levels of grass cover within the arenas could be used as proxies of habitat disturbance that could have important implications for pastoral and forest management. Rank grass cover could be treated as a low disturbance habitat, short grass cover as a habitat with an intermediate level of disturbance, and bare ground representing a highly disturbed habitat. Multiple studies have investigated the role of habitat disturbance plays in the community assemblage of rodents (Howe and Brown 1999, Malcolm and Ray 2000, Avenant and Cavallini 2007). There are fewer rodents in New Zealand but disturbance may still play a role in rodent communities.

Disturbances within or surrounding forests which create gaps in the canopy would initiate early successional vegetation forming dense low cover, suiting the habitat preferences of *M. musculus*. *R. rattus* are known to prefer arboreal habitats (Hooker and Innes 1995, King *et al.* 1996) so a forested landscape mosaic (Lertzman *et al.* 1996) could support both species. The community relationships of rodents would change in unforested areas. Further investigation is needed of the terrestrial habitat preferences of *R. rattus*, but from the interpretation of this study intermediate disturbance may benefit them. Undisturbed habitats or severely disturbed habitats with frequent refuge would be preferred by *M. musculus*. Singleton *et al.* (2007) investigated the relationship between landscape ecology and mouse plagues in Australia, where permanent refuge combined with cereal crops that have low disturbance rates and supply food augmented population outbreaks. Ylönen *et al.* (2002) explored trade-offs through varying population densities between safety afforded by habitat and food availability where mice used feeding trays in the open near the refuge around fences more readily than further away in the pasture. The findings of my study correspond with and support both of these studies.

Commercial logging is a widespread industry throughout New Zealand, which disturbs the forest by selective logging or clear felling. The findings of this study would suggest that skid sites, logging tracks and clear felling would be preferred by *M. musculus*. King *et al.* (1996) showed that *M. musculus* abundance was higher in roadsides and young stands of *Pinus radiata* where the canopy was not continuous, a exotic species widely used in timber plantations. If patches of forest remain intact near areas that have been logged then both *M. musculus* and *R. rattus* could persist. This was observed in King *et al.* (1996) and logging has promoted diversity in small mammal communities elsewhere (Malcolm and Ray 2000).

Another large scale disturbance of forest in New Zealand that could alter the rodent communities is fire. New Zealand's forests have not evolved to mitigate the effects of fire so the damage can be severe and succession slow (Ogden *et al.* 1998). Disturbance of habitats by fire has been shown to promote species diversity (Haim and Izhaki 1994, Valone and Kelt 1999). Although the restricted distribution of *R. norvegicus* and *R. exulans*, and the use of arboreal habitats by *R. rattus* and possible avoidance of open areas means that fire disturbance would likely only benefit *M. musculus*, thus reducing the diversity of rodent communities in New Zealand.

In pastoral agricultural systems *M. musculus* populations may be suppressed by livestock grazing where pasture is generally kept a low level throughout the year without completely removing the grass. This intermediate level of grass could restrict *M. musculus* use of this habitat if *R. rattus* were present, and *R. rattus* are often seen around livestock carcasses (*pers. obs.*). A probable scenario of bare ground occurring in a pastoral system is during drought conditions, this highly disturbed situation may favour *M. musculus* if sufficient refuge was available. In the arenas, *M. musculus* showed a slight preference for bare ground over short grass ground cover but pastoral paddocks are larger areas without regular reachable refuge. If refuge was nearby it would be expected that bare ground would be utilised as observed in Ylönen *et al.* (2002).

Further investigation of small mammal communities in New Zealand would be required before findings from this study could be implemented into practice. Understanding the influence of mustelids on the behaviour of *M. musculus* and the habitat preferences of *R. rattus* would improve the knowledge base of these communities, and then accurate predictions of their dynamics could be made to advance management of these pest species.

## **Chapter 4:**

### **The role of canopy as an indirect cue in house mouse (*Mus musculus*) habitat selection**

## Abstract

How a species interacts with its surrounding habitat and associated species is a fundamental element of ecology. Individuals can use features of the environment as indirect cues to indicate vulnerability and occurrence of adverse species. *Mus musculus* have been shown to be abundant in habitats with dense ground cover and infrequent in habitats with continuous canopy where a dominant arboreal competitor, *Rattus rattus*, occurs. Both species are introduced to New Zealand and many other island ecosystems, negatively impacting the native flora and fauna. Arenas were created for the mice with variations of ground cover and canopy treatments. Feed trays within different combinations of ground cover and canopy treatments were sampled to acquire quitting harvest rates (QHR), which indicate habitat preferences. Canopy treatments did not appear to significantly influence habitat preferences of *M. musculus* though two possible patterns of canopy influence did emerge. As canopy provided more direct cover (low canopy or understory), diurnal foraging increased. Nocturnal foraging was decreased in the potentially hazardous short grass cover under high canopy, which may indicate *R. rattus* presence to *M. musculus*. These patterns provide possible evidence contrary to previous accounts of house mice not considering higher vegetation when selecting suitable habitat. The relationship of *M. musculus* using dense ground cover use and higher nocturnal activity complements the current literature. Combining the possible use of canopy cover with investigations of more specific community interactions may strengthen and clarify the use of indirect cues by *M. musculus*.

## Introduction

Understanding the relationship between the physical structure of the environment and habitat-use by species within is an important goal for ecology. The physical structure of a rodents environment has been shown to be important for providing refuge from predators (Brown *et al.* 1992), foraging (Brown 1988), reproduction (Arthur *et al.* 2004), intra-specific interactions (Dickman *et al.* 1991), and inter-specific interactions (Kotler *et al.* 1988, Kotler *et al.* 2001).

By evaluating features of a habitat structure, species can reduce contact with a dominant competitor or predator (Stamps and Krishnan 2005). These features, indirect cues, are not created by the competitor or predator but indicate higher vulnerability or are associated with their presence. Structural complexity, escape substrate or a habitat type suitable for dominant competitor or predator species are features that species could use as indirect cues. Indirect cues have been shown to be important in habitat selection by various species of rodents (Roche *et al.* 1999, Mandelik *et al.* 2003, Orrock *et al.* 2004). Alternative to indirect cues are direct cues such as sight, sound and smell from the competitor or predator (Orrock *et al.* 2004). The presence of the competitor or predator inhibits the activity of the species or displaces them from the habitat.

*Rattus rattus* and *Mus musculus* have been shown to be abundant in different habitats. *M. musculus* are more common in dense ground cover and non-continuous canopy while *R. rattus* are more common in natural habitat with continuous canopy (King *et al.* 1996) and are predominantly arboreal (Hooker and Innes 1995). *R. rattus* are considered the dominant competitor in this relationship (Caut *et al.* 2007). The use of indirect cues by *M. musculus* may be one reason for the lack of overlap in habitat



use between these species, though vegetation above 1m has been considered not to influence *Mus domesticus* (Dickman 1992).

By isolating and examining *M. musculus* responses to variations of habitat structure, insight into how communities with *M. musculus* are assembled can be gained. Comprehension of these relationships improves the understanding of how rodents have adapted to New Zealand's environment and tools to managing these invasive pests.

*R. rattus* and *M. musculus* are the most widespread small mammals in New Zealand (Innes 2005b, Ruscoe and Murphy 2005) and also occur on other islands of the Pacific, Indonesia, sub-Antarctic, and Madagascar (Caut *et al.* 2007). Historically, the focus of ecological research has been on the detrimental ecological effects and management of *R. rattus* (Towns *et al.* 2006, Caut *et al.* 2007) with limited consideration of the ramifications with *M. musculus* persisting (Caut *et al.* 2007). *M. musculus* populations have increased with the reduction or removal of *R. rattus* populations (Innes *et al.* 1995, Miller and Miller 1995, Caut *et al.* 2007). *M. musculus* have been shown to directly and indirectly impact on New Zealand's avifauna (King 1983), herpetofauna (Newman 1994, Lettink and Cree 2006), flora (Fitzgerald *et al.* 1996, Duthie *et al.* 2006), freshwater vertebrates (Baker 2006), invertebrates (Fitzgerald *et al.* 1996), and forest succession (Wilson *et al.* 2007).

If *M. musculus* were to use indirect cues for *R. rattus* occurrence then it would be expected that canopy cover may be used as a cue because *R. rattus* are known to utilise arboreal habitats (Hooker and Innes 1995). This is likely to be important to *M. musculus* ecology because *R. rattus* are a widely distributed species (Ruscoe 2001) and dominant competitor (Caut *et al.* 2007). The use of canopy as an indirect cue by *M. musculus* would be inferred if they were less active or avoided habitats under

canopy. *M. musculus* could respond to indirect cues by spending more time in safer habitat patches (Dickman 1992), becoming more active at times when *R. rattus* is less active (Jones *et al.* 2001), or putting more effort into behaviours such as vigilance at the cost of other behaviours like foraging (Abramsky *et al.* 2002, Arthur *et al.* 2004). Forced changes in habitat choice and activity may be mitigated if refuge or a favourable habitat occurred under the canopy cover, such as long rank grass (King *et al.* 1996), whereas a lack of response to habitat features might be due to *M. musculus* using direct cues or *R. rattus* not influencing *M. musculus* ecology. A lack of influence is unlikely because *R. rattus* removal benefits populations of *M. musculus*, although if their use of habitat is so different that *M. musculus* may not need to readily avoid *R. rattus*. Alternatively, predator species of *M. musculus* may have greater influence on *M. musculus* distribution and activity, overriding any responses to cues of *R. rattus*.

In this chapter, I investigate the interactions between ground and aerial cover on *M. musculus* foraging activity and habitat choice. Based on the role that *R. rattus* appears to play in *M. musculus* population dynamics and their use of arboreal habitats, I predict that high canopy cover will affect *M. musculus* activity and habitat-use in a similar pattern that the direct presence of *R. rattus* does.

## Methods

In this chapter the arenas and ground cover treatments are retained from chapter 3, though instead of the *R. rattus* scent treatment varying canopy heights were introduced.

### Arena location, construction and dimensions

Six 23.4 m<sup>2</sup> arenas were built amongst rank grass within a fenced area on the brow of a low-lying flat topped ridge (41°14'42.13"S, 175°29'2.91"E) between pastoral fields near Martinborough (Figure 3.1). Vegetation within the fenced area was dominated by *Chamaecytisus palmensis* (Leguminosae) (tree lucerne) and rank pastoral grasses but also consisted of a variety of native and exotic trees, shrubs and flaxes. Livestock pasture surrounded this site with shelter belts nearby (Figure 3.1).

Hexagon shaped arenas were built because of the simplicity of construction and because they could be divided into equal diamond shaped thirds for different internal treatments. Sheets of plywood (3 x 0.65 x 0.025 m) were fixed in a hexagon shape and placed into a narrow trench approximately 50 mm deep. The loosened sod along the trench was pressed down by foot on the interior side of the wall and compressed down on the exterior side by a hand soil compactor. The entire wall was approximately 50 mm underground to prevent mice from digging under the wall. The height of the wooden wall was approximately 0.6 metres similar to other arena trials (Kotler *et al.* 1988, Arthur *et al.* 2004). Strips of corflute plastic 250 mm wide were nailed to the top of the plywood sheets to prevent mice from climbing over the fence. Joins between corflute sheets were taped together so there were no edges that mice might use to climb the wall. The corflute plastic increased the height of the arena walls to just over 0.8 m. Grass around the internal perimeter was cut to 250 mm and

stalks of seed heads throughout the arena were cut to approximately 500 mm to prevent mice using the grass to climb over the fence.

### **Ground cover treatments**

Each third of the arena was randomly assigned a different height of ground cover. The three heights of ground cover used were bare ground, short grass (80-130 mm), and rank grass (max. 500 mm) (Arthur *et al.* 2004). To create bare ground, the grass was cut as close as possible to the soil surface (Figure 3.2 and 3.3). An edge-trimmer with a whipping nylon cord was used to cut the grass because it would not dig up the soil or damage the arena walls. Between each trial the grass was trimmed to the appropriate height and any clippings raked and removed from the arena.

One feed tray filled with a litre of sand was placed in the middle of each ground cover treatment. Holes were dug for the 200mm round x 40mm deep trays so the upper edge was flush with ground level. The shortest distance from the tray to the adjacent ground cover type was 1.299m. This distance prevents the neighbouring patch providing cover. From 1m to 1.5m has been used previously to separate covered and open foraging patches or as a minimum distance to a refuge (Kotler *et al.* 1991, Kotler *et al.* 2001, Orrock *et al.* 2004).

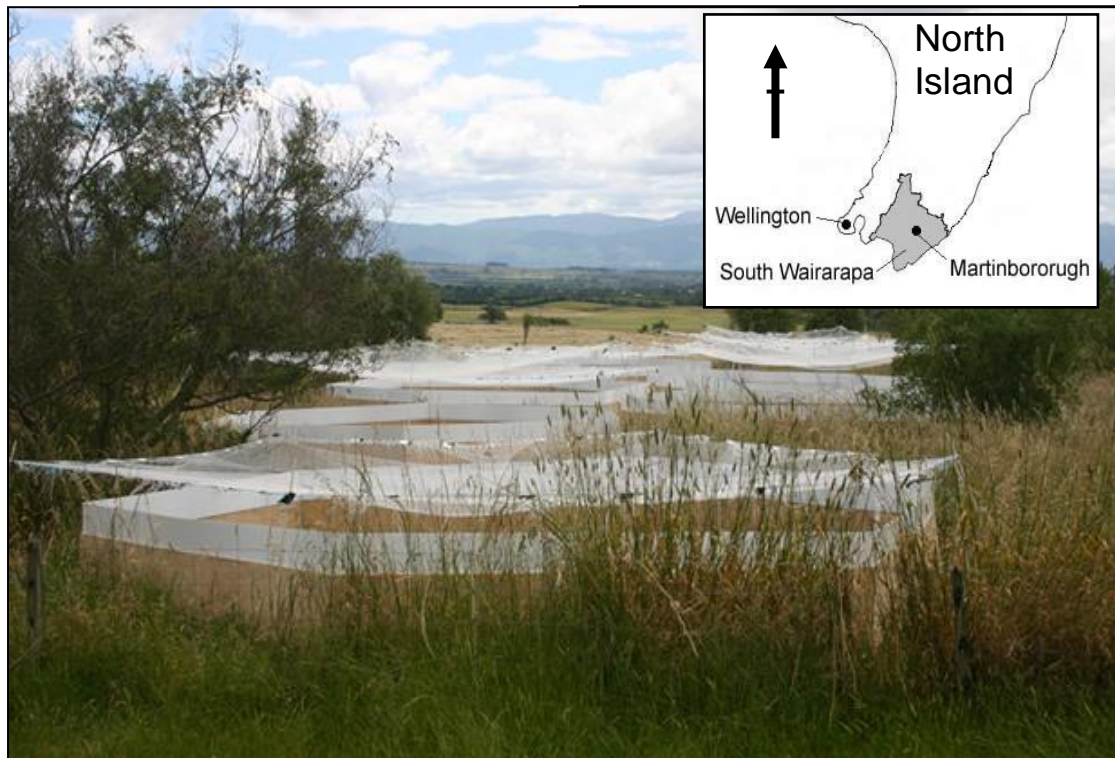


Figure 4.1. Arenas situated in area fenced from livestock and surrounded by trees and rank grass facing west. Inset in the top-right corner displays the location of Martinborough in New Zealand, Martinborough is located beyond the fields in the background.

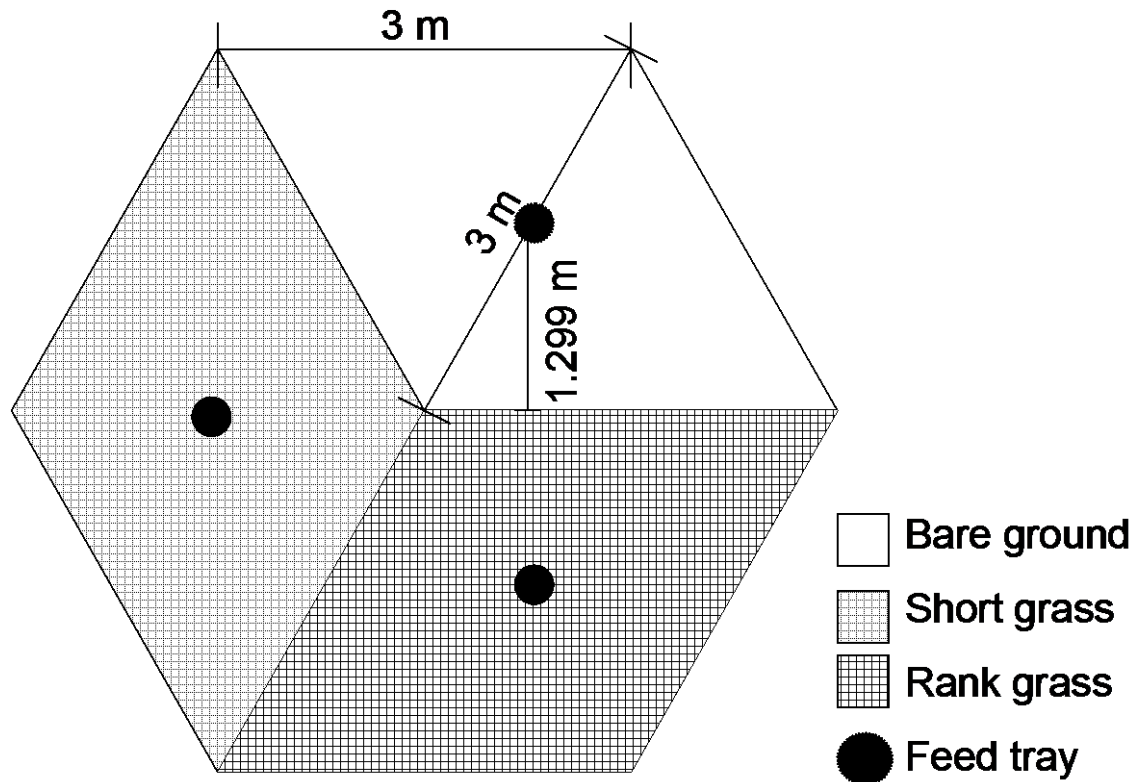


Figure 4.2. Dimensions of hexagon shaped arena with 3 m sides and 3 ground cover treatments: bare ground = no cover, short grass = 80-130 mm, rank grass < 500 mm within the arena that *M. musculus* could move between. In the centre of each ground cover patch is a feed tray.



Figure 4.3. Three levels of ground cover as treatments with a feed tray in the foreground within an arena. The three ground cover treatments were: bare ground = no cover, short grass = 80-130 mm, rank grass < 500 mm.



Figure 4.4. Four arenas with canopy treatments made of baleage netting are shown.

The low canopy treatment (0.8 - 1 m) above an arena in the foreground and two arenas with the high canopy treatments (1.75 - 1.9 m) behind, arenas with no canopy treatment are not shown



## **Canopy cover treatment**

Canopy cover treatments were placed at different heights to represent three natural canopy cover conditions. Dickman (1992) deemed vegetation over 1m was not used in habitat selection by *M. musculus* so one canopy treatment was set just below this level (0.8-1m), one clearly above this level (1.75-1.9m) and one treatment without any form of canopy cover (Figure 4.4). The canopy covers were made of baleage wrap (a white, light weight netting that is conventionally used to bind bales of green grass feed) and supported by fibreglass rods. Each canopy treatment was randomly assigned to two of the six arenas, once a round of trials was complete the artificial canopies were rotated between arenas.

## **Quitting harvest rate trial protocol**

A method of measuring the quitting harvest rate (QHR) (Schmidt and Ostfeld 2003) was used to examine the habitat preferences of *M. musculus* (Brown 1988, Brown 1992). A giving up density (GUD) gives more absolute values of habitat quality while QHR gives relative rates of harvesting between the habitats. Trays were filled with a substrate and a designated amount of granule food mixed through it. The rate at which that food was harvested was at a rate relative to the perceived risk and harvesting opportunities in surrounding habitats. The rate of harvest decreases as the individual spends more time depleting the food tray. The amount of food remaining gives a value of the minimum harvest rate of an individual for that time period relative to the other available patches. Different harvest rates between different habitats indicate habitat preference. In this study, the food in each tray was limited so that an individual could not be satiated by feeding in only one habitat type. Thus, mice have to select between multiple ground cover types when foraging to meet their metabolic requirements.

Nevertheless, food trays were adequately stocked with food such that a mouse would not exhaust itself searching through trays trying to meet its needs. The QHRs taken from trays were relative to harvest rate and perceived risk of the other habitat patches available to the individual over a twelve hour period. The conventional GUD method (Brown 1988) repeatedly leaves trays until they are depleted to a level relative to the surrounding environment, then the amount of food at which the species quits foraging in the patch was averaged.

A preliminary trial was conducted to ensure that an adequate amount of food for the mice to meet their metabolic demands for a twelve hour period was placed in each arena while still requiring the mouse to search between the habitat patches. *M. musculus* require approximately 3 g of dry matter per day (Crowcroft 1966). One gram mixed through 1 litre of sand in each of the three trays of the arena every 12 hours was therefore thought sufficient and most likely for selective consumption from trays to reflect the influence of treatments. The preliminary trial also created a presence of prior activity in each of the arenas for the first round of trials that were sampled thus creating similar conditions for each of the sampled trials that followed. Sampling every twelve hours would identify any diurnal or nocturnal changes in *M. musculus* foraging activity.

Every feed tray was stocked from the first morning between 7-7:30am with 1 g of Sharpes® feed wheat mixed through a litre of sand in each tray. The sand and wheat were mixed in a twenty litre bucket and poured into the feed tray. The tray was gently shaken so that the sand levelled to a smooth surface so that *M. musculus* tracks and foraging activity on its surface could be detected. Trays were replenished with wheat every twelve hours for three days and all at the same time to reduce human activity in the vicinity and within the arenas. Before removing a tray for

replenishment they were examined for evidence of track and sign according with previous studies (Arthur *et al.* 2004, Orrock *et al.* 2004). Those trays with mice sign were sieved into a twenty litre bucket and any seeds that remained removed and placed into a small labelled paper envelope. Envelopes were labelled detailing; the trial number, arena number, sample period, and ground cover type from which the sample was taken. Seeds from samples were dried in a oven at 60°C for seven hours and weighed to the nearest 0.01g (Orrock *et al.* 2004). If sand had been lost from the tray it was replaced so the volume was returned to 1 litre and the next 1g of seed mixed through it. Trays that did not have any sign of mice were re-mixed and deposited back into the tray. Trays were put randomly back into the holes in the arenas for another twelve hours. QHRs from the first 24 hours that the mice were in the arena were discarded as habituation time, giving 48 hours of sampling.

## Study specimens

Wild *M. musculus* from the surrounding farm environment were used in arena trials because they were likely to have been exposed to the local potential predators and competitors. *Circus approximans* (harrier hawk), *Ninox novaeseelandiae* (morepork), *Mustela erminea* (stoat), *Mustela nivalis* (weasel), *Felis catus* (feral cat), *Canis familiaris* (domestic dog) and *R. rattus* all occurred on the surrounding farmland (*pers. obs.*). The responses of wild *M. musculus* were more likely to reflect behaviour in a natural setting than the behaviour naïve or commensal mice. *M. musculus* have been shown to retain anti-predator behaviour when moved to an environment in which predators were absent (Dickman 1992).

Up to seventeen Longworth® live mouse traps were used on the surrounding farmland to catch six mice in one night. Traps were baited with a half teaspoon of Sanitarium® peanut butter and with Nestle® chocolate melt buttons. The traps were

placed around shelterbelts, unused timber and stacked debris on the farm and in shade where direct sunlight would not heat the traps. Two nights prior to the night of actual trapping, the traps were baited and placed with the trap door locked open so mice became acclimatised to the traps and feeding from them. About an hour prior to dusk on the day before mice were required, the traps were re-baited and the doors set. All traps were checked the following morning and the mice caught released into the arenas between 7-7:30 am. Only one mouse was released into each arena to prevent dominant-subordinate mouse interactions confounding habitat-use preferences (Dickman *et al.* 1991). Any surplus mice were released where they were caught. If less than six mice were caught in a single night, the trial would be delayed and trapping continued until six had been caught in a single night so that every arena could be occupied over the same period.

Mice of previous trials were removed from arenas by placing a baited and set live trap while the feed trays from the previous night were sieved. If a mouse was not caught in the arena by the time the new mice were ready to be released, the new mouse was placed in the shade near the assigned arena until the old mouse was caught.

## **Analysis**

Data was analysed with SPSS 16.0 (SPSS, Inc., Chicago, IL) general linear models procedure. I used an analysis of variance (ANOVA) with repeated measures to test for the influence of the three canopy treatments (between subjects factor) on the two levels of diurnal foraging behaviour and three levels ground cover usage (within subject factors). This analysis is generally done for repeated measures over time

(Gotelli and Ellison 2004). Repeated measures ANOVA was used because the diurnal and grass cover factors occurred within each of the canopy treatments. Data from both days were pooled for each arena to remove issues of pseudo-replication when sampling was done from the same enclosures with the same mouse and treatment. Pillai's Trace test was used to identify significant treatment effects and interaction after Mauchly's test of sphericity showed that the assumption of sphericity was met.

## Results

Contrary to expectations, the canopy treatments did not appear to affect the foraging behaviour of *M. musculus* during these trials. There were no significant interactions between canopy cover treatments and ground cover use (Pillai's trace,  $F_{4, 24} = 1.017$ ,  $P = 0.418$ , Figure 4.5) or between canopy cover treatments and temporal activity (Pillai's trace,  $F_{2, 12} = 0.920$ ,  $P = 0.425$ , Figure 4.6).

Overall, the strongest effect was ground cover (Pillai's trace,  $F_{2, 11} = 49.256$ ,  $P < 0.001$ ). *M. musculus* harvested 55% more seed in rank grass than in short grass, and 26% times more in short grass than on bare ground (Figure 4.5). During nocturnal foraging 59% more seed was harvested than during diurnal foraging (Pillai's trace,  $F_{1, 12} = 49.256$ ,  $P < 0.001$ ) (Figure 4.6).

*M. musculus* foraging activity was higher at night for each ground cover type than during the day but the magnitude of change between each ground type varied (Pillai's trace,  $F_{2, 11} = 6.841$ ,  $P = 0.012$ , Figure 4.7). Foraging activity in short grass cover was higher than on bare ground throughout the day and night and both increased by similar amounts at night (0.90 g and 1.04 g more harvested respectively). In the short

grass, *M. musculus* harvested only 20% of the amount harvested from the rank grass cover than the short grass cover, though at night this increased to 71%.

A three-way interaction between the canopy cover treatments, use of different ground cover types and temporal activity was not significant (Pillai's trace,  $F_{4, 24} = 1.808$ ,  $P = 0.160$ ) but the sample size for each combination of factors for this analysis was low ( $n = 5$ ). Two possible trends (Figure 4.8) warranted consideration. The change in foraging activity in rank grass ground cover under different canopy treatments between night and day, and the low increase in seed harvested in short grass cover under high canopy treatments from day to night.

In rank grass ground cover, there was greater variation in foraging activity between canopy treatments diurnally than at night (0.73 g diurnal range of the seed harvested compared with 0.07 g range at night) (Figure 4.8). When excluding the rank grass ground cover from consideration, the short grass ground cover and high canopy combination had the most of food removed during the day but the lowest at night (day, 0.29 g eaten compared with 0.92 g at night) (Figure 4.8). The change of 0.63 g between night and day was the smallest of the short grass and bare ground cover treatments, the next smallest was 0.93 g (bare ground and no canopy treatment). Though three-way interaction was not significant, short grass ground cover under high canopy was the most preferred ground cover outside of rank grass during the day but becomes the least preferred combination overall at night.

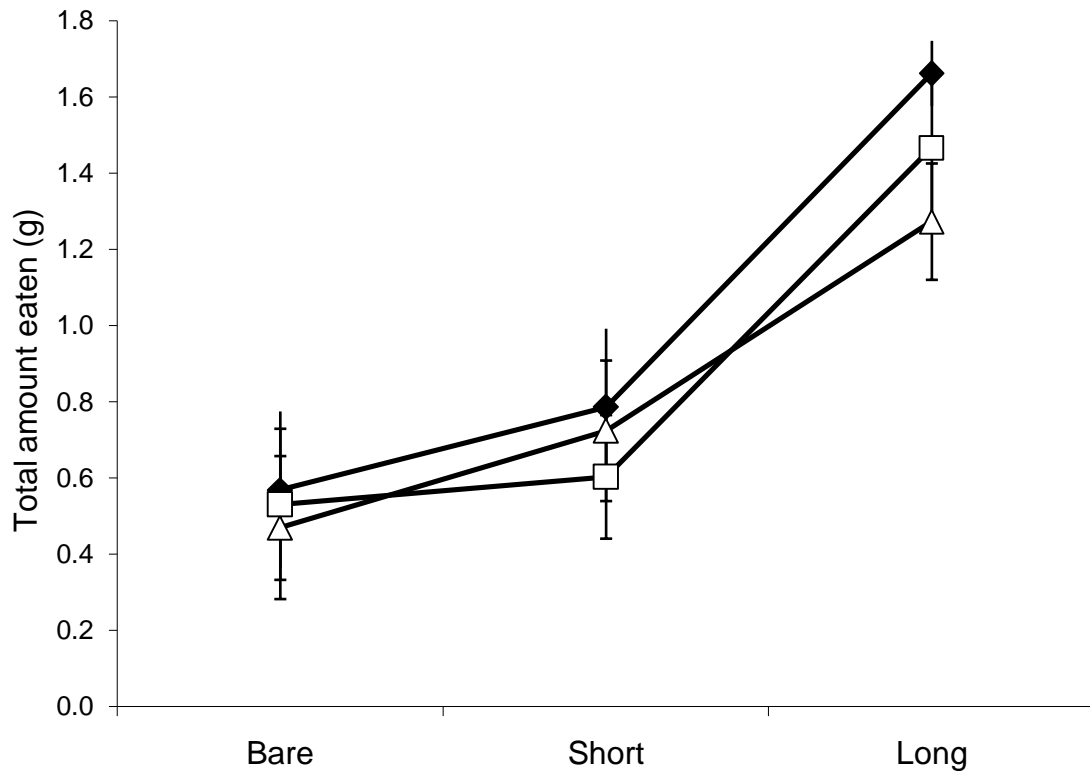


Figure 4.5 Total amount eaten (g) in low canopy cover  $\blacklozenge$ , high canopy cover  $\square$ , and no canopy cover  $\triangle$  treatments, displaying the interaction between canopy cover height and use of ground cover of *M. musculus* during foraging ( $F_{4, 24} = 1.017$ ,  $P = 0.418$ ) ( $n=10$ ).

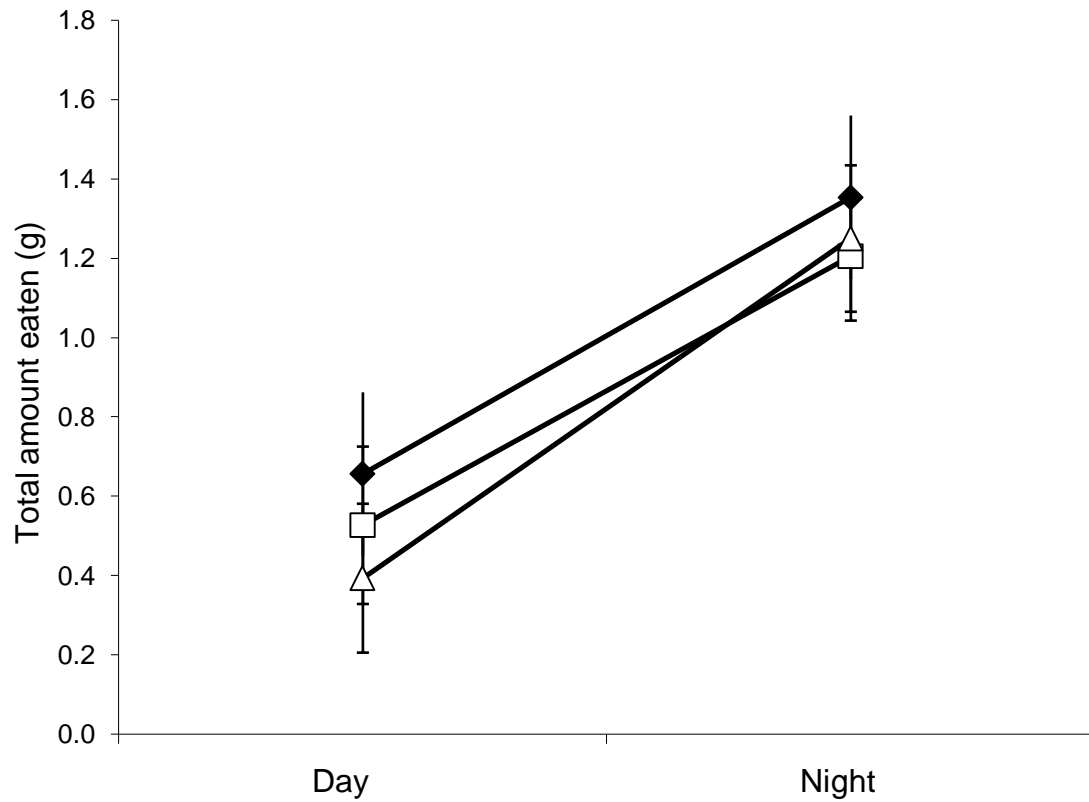


Figure 4.6 Total amount eaten (g) in low canopy cover ◆, high canopy cover □, and no canopy cover △ treatments, displaying the interaction between canopy cover height and temporal *M. musculus* foraging activity ( $F_{2, 12} = 0.920$ ,  $P = 0.425$ ) (n=15)



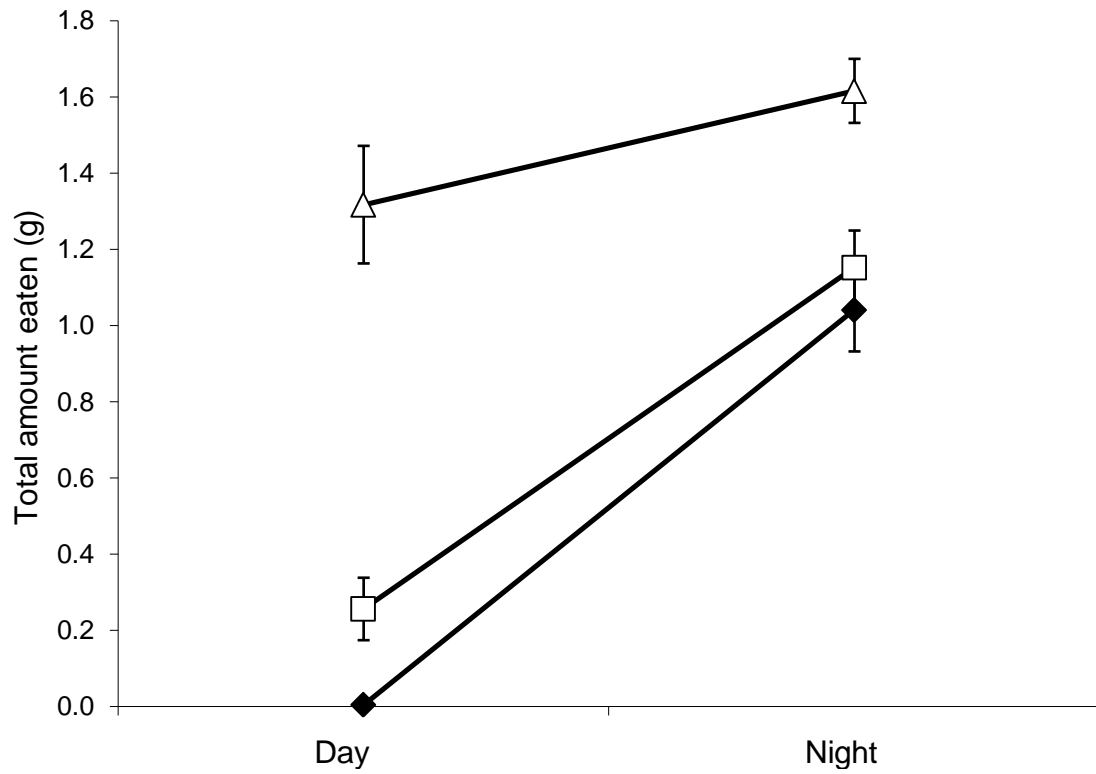


Figure 4.7 Total amount eaten (g) in no ground cover ◆, short grass cover □, and rank grass cover △ treatments, displaying the interaction between ground cover and temporal *M. musculus* foraging activity ( $F_{2, 11} = 6.841$ ,  $P = 0.012$ ) (n=15).

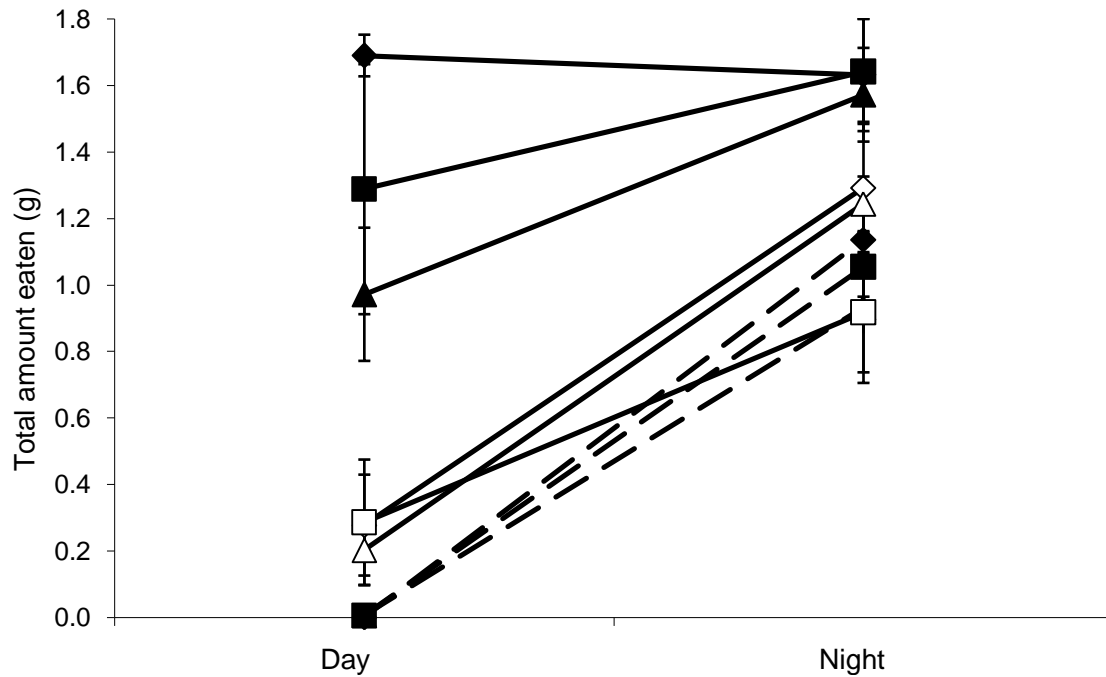


Figure 4.8 Total amount eaten (g) in no ground-low canopy cover -◆-, no ground-high canopy cover -■-, no ground-no canopy cover -▲-, short grass-low canopy cover ◇, short grass-high canopy cover □, short grass-no canopy cover △, rank grass-low canopy cover ◆, rank grass-high canopy cover ■ rank grass-no canopy cover ▲ treatments, displaying the interaction between canopy cover height and both ground cover use and temporal behaviour of *M. musculus* during foraging ( $F_{4, 24} = 1.808$ ,  $P = 0.160$ ) (n=5)

## Discussion

The high amounts of nocturnal foraging and use of the rank grass habitat observed here fits with the two previous chapters and the literature (Dickman *et al.* 1991, Dickman 1992, King *et al.* 1996, Singleton *et al.* 2007). Canopy treatment had no significant effects on the foraging activity of *M. musculus* but the trends of both diurnal and nocturnal foraging did give reason to examine further.

The lack of a significant influence of canopy treatments on the foraging behaviour of *M. musculus* was unexpected considering the habitat partitioning previously observed (King *et al.* 1996). Because *R. rattus* and *M. musculus* use habitats that differ in canopy cover (King *et al.* 1996), it was predicted that *M. musculus* would use aerial cover as an indirect cue to reduce encounters with their dominant competitor, *R. rattus* (Caut *et al.* 2007).

When focussing on the nocturnal short grass interactions displayed in Figure 4.8 there are possible indications of high canopy as an indirect cue for *R. rattus*. Foraging activity under the high canopy treatment increases less at night time relative to the two other short grass interactions. The low canopy treatment represents a level of low vascular vegetation or sub-canopy in a natural environment, whereas the high canopy treatment provided an imitation of higher arboreal canopy.

Chapter 3 provided evidence that short grass at night was a ground cover treatment that was less preferred in the presence of *R. rattus* scent, suggesting that they may be more prone in this habitat when both species are more active. Orrock *et al.* (2004) showed an example of rodents using vegetation as an indirect cue of predation risk over direct scent cues of predator species when considering habitat preferences, though does not appear to occur here. The combination of short grass, a

ground cover type that was not preferred in the presence of *R. rattus*, and high canopy cover, a habitat that *R. rattus* are abundant in, may create an environment that *M. musculus* may be apprehensive in but does not significantly avoid.

The patterns of foraging activity observed in rank grass patches during the daytime was likely due to lower canopy providing more direct cover and therefore more protection from avian predators. Diurnal *Circus approximans* (Harrier hawks) were considered the main form of avian predation because of their diet (Baker-Gabb 1981b) and were common in the area (*pers. obs.*). The other diurnal raptor species of New Zealand, *Falco novaeseelandiae* (New Zealand falcon), was not present (*pers. obs.*) and *M. musculus* are not a frequent constituent of *F. novaeseelandiae* diet (Lawrence and Gay 1991, Barea *et al.* 1999). *C. approximans* hunts for prey by soaring or hovering then dropping to the prey (Baker-Gabb 1981a). Therefore, canopy treatments would provide cover for *M. musculus* from *C. approximans*. The lower the canopy the more direct the cover was and more foraging activity resulted.

The patterns of *M. musculus* ground cover use and the weaker relationship with canopy cover suggest that ground cover may be a more significant (primary) factor in *M. musculus* habitat choices and canopy cover a secondary factor. Preference for rank grass remained clear whereas possible choices of canopy were not so apparent. These findings provide possible support for the use of indirect cues by *M. musculus* as secondary features in habitat selection.

Dickman (1992) stated that *M. domesticus* did not use vegetation over 1m high when selecting habitat. Dickman (1992) was conducted in an Australian environment where there are more mammalian, avian and reptilian predator species (MacDonald 1992, Menkhorst 2001, Wilson and Swan 2003) as well as more rodentia species (Menkhorst 2001). The community relationships with different predators and

competitors may have altered the processes and value of certain habitat preferences. In this study, increased ground cover was preferred (Figure 4.5) but there are two examples shown in these arena trials that display potential examples of *M. musculus* evaluating canopy cover. Evaluation of canopy features by *M. musculus* may need more study with more natural canopy materials and choices of canopy heights available within an arena.

If the ungulates were removed then regeneration may benefit from *R. rattus* presence and the absence of *M. musculus*. There are no native ungulate species to New Zealand and their abundance has been negatively correlated with understory and seedling density (Sweetapple and Nugent 2004). Low amounts of ground cover due to ungulate browsing and *R. rattus* presence because of a continuous arboreal habitat (Hooker and Innes 1995) would be alike the combination of short grass and high canopy that was not preferred by at night *M. musculus*. Post-dispersal seed predation would decrease without *M. musculus* and with the removal of ungulates seedling survival would increase, aiding regeneration of the forest. Though this would be counteracted by pre-dispersal destruction of fruits, flowers, buds and seedlings by *R. rattus* (Towns *et al.* 2006), and as the forest regenerates, the habitat would become more suited to *M. musculus*.

The interaction between rank grass and canopy treatments during the day may suggest that the relationship between *M. musculus* and *C. approximans* is a  $\mu$ -type predator-prey relationship. A  $\mu$ -type relationship is a system where the prey species avoids contact with another species through behavioural changes (e.g. habitat shift, diet change, diverting time from foraging to vigilance or altering foraging times). If individuals are physically removed from a habitat through direct contact with a predator species then it is treated as an N-type system (Brown *et al.* 1999). There was

the possibility that *M. musculus* avoided the habitat where they are prone to *C. approximans*, though none were depredated. A study looking directly at this relationship would be more conclusive.

The presence of canopy cover may have promoted some diurnal foraging and limited some nocturnal foraging by *M. musculus*. *M. musculus* are more active nocturnally and so the negative effects of canopy at night time may have a stronger influence on their overall habitat choice. The decrease of foraging activity in short grass ground cover under high canopy would add further detail to the distribution patterns of *M. musculus* and *R. rattus* in King *et al.* (1996).

The main effects of high activity in dense ground cover and at night are aligned with previous studies. Nocturnal behaviours of *M. musculus* and other rodent species are inherent whether in natural or artificial environments to reduce activity when they more visually conspicuous (Mackintosh 1981). The high use of ground cover is widely supported in the literature (Brown 1988, Dickman 1992, Krebs *et al.* 1995, Arthur *et al.* 2004, Singleton *et al.* 2007) and adds to the correlation found in King *et al.* (1996) of high mice abundance in dense ground cover and absence in closed canopy habitat. The patterns found in King *et al.* (1996) were partially explained from these arena trials. Foraging increased amongst rank grass ground cover and decreased under canopy and with low level ground cover. Other benefits provided by the dense ground cover could be refuge, nesting habitat or food resources that relate to success of the population and fitness of the individual (Brown 1988, Krebs *et al.* 1995, King *et al.* 1996, Gray *et al.* 2000, Arthur *et al.* 2004, Singleton *et al.* 2007). In Chapter 2, ground cover was found to be a strong estimable parameter of mouse abundance and was also a contributor to the second strongest model that concerned suitable breeding habitat. Chapter 3 suggested that the complex ground

cover substrate that does not provide refuge for *M. musculus* can be a hindrance for vigilance and escape.

Further trials could be done to support the evidence from the interactions of nocturnal foraging use of short grass under different canopy treatments and the effect of canopy treatment on daytime foraging behaviour. Arenas with consistent levels of ground cover throughout and varying levels of canopy treatment over each arena may clarify the canopy preferences of *M. musculus*. *M. musculus* are more active nocturnally (Mackintosh 1981) so the changes of activity due canopy cover at night this may play a bigger role in the patterns of preference displayed than during diurnal foraging.

The use of canopy as an indirect cue was not conclusive though there was potentially a weak response. There may be other environmental features that *M. musculus* use not only for *R. rattus* but other species, i.e. soil moisture or proximity to bodies of water may act as cues of the larger *Rattus norvegicus* (Norway rat), (King *et al.* 1996). There is scope for further investigation of indirect cues by *M. musculus* for *R. rattus*, whether with canopy cover of alternative features, or other species that are part of *M. musculus* ecology.

## **Chapter 5:**

## **Conclusions**



The objective of this study was to examine the competitive relationship between *Mus musculus* and *Rattus rattus*. I expected that *R. rattus* would have affected *M. musculus* habitat preferences via direct and indirect cues of *R. rattus* presence because of the degree of influence that *R. rattus* appears to have on *M. musculus* populations (Innes *et al.* 1995, Miller and Miller 1995, King *et al.* 1996, Caut *et al.* 2007).

The common theme from the three investigations was that ground cover in the form of rank grass was preferred by *M. musculus*. From the observations on the landscape scale, rank grass was the strongest parameter for estimating *M. musculus* abundance. During both arena experiments rank grass was used the most regardless of the time of day or treatments of canopy cover and *R. rattus* presence. The use of dense ground cover is by no means a novel concept for *M. musculus* or a majority of small mammal species (Dickman *et al.* 1991, Dickman 1992, Twigg and Kay 1994, King *et al.* 1996, Kotler *et al.* 2001, Singleton *et al.* 2007), although there are some species that have adapted to foraging in open micro-habitats (Randall 1992, Kotler *et al.* 2001). This habitat preference fits with King *et al.* (1996) where in Pureora Forest Park *R. rattus* were more abundant in continuous canopy habitats and *M. musculus* were more common in areas of rank grass and broken canopy.

The point of interest throughout the study was how the relationship with *R. rattus* influenced *M. musculus* habitat preferences. There has been a demand for further work to be done to improve our grasp of the dynamics between these two rodent species (Innes *et al.* 1995, Brown *et al.* 1996, Sweetapple and Nugent 2005, Caut *et al.* 2007). Increases in *M. musculus* populations have been recorded after the removal of *R. rattus* (Innes *et al.* 1995, Miller and Miller 1995, Murphy *et al.* 1999) but it has been suggested that these increases were not solely due to removal of a competitor.

Behavioural changes may play a role in the increased detection of *M. musculus* (Brown *et al.* 1996, Sweetapple and Nugent 2005, Caut *et al.* 2007).

During the arena trials where scent, a direct cue of *R. rattus* presence, was introduced there was evidence supporting a behavioural change in *M. musculus*. Mice in the arenas with the scent of *R. rattus* present decreased their foraging activity in short grass patches but did not increase activity in the other patches, suggesting that their foraging activity was suppressed. Therefore, it is possible that increases in foraging activity in the absence *R. rattus* of could incite higher reproductive rates (Arthur *et al.* 2004). The increase of *M. musculus* populations benefiting from the removal of *R. rattus* maybe due to higher reproductive rates with improved access to food resources (Brown *et al.* 1996) but also higher detection rates of *M. musculus* (Sweetapple and Nugent 2005), as they are more active.

Combining the findings of *M. musculus* behavioural changes due to *R. rattus* presence in the arena trials and with similar suggestions of behavioural changes (Brown *et al.* 1996, Sweetapple and Nugent 2005) it would be reasonable to be wary of estimates of the extent and number of *M. musculus* where *R. rattus* densities are modified or different. It is probable that in the presence of *R. rattus* in natural settings *M. musculus* populations are underestimated. The potential impacts of *M. musculus* may not be apparent in the presence of *R. rattus* because their activity, particularly foraging behaviour, are suppressed. The negative impacts of *M. musculus* may be attributed to *R. rattus* because the true extent *M. musculus* abundance is not apparent in natural settings where both species occur. Moreover, studies of behaviour solely on one of these species isolated from the other have to consider how the results would be represented in natural environments where both species are present.

A finding with potentially important ramifications was the shared preference of *M. musculus* and *R. rattus* for warm dry slopes. A management focus on the removal of rats (Towns *et al.* 2006, Caut *et al.* 2007) may not be sufficient to conserve or restore native species and habitats because of the potential increase of the impact of *M. musculus* in these preferred habitats (Tompkins and Veltman 2006). The strongest parameter in the landscape scale observations was the aspect of slopes with *M. musculus* abundance positively correlated with north facing slopes and negatively correlated with slopes facing north-east around to the west. King *et al.* (1996) found that *R. rattus* were also more abundant on warmer and dryer slopes. Regeneration of forest communities and species adapted to warmer dryer areas might be restricted by rodents.

Imagine a forest flora adapted to warm dry sites that have suffered a decrease in range and a survey of pests in the area showing an abundance of *R. rattus* but, perhaps mistakenly, low levels of *M. musculus*. A management plan aimed at reducing the *R. rattus* population without considering *M. musculus* could lead to population irruptions of *M. musculus* (Innes *et al.* 1995, Miller and Miller 1995, Tompkins and Veltman 2006, Caut *et al.* 2007). Therefore, the management for this forest would be ineffective at promoting the forest species regeneration because high *M. musculus* numbers would not benefit seed or seedling survival and possibly invertebrates involved with regeneration of the forest (Miller and Miller 1995, Fitzgerald *et al.* 1996, Duthie *et al.* 2006, Wilson *et al.* 2007).

Reoccurring increases of *M. musculus* abundance with the removal of *R. rattus* (Innes *et al.* 1995, Miller and Miller 1995, Ruscoe 2001, Caut *et al.* 2007) and the increase of *Mustela erminea* (stoat) with irruptions of *M. musculus* and their subsequent prey-swapping (King 1983, O'Donnell and Phillipson 1996, King and

White 2004) create cause for concern for pest management programs without adequate foresight. For example, if *M. erminea* and *R. rattus* are removed from an area or habitat to protect a species that is prone to predation from these species, it would be expected that *M. musculus* populations would benefit from their absence. However, an abundance of *M. musculus* would benefit the reinvasion of *M. erminea* to the area, potentially nullifying the gains made by removing the predators. The relationships within these communities need to be understood and considered to improve the efficiency and long-term success of controlling mammalian pests.

In New Zealand plagues of mice like those that occur in Australian grain growing regions (Singleton and Redhead 1990) have not taken place, but there have been irruptions of *M. musculus* populations coinciding with mast seeding of New Zealand beech forests (*Nothofagus spp*) (King 1983). These irruptions lead to an increase in rodent predators, particularly *M. erminea* (King 1983, O'Donnell and Phillipson 1996), increasing predation on *Mohoua ochrocephala* (mohua, yellowhead) (King 1983, O'Donnell *et al.* 1996) an endangered species (O'Donnell *et al.* 2001).

Those conserving *M. ochrocephala* may be able to pre-empt these irruptions to minimize the impact of *M. musculus* irruptions. Between plagues in Australia, *Mus domesticus* persist in refuge sites, but expand their range when the conditions are suitable (Singleton *et al.* 2007). Outside of mast seasons *M. musculus* are scarce in *Nothofagus* forest (Fitzgerald *et al.* 1981) so are likely to persist in the area at refuge sites. By concentrating on potential refuge sites in the lead up to a mast year the irruption of *M. musculus* populations may be reduced. From this study the northern facing sites with dense cover would be conducive as refuge sites. Singleton *et al.* (2007) observed that habitats previously utilised rarely by *M. domesticus* became centres of source populations (positive emigration) in favourable conditions. Pre-

emptying *M. musculus* irruptions may limit their increase initially but would not stop them completely. The behavioural preferences shown here, combined with demographic and spatial studies of *M. musculus* (Fitzgerald *et al.* 1981, Dickman 1992, Arthur *et al.* 2004, Singleton *et al.* 2007) begin to draw a picture of potential source-sink dynamics (Pulliam 1988).

Consideration of *M. musculus* when conserving cold blooded vertebrates is also imperative. *M. musculus* have previously been recorded impacting on native reptiles in New Zealand (Newman 1994, Lettink and Cree 2006). Reptiles need external sources of warmth and utilise habitats with dense ground cover (East *et al.* 1995) so they could overlap in habitat with *M. musculus* and suffer from *R. rattus* eradication that does not factor in the response of *M. musculus*.

Other vertebrates may need to be considered when managing rodent species. *Galaxias maculatus* (inanga, whitebait) eggs have been depredated by *M. musculus* (Baker 2006). Their eggs are laid on the banks generally minor waterways (Baker 2006), where contact with *M. musculus* might ordinarily be low because of the damp conditions. Reducing the *R. rattus* densities may increase *M. musculus* activity and increase egg predation.

Extant species of frog that are endemic to New Zealand, *Leiopelma hamiltoni* (Hamilton's frog), *L. pakeka* (Maud Island frog), *L. archeyi* (Archey's frog) and *L. hochstetteri* (Hochstetter's frog) are all threatened species (Daugherty *et al.* 1994). *M. musculus* have not been shown to be a cause of decline in native frogs (Towns and Daugherty 1994, Baber *et al.* 2006), despite their varying degrees of terrestrial habitat use that could make them prone. Perhaps *M. musculus* avoid their damp cool habitats. This is potentially supported by the most aquatic species, *L. hochstetteri*, which would

be less likely to come into contact with *M. musculus* is also the most widespread frog species (Daugherty *et al.* 1994).

There was weak evidence from the arena trials that *M. musculus* used physical features of the habitat other than ground cover as cues to preferred foraging habitats. The possible use of differing levels of canopy cover differs from Dickman's (1992) suggestion that cover over 1m did not influence *M. musculus* habitat choice. There was a trend for nocturnal foraging activity to decrease in short grass under the high canopy treatment. This fitted with the decreased foraging activity in short grass with the scent of *R. rattus* present. The use of indirect cues did not only concern the relationship with *R. rattus* but also diurnal avian predators. There was potentially a predation risk created by *Circus approximans* (Australasian harrier), this was the most probable explanation of higher diurnal foraging activity as canopy cover treatments became lower and provided direct cover. These patterns were not seen at night which suggests that *Ninox novaeseelandiae* (morepork, ruru) may not be a major predator of *M. musculus* though they were present in the area (*pers. obs.*). The lack of predatory risk posed *N. novaeseelandiae* is supported by the low proportion of *M. musculus* in their diet (Haw and Clout 1999, Haw *et al.* 2001). Ground cover has repeatedly been shown to be important in habitat use for *M. musculus* and other rodent species but my arena trials show that there may have been a secondary preference for canopy cover.

Nocturnal foraging behaviour in rank grass patches by *M. musculus* was not affected by canopy treatments during the arena trials. This suggests that there was the potential for coexistence with *R. rattus* where dense ground cover exists under continuous canopy. Overlap in both of these rodents species diet (Miller and Miller 1995) was not factored in the arena trials. At higher *R. rattus* densities, it would be expected that *M. musculus* would be excluded from some of the food resources

(Brown *et al.* 1996, Caut *et al.* 2007). At lower densities coexistence of both species could arise with less competition for food (Caut *et al.* 2007).

The change in foraging behaviour of *M. musculus* during the arena trials was assumed to be caused by *R. rattus*, which compete with *M. musculus* in natural settings (Brown *et al.* 1996, Caut *et al.* 2007). It is feasible that *R. rattus* also attract predators of both species, such as *M. erminea*. King *et al.* (1996) reported a correlation in abundance between *M. erminea* and *R. rattus* and between *Mustela nivalis* (weasel) and *M. musculus*. *M. nivalis* are not common throughout New Zealand and *M. erminea* are more numerous (Murphy *et al.* 1998a, King *et al.* 2001). Therefore, an overlap in habitat with *R. rattus* may increase *M. musculus* contact with *M. erminea* and reduce *M. musculus* activity. *R. rattus* may be used by *M. musculus* as an indirect cue for *M. erminea* causing the reduction in foraging activity, not the competitive relationship between *M. musculus* and *R. rattus* supposed. The behavioural responses of *M. musculus* to *M. erminea* need to be investigated exclusively to make more precise conclusions on their relationship. Similar but larger arena experiments with *R. rattus* physically present may comprehensively clarify the type of relationship between *R. rattus* and *M. musculus*. Additional research into the dynamics between more invasive small mammal species, whether competitive or predatory, would further our comprehension of these communities and improve the management of them.

The arena trials made it possible to control the access to the feed trays that were interfered with by other species in the giving up density trials on the landscape scale (Chapter 2). This made it possible to identify the preferences of *M. musculus*. Excluding other species and individuals from the enclosures meant that the responses of *M. musculus* may not have been completely representative of a natural setting but

did provide insight that can help to explain patterns that are observed in the environment.

By advancing our understanding of *M. musculus* habitat preferences the amount of effective effort put into pest management can be improved. Depending on the habitat preferences and ecology of the species of conservation interest, the degree of *M. musculus* eradication required can be determined or whether control is needed at all. If management of *M. musculus* is required, then effort can be asserted more effectively in habitats favoured by *M. musculus*. Further investigations into source-sink dynamics of *M. musculus* would strengthen this concept as a tool for conservation.



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