Interactions between ship rats and house mice

A thesis submitted in fulfilment
of the requirements for the degree of

Doctor of Philosophy
in
Biological Sciences
at
The University of Waikato
by

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The University of Waikato
2012

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

The ship rat (*Rattus rattus*)

The house mouse (*Mus musculus*)

Abstract

Interactions between coexisting invasive species can cause complications when their populations are managed to protect native biodiversity. The ship rat (*Rattus rattus*) is a widespread invasive species often targeted for management because of its negative impacts on native wildlife, particularly in otherwise mammal-depauperate ecosystems such as in New Zealand. However, where ship rats are removed, another common, coexisting invasive species, the house mouse (*Mus musculus*), is often detected more frequently, which may undermine the benefit of the management operation for biodiversity. The aim of this study was to better understand why house mice become more abundant, or potentially also more active and detectable, when released from suppression by ship rats through determining the mechanism involved. The hypothesised mechanisms were: exploitation competition, interference competition and intraguild predation.

Focusing on New Zealand, I reviewed diet studies of ship rats and house mice to have a clearer understanding of the resources they may share. I found that whilst some features of their diets differ, ship rats and house mice do show overlap in the range of food items they consume. Therefore they could compete for these shared resources if they were limited. However, in captive experiments I confirmed that ship rats exhibit predatory aggression towards house mice and therefore have potential to directly negatively influence mouse populations regardless of resource availability.

In response to the threat of predation by ship rats, house mice exhibited avoidance of caged rats during further captive experiments and this restricted their foraging choices. In the field, the foraging behaviour of mice in podocarp-broadleaf forest was also limited by the risk posed from abundant ship rats, which prevented them from accessing resources. In similar habitat at Pureora Forest Park during a longer term study of mouse populations, mice captured when ship rats were abundant had lower body mass compared to those captured

when ship rats were controlled, an effect that was not offset by supplementary feeding.

At Pureora, the ship rat control operations did not achieve optimal low ship rat levels, however, despite small mouse sample sizes, both the abundance of mice measured by live-trapping and their activity in tracking tunnels were positively affected. These measures were moderately correlated indicating that activity was related to mouse abundance. However, capture probability varied seasonally and according to rat abundance in unexpected ways, indicating more subtle and complex potential influences of ship rats on the probability of detecting mice.

My results indicate that the main mechanism by which ship rats suppress house mice is intraguild predation. This is because though apparently food restricted, house mice did not access resources I provided for them when ship rats were abundant, which rules out exploitation competition. Ship rats appear to view house mice as prey and opportunistically consume them, which differentiates intraguild predation from interference competition as the latter is primarily driven by resource defence. Even if predation events are rare, my research demonstrates that the risk effects of avoiding an abundant opportunistic predator appear to have a strong influence on the abundance and distribution of house mice.

Acknowledgements

I thank the following organisations for funding or support: The University of Waikato (main scholarship), Landcare Research (host organisation), Department of Conservation, The Royal Forest and Bird Protection Society (JS Watson Conservation Trust and Valder Conservation Grant), The Royal Society (Hutton Fund) and Waikato Regional Council (Environmental Initiatives Fund).

At the top of my list of people to thank are my supervisors Carolyn (Kim) King (University of Waikato), John Innes (Landcare Research) and Craig Gillies (Department of Conservation). I'm so grateful for their support, encouragement, wisdom and good humour. Kim gave me the opportunity to come to New Zealand in the first place and she and her husband Ken helped me settle in and start to understand the many ways in which this country is a unique and fascinating place. John allowed me to be based at Landcare Research where I've learned so much from working with him and his team members and from our stimulating discussions about animal behaviour and ecology. Craig has helped me keep in mind the applied aspects of my research as well as being a wealth of knowledge about mammalian pests and a great help with arranging field sites.

Thank you to everyone who was generous with their time and enthusiastically chatted about aspects of my research, especially at the start of the project. Staff at Landcare Research have been so helpful, especially Wendy Ruscoe, Penny Fisher and Deb Wilson. Yuki Fukuda and Dai Morgan were always willing to talk things through with me and offer advice. Stacey Foster shared rodent woes with me and helped in the field on numerous occasions. Bruce Patty was a massive help with technical stuff for the captive experiments. Bobby Smith of Agresearch loaned me cages and taught me procedures with mice. Jamie Mackay loaned me traps and answered mouse questions. Mark Smale made me laugh and was kind and encouraging during the final write-up stages.

Thank you to Matamata-Piako District Council for allowing me to study animals at the Water Treatment Reserve, and to the Department of Conservation (DOC) for letting me work at Pureora Forest Park. DOC Staff associated with Pureora

were helpful and supportive of the project, in particular, Howard Matthews and Dave Smith. A succession of people were unfortunate enough to be my field assistants at Pureora: Toni Cornes, Stacey Foster, Melissa Yeoman, Kelly DeVoy, Laura Bergner, Kane Lynn, Barry O'brien, Warrick Powrie, Jean-Baptiste Michael and Erin Bowkett. Thanks so much, especially those of you who suffered torrential rain, floods, trees falling over, exhaustion, vegetarian food, and my misery when we were catching so few mice and detecting so many rats.

I'm grateful to Maheswaran Rohan and Ian Westbrooke of DOC for allowing me to do their statistical modelling courses. Rohan gave further guidance about implementing what I learned. Steven Miller and Deb Wilson also gave advice about different aspects of analysis, thank you.

I apologise to friends and relatives who came to visit me here in NZ and had to entertain themselves because I had rodents to look after or field work to do. During her holiday, poor Hannah Ford donned a high viz vest and some 'tramping' boots and helped me put out DOC250 traps at Pureora. Thanks Han. I told her she was getting a unique New Zealand experience, but I don't think she's quite forgiven me.

Thanks to my family in England, particularly my parents Steve and Mandy Bridgman, for supporting my passion for wildlife research and going to live in faraway places. I acknowledge my mum and her compassion for all animals, which I keep in mind when working with pests. Thank you to my stepson Izach Fitzgerald for putting up with disrupted weekends and being dragged along to do field work. Zach's good humour, intelligence and curiosity are an inspiration.

Last but not least there's my partner Neil Fitzgerald who's put up with an awful lot these last few years. He's helped with field work, building stuff and other technical aspects of my project, not to mention being a general sounding board for my crazy ideas. Neil let me use his photos of ship rats and house mice for various presentations and for the second page of this thesis. It seems he can even make vermin look beautiful. I hope I haven't been too much of a moaning pom the last few years Neil, thanks loads for your support, you're the best.

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1 Main introduction

1.1 Intraguild interactions

Understanding the influence of interspecific interactions on the behaviour and ecology of organisms is a core area of scientific research (Begon *et al.* 2006). Relationships between species influence their abundance, distribution and evolution. Any change within an ecological community, which results in the addition, loss or alteration of the relative abundance of species, can therefore have cascading effects on other species present (Paine 1980; Pimm 1987; Brown *et al.* 2001; Zavaleta *et al.* 2001).

A guild is defined as a group of sympatric species that use similar resources (Root 1967). Intraguild (IG) interactions are therefore often characterised by competition for those resources that are in limited supply. Competition can manifest as exploitation (consumptive competition, Schoener 1983), where resources are depleted by individuals of one species and are therefore no longer available to those of another (Begon *et al.* 2006). Common examples of resources that may be exploited by two or more species are food and nest sites.

Competition can also involve one species directly interfering with the ability of another to access resources. Amongst vertebrates, this often involves antagonistic behaviour. Interference may be territorial or simply depend on individuals encountering each other and can involve varying levels of aggression, and may even be lethal (Schoener 1983). Whilst resources must be limited for exploitation competition to occur, interference competition can be evident even when resources are plentiful if individuals of either or both species harm one another (Schoener 1983).

Some species also exhibit IG predation where they kill and eat organisms that use similar resources as they do themselves (Polis *et al.* 1989). IG predators benefit from both the food acquired by killing their IG prey and also from some reduction in competition for other resources (Polis *et al.* 1989). IG predation may be predominantly an extreme form of interference competition resulting from

territorial aggression or resource defence (Sunde *et al.* 1999). Alternatively, IG predation may be predominantly associated with feeding, and reduced competition is incidental (Polis *et al.* 1989).

IG interactions are usually asymmetric with one species dominating another (Lawton & Hassell 1981). In the case of exploitation competition, the dominant will be whichever species is better able to use the resources of a particular habitat more effectively. Often smaller species have an advantage because they require less food in total and are therefore better able to withstand reduction in relative availability of resources caused by their competitor (Persson 1985). However, interference competition can redress this balance or allow larger species to be dominant, because being bigger is an advantage during antagonistic encounters (Persson 1985). IG predators are also usually larger than their IG prey (Polis *et al.* 1989; Donadio & Buskirk 2006).

IG interactions can sometimes lead to exclusion of subordinate species by those that are dominant. This can happen at different scales from microhabitat to landscape (Grant 1972; Ritchie & Johnson 2009). The more similar the niches occupied by two species, the more likely they are to compete (Macarthur & Levins 1967). According to Gause's competitive exclusion principle two competing species can only coexist in a stable environment by differentiation of their niches, otherwise one species will exclude the other (Gause 1934). There is evidence that IG predation is most common amongst species that are similar enough in size that they have a high probability of resource overlap, but where the IG prey is sufficiently smaller than the IG predator that the latter is unlikely to be injured (Donadio & Buskirk 2006).

1.2 Studying intraguild interactions within terrestrial vertebrate communities

Observations of negative correlations in abundance or distribution of species with similar niches were some of the early indicators to researchers that IG interactions may have consequences for ecological community structure (Grant 1972; Eccard & Ylönen 2003). For example, sympatric chipmunk (*Eutamias*)

species in North America and Canada are more abundant in different habitat types even though they occupy similar habitat when in isolation and appear to use similar resources (Brown 1971; Heller 1971).

In response to growing concern that such correlative studies provide only circumstantial evidence of the importance of IG interactions, there has been a move towards designing experiments to test the effects of these relationships by determining how interactions influence resource use and impact species at the population level (MacNally 1983). To have a better understanding of how species interact and to be able to generalise results to wider situations Tilman (1987) described the need to determine the mechanisms underpinning interactions. In order to achieve this, different approaches are required which include observations and experiments (Tilman 1987). Numerous methods have been used which broadly consist of studying niche overlap; the nature of direct interactions; effects on resource use; impacts on fitness parameters and life history characteristics; and effects on populations. These are discussed in the following sections.

1.2.1 Niche overlap

Whether or not species exhibit niche overlap may be inferred from what is already known about the resources they use. Resource use is mainly determined by the spatial ecology and diet of a species. Radio tracking, spool and line and trapping are examples of methods used to determine range and habitat use (e.g. Wijesinghe & Brooke 2004; Vieira *et al.* 2005; Glen & Dickman 2008; Stokes *et al.* 2009b). Diet can be assessed by stomach content analysis or by faecal analysis (e.g. Vieira 2003; Sweetapple & Nugent 2007; Glen & Dickman 2008). Various indices have been developed to measure niche overlap e.g. Pianka's index (Pianka 1973).

1.2.2 The nature of direct interactions

1.2.2.1 Identifying intraguild killing and predation

IG predation may be directly observed when, for example, researchers have witnessed large carnivores in open savannah habitat attacking and killing guild

members (Laurenson 1994; Durant 2000) and multiple observations of coyotes attacking red foxes have been compiled (Sargeant & Stephen 1989). Some observations of IG predation have been made in captivity by arranging staged encounters. For example, Takahashi and Blanchard (1982) observed the response of Norway rats and ship rats to intruders of the opposite species into their pen: Norway rats killed and partially ate ship rats. Observing animals in captivity can alleviate some of the practical difficulties of studying them in the field. However, ethical constraints usually prevent forced encounters between individuals of species that are likely to harm each other, because the situation is artificial and there is potential for suffering.

IG predation is also determined when the remains of IG prey are found and there is compelling evidence that death was caused by an IG predator (e.g. Doncaster 1992; Sunde *et al.* 1999). The remains of IG prey may also be found within the diet of potential IG predators as assessed by stomach content analysis (Stapp 1997). This evidence is circumstantial however, as scavenging may have occurred (Palomares & Caro 1999).

IG predation is most common amongst generalist predators (Polis *et al.* 1989). The terrestrial vertebrate IG predation literature is dominated by research on large terrestrial carnivores (Ritchie & Johnson 2009), and raptors also feature in a number of studies (Sergio & Hiraldo 2008). Examples from other groups exist, but are rarer. Amongst the rodents, one of the few examples is the grasshopper mouse (*Onychomys leucogaster*) which is an IG predator of other mouse species (Stapp 1997). It is difficult to determine to what extent IG predation is more prevalent amongst large terrestrial carnivores or easier to detect in large conspicuous species compared to small elusive ones (Palomares & Caro 1999).

1.2.2.2 Identifying non-lethal aggression

Like IG predation, in some cases, non-lethal aggressive behaviour may also be directly observed, particularly in conspicuous diurnal animals. For example, aggressive behaviour from dominant chipmunk (*Eutamias*) species excludes subordinates from preferred habitat (Brown 1971; Heller 1971). Conversely,

aggressive dominance was not observed in grey squirrels (*Sciurus carolinensis*) interacting with red squirrels (*Sciurus vulgaris*) so interference competition is not supported as an explanation for why the former has replaced the latter in the UK (Wauters & Gurnell 1999).

To address practical difficulties of studying behaviour in the wild, observations of non-lethal aggression have also been made in captivity by staging encounters. Many of these studies involve small mammals such as rodents and there may be some expectation that the species are unlikely to be predatory because they are granivorous or herbivorous. However the observed lack of predatory behaviour can provide further support for interference competition rather than IG predation as a mechanism of interaction (e.g. Maitz & Dickman 2001).

To determine which species is the dominant competitor during encounters behaviour patterns are observed. For example, Bleich and Price (1995) investigated the dominance hierarchy between kangaroo rat species *Dipodomys agilis* and *D. stephensi* in a terrarium. Dominance hierarchy was determined by which species exhibited aggressive or submissive behaviour, or initiated or retreated from interactions most frequently. Staged encounters provide information about the relationship between species, but are only useful as part of a wider study because animal behaviour under artificial conditions may not reflect what occurs naturally. Furthermore, dominance hierarchies do not always explain patterns of temporal or spatial distribution observed in the wild. For example, Pinter-Wollman *et al.* (2006) found that captive spiny mice *Acomys cahirinus* and *A. russatus* showed an opposite dominance relationship to what was hypothesised from field studies.

1.2.2.3 Avoidance

A number of studies have investigated whether subordinate or IG prey species perceive risk associated with the direct presence or indirect cues of a dominant competitor or IG predator and exhibit avoidance. Dickman (1991) showed that the small insectivorous mammal species *Antechinus stuartii* avoids interactions with a larger species: *A. swainsonii*. Conversely Wauters and Gurnell (1999)

found no difference in the time that red squirrels spent in habitat occupied by a dominant competitor, the grey squirrel, compared to other habitat, which supported the observed lack of aggressive dominance by grey squirrels, indicating that interference competition is not the mechanism by which grey squirrels replace reds (Wauters & Gurnell 1999).

Using playback, Durant (2000) showed that the sound of IG predators (lions and hyenas) caused cheetahs to leave the area. Scent can also elicit avoidance (Barreto & Macdonald 1999), although not always (Mukherjee *et al.* 2009). Avoidance can occur at different scales as animals may refrain from occupying habitat preferred by a dominant or predatory species or they may be present within the same habitat, but alter their activity or foraging behaviour (Sergio & Hiraldo 2008; Ritchie & Johnson 2009).

1.2.3 Effects on resource use

Optimal foraging theory has been used to demonstrate the effects of predators and competitors on resource use by measuring the giving up density (GUD) of resources left by foraging animals (Brown 1988). An animal should leave a resource patch when the harvest rate (H) is less than or equal to the metabolic cost (C), predation cost (P) and missed opportunity cost (MOC) of foraging there (Brown 1988):

$H \leq C + P + MOC$

Therefore the density of the resource left once the animal has given up foraging reflects the point at which foraging at this patch results in no perceived net gain (Ziv & Kotler 2003).

Often the resource used by an animal is difficult to measure directly. Brown's method involved the use of trays filled with sifted sand and millet seed to represent resource patches. Embedding the resource in a substrate causes harvest rate to decline with resource density (Brown 1988). By keeping resource availability constant, it is possible to measure the effect of different conditions on the foraging response of the animal.

GUDs have been investigated to identify the effects of exploitation and interference competition and also IG predation. For example, Ziv and Kotler (1993; 2003) demonstrated the effects of exploitation competition and interference competition for *Gerbillus andersoni allenbyi* and *G. pyramidum* by manipulating the presence or absence of the larger *G. pyramidum* within the environment at different scales. Mukherjee *et al*. (2009) found that the GUDs of red foxes were positively related to risk of IG predation from hyenas.

1.2.4 Impacts on fitness parameters and life history characteristics

Studying the effects of IG predation on life history characteristics can link resource limitation or direct mortality caused by exploitation, interference or IG predation to population size and distribution by determining how survival, reproduction and juvenile recruitment are influenced (Eccard & Ylönen 2002, 2003). Exploitation competition is expected to be manifested in fitness parameters which relate to food supply such as body mass, condition and growth which have consequences for survival, reproduction and juvenile recruitment (Wauters *et al.* 2000; Eccard & Ylönen 2002; Gurnell *et al.* 2004; Stokes *et al.* 2009a).

If body mass, condition and growth remains unchanged, but survival, reproduction or juvenile recruitment are affected, exploitation competition is unlikely to be the mechanism of interaction and direct interference or IG predation may be suspected (Stapp 1997; Eccard & Ylönen 2002; Stokes *et al.* 2009a). Reproduction may be limited by stress due to antagonistic encounters with competitors or fear of an IG predator (Kelly *et al.* 1998; Eccard & Ylönen 2002). Reduced survival may be due to antagonistic encounters resulting in lethal injuries or IG predation. However, in open field studies survival can be difficult to distinguish from residency and animals that disappear, classed as having died, may merely have been driven from an area due to interference competition or fear of IG predation (Palomares & Caro 1999; Eccard & Ylönen 2003; Ritchie & Johnson 2009).

Juvenile animals may be more vulnerable to interference competition or IG predation. Sometimes evidence for this is observed directly, for example red foxes have been observed killing arctic fox pups (Tannerfeldt *et al.* 2002). However, the effects of competition or IG predation on life history characteristics are best demonstrated via perturbation experiments.

1.2.5 Population level effects

1.2.5.1 Perturbation experiments

To determine the effects of IG interactions at the population level perturbation experiments are required where one species is removed from the system and the population sizes of other species are measured. Sometimes a reciprocal removal is carried out, but often there is already some evidence that one species is dominant so only these individuals are removed (Eccard & Ylönen 2003).

Some experiments use a 'Pulse' removal technique whereby a single, short term removal event is used to detect direct interactions within the community (Bender *et al.* 1984). For example, Dickman (1991) found that the insectivorous small mammal *Antechinus stuartii* was captured more frequently within hours of the removal of a dominant species *A. swainsonii*. Such a rapid response to the removal of another species is argued to reflect release from direct interference rather than exploitation competition because the latter would require recovery of resources, which takes time (Dickman 1991; Maitz & Dickman 2001). Longer term continuous removal of a species, known as 'press' experiments, are needed to detect indirect effects (Bender *et al.* 1984) and are used to determine the influence of interactions on fitness parameters and life history characteristics. For example, Stokes *et al*. (2009a) removed ship rats (*Rattus rattus*) to investigate competitive release of bush rats (*Rattus fuscipes*).

Removal studies, particularly over long periods of time, have inherent difficulties. Where removal takes place on open grids, recolonisation by the species being removed is often a problem (e.g. Higgs & Fox 1993; Thompson & Fox 1993). Removal treatment grids may act as 'sink' sites and draw in animals from the surrounding area. This may even reduce the numbers of animals on control grids

if they are too closely situated (Thompson & Fox 1993). Some researchers have opted to study animals within enclosures to avoid these effects (e.g. Grant 1970; Brown & Munger 1985; Eccard & Ylönen 2002). However, enclosures may not be viable for studying species in structurally complex habitats and they are expensive to construct and maintain.

1.2.5.2 Resource supplementation

Supplementing food can determine whether species are limited by food shortage in the presence of a competitor (Schoener 1983). Resource supplementation has been used extensively in field trials to test links between food availability and population responses (Boutin 1990). However, investigation of resource supplementation in a community context is rarer (Harris & Macdonald 2007).

If supplementary food is available to all species in the community, those limited by food shortage are expected to increase in population size. Those limited by interference or IG predation are expected to remain unchanged, or even decrease if the dominant species becomes more abundant. For example, studying small mammals in Australia, Banks and Dickman (2000) found that resource supplementation at food stations increased immigration and reproductive activity for two *Rattus* species whilst a smaller marsupial species, *Antechinus stuarti,* avoided areas with high rodent density indicating that interference competition prevented it from benefiting from increased resources.

1.2.6 Distinguishing between mechanisms

By studying the different behavioural and ecological attributes of species interactions described above it is possible to distinguish between IG predation, interference competition and exploitation competition as mechanisms underpinning them (summarised in Table 1. 1). However, a holistic approach is essential because some hypotheses considering different mechanisms may produce similar results (Table 1. 1) (Stapp 1997; St-Pierre *et al.* 2006).

In addition, it can be difficult to determine the proximate and ultimate factors that determine how and why species are limited by other guild members (Sergio

& Hiraldo 2008; Ritchie & Johnson 2009). For example, IG prey often avoid IG predators, which means death by predation is rare, but avoidance itself causes IG prey to suffer negative effects due to limited habitat use or restricted foraging opportunities (Ritchie & Johnson 2009). This situation is similar to limitation due to interference competition from an aggressive, but non-predatory guild member and may result in starvation which is associated with exploitation competition. In this scenario the proximate cause of death for the IG prey is resource shortage, but the ultimate cause is threat of predation. There is growing evidence that non-lethal effects of predation can have a major influence on prey populations even in classic predator-prey systems (Lima 1998; Preisser *et al.* 2005; Creel & Christianson 2008).

Alternatively, during times of food shortage, IG prey may take more risks when foraging and are thus more susceptible to predation. IG predators may also be hungrier due to shortage of the shared prey and more likely to exhibit IG predation. The proximate cause of death is therefore predation, but the ultimate cause is food shortage (Sergio & Hiraldo 2008).

As IG predation may be considered an extreme form of interference competition these two mechanisms are linked and difficult to distinguish and may even be context dependent (Polis *et al.* 1989). This is reflected in the carnivore literature where the terms IG predation or interference competition often appear to be used interchangeably. Researchers may simply acknowledge that either might take place and not attempt to discriminate between them (St-Pierre *et al.* 2006). However, where possible, a distinction can be made based on the potential evolutionary benefit of the killing behaviour, whether it is primarily a mechanism to reduce competition or more simply opportunistic predation of a profitable prey item (Polis *et al.* 1989; Stapp 1997; Sunde *et al.* 1999).

Table 1. 1 Ecological or behavioural attributes of intraguild interactions and how they have been interpreted in the literature as intraguild predation, interference competition or exploitation competition (compiled based on the reviews in: Grant 1972; Schoener 1983; Tilman 1987; Palomares & Caro 1999; Eccard & Ylönen 2003; Sergio & Hiraldo 2008; Ritchie & Johnson 2009)

	Direct mechanisms		**Indirect mechanism**
	Intraguild predation	**Interference competition**	**Exploitation competition**
Niche overlap	Diet or other resource overlap is evident and may be limiting	Diet or other resource overlap is evident and may be limiting	Diet or other resource overlap is evident and is limiting
Direct interactions	Direct interactions involve killing and eating of individuals of one species by those of another IG prey may show strong avoidance of IG predators The IG predator is usually larger than the IG prey	Direct interactions involve antagonistic behaviour by the dominant species towards the subordinate species Antagonistic encounters may be lethal, but are not predatory Subordinate species may avoid dominant species The dominant species is usually larger than the subordinate species	Direct interactions do not occur or are neutral Subordinate species do not avoid dominant species The dominant species in the environment may be smaller than the subordinate species

Effects on resource use	IG predator may limit access to resources for the IG prey as a result of the latter avoiding predation	Dominant species interferes with access to resources for the subordinate species due to territorial aggression or antagonistic encounters	Dominant competitor uses resources causing shortage for the subordinate competitor Dominant competitor may use resources more efficiently or effectively Food shortage may cause subordinate species to take more risks when foraging
Impacts on fitness parameters and life history characteristics	Survival may be reduced by direct effects of the IG predator Vulnerable life stages may be disproportionately affected No effect on body condition or growth indicates that poor survival was due to direct effects of predation However, body condition, growth, reproduction and residency may be influenced due to risk effects and stress	Survival may be reduced by direct effects of the dominant competitor Vulnerable life stages may be disproportionately affected No effect on body condition or growth indicates that poor survival was due to direct effects of antagonistic encounters However, body condition, growth, reproduction and residency may be influenced due to risk effects and stress	Survival, reproduction and juvenile recruitment may be affected indirectly by resource shortage Poor body condition or decreased growth rates of the subordinate species may be evident indicating food shortage rather than direct effects due to interference or predation Vulnerable life stages may be disproportionately affected

Population level effects	Abundance or distribution may be spatially or temporally negatively correlated with that of the IG predator Pulse removal of the IG predator may lead to increased abundance usually through immigration Press removal of IG predators may lead to increased abundance through enhanced survival, reproduction or recruitment Food addition does not increase population size	Abundance or distribution may be spatially or temporally negatively correlated with that of the dominant competitor Pulse removal of the dominant competitor may lead to increased abundance usually through immigration Press removal of dominant competitors may lead to increased abundance through enhanced survival, reproduction or recruitment Food addition does not increase population size	Abundance or distribution may be spatially or temporally negatively correlated with that of the dominant competitor Pulse removal of dominant competitor does not influence abundance Press removal of dominant competitors leads to increased abundance through enhanced survival, reproduction or recruitment Food addition increases population size

1.3 The study of intraguild interactions: relevance for terrestrial invasive species management

An area of applied ecology where knowledge about how species interact is particularly important is invasive species management. Invasive species are a major threat to biodiversity worldwide (Clavero & Garcia-Berthou 2005; Blackburn *et al.* 2010) and it is vital to understand how they interact with native flora and fauna in order to determine their effects and prioritise management for conservation (Gurevitch & Padilla 2004). Mechanisms can be varied and complex and include competition (Harris & Macdonald 2007; Dolman & Waber 2008; Stokes *et al.* 2009a) and IG predation (Hall 2011).

As the science of invasive species management has progressed, allowing control or even eradication of species over increasingly larger areas, it has become apparent that interactions between sympatric invasive species must also be thoroughly understood (Veitch & Clout 2002; Parkes & Murphy 2003; Towns & Broome 2003; Howald *et al.* 2007). This is because removal of one can cause an increase in another through mesocompetitor or mesopredator release (Soulé *et al.* 1988; Courchamp *et al.* 1999; Caut *et al.* 2007; Rayner *et al.* 2007; Witmer *et al.* 2007). Such unexpected consequences can undermine the net benefit of management for conservation and in some circumstances lead to even greater loss of native species (Soulé *et al.* 1988; Courchamp *et al.* 1999; Zavaleta *et al.* 2001; Tompkins & Veltman 2006; Caut *et al.* 2007).

In addition to the overall effects on abundance and distribution, interactions between multiple invasive species can also complicate management when species compete for the same devices or toxins used to control them. For example, during control operations exploitation competition for toxic bait may potentially lead to target animals having access to insufficient quantities (Morriss *et al.* 2011). Alternatively, interference from a dominant competitor or avoidance of an IG predator may hinder the access of a subordinate or prey species to bait or killing devices. Monitoring may also be influenced if a subordinate or IG prey species is prevented from accessing or unwilling to approach devices such as traps or footprint tracking tunnels used to detect them

(Brown *et al.* 1996; Harper & Veitch 2006). This can lead to misrepresentation of the abundance and distribution of this species in field surveys (Brown *et al.* 1996). The worst case scenario is that a subordinate or prey species is undetected prior to eradication of a dominant competitor or IG predator, but becomes abundant following (Witmer *et al.* 2007).

1.4 House mice and ship rats in New Zealand

Invasive species are the primary threat to native biodiversity in New Zealand, and mammals are the most destructive of the species that have been introduced (Atkinson 1989; Tennyson 2010). The main reason for this is that New Zealand has few native terrestrial mammals (only two surviving species of bats). Therefore many native species are not adapted to coexist with mammalian predators, so exhibit characteristics that make them particularly vulnerable to them (King 2005; Innes *et al.* 2010a). Controlling or where possible eradicating invasive mammals is essential for preserving what is left of New Zealand's native flora and fauna, a high proportion of which is rare and endemic (Towns & Broome 2003; Towns *et al.* 2006; Innes *et al.* 2010a).

Rodents feature amongst the most damaging of the mammals introduced to New Zealand (Towns *et al.* 2006). Of the four rodent species present, the most widely distributed are the house mouse (*Mus musculus*) and ship rat (*Rattus rattus*) (Innes 2005b; Ruscoe & Murphy 2005). Both species can live commensally with humans, and both have been accidentally transported around the world as stowaways. House mice reached New Zealand in the early to mid-nineteenth century via Australian and European merchant ships, and were transported inland along with the cargo they travelled in (Ruscoe & Murphy 2005). Ship rats reached New Zealand via trade ships in the mid to late nineteenth century and colonised the mainland and numerous islands in a relatively short time (Atkinson 1973).

House mice and ship rats are now found throughout the New Zealand mainland and on some offshore islands. They live both commensally with humans and also in native and exotic habitats (Innes 2005b; Ruscoe & Murphy 2005). Ship rats are

found in a range of habitats, but are abundant in structurally complex habitat, in particular, lowland podocarp-broadleaf forests (King *et al.* 1996c; Innes 2005b). Mice are also fairly ubiquitous, but are most abundant in habitat with dense ground cover (King *et al.* 1996c; Ruscoe & Murphy 2005). King *et al* (1996c) observed a negative correlation in the distribution of house mice and ship rats.

Ship rats prey on native wildlife including birds, bats and invertebrates and have contributed to or caused the decline or extinction of many species (Towns & Broome 2003; Innes 2005b; Towns *et al.* 2006; Innes *et al.* 2010a; Tennyson 2010). For example, when ship rats invaded Big South Cape in 1962 the bush wren (*Xenicus longipes*), greater short-tailed bat (*Mystacina robusta*) and at least one species of large invertebrate disappeared (Atkinson 1989). Predation of eggs and chicks by mammals, predominantly ship rats, limits Kōkako (*Callaeas cinerea*) populations on the New Zealand mainland (Innes *et al.* 1999; Flux *et al.* 2006).

The effects of house mice on native species are not as clear as those of ship rats and often cannot be separated from the effects of other introduced species present (Ruscoe & Murphy 2005). Mice prey on invertebrates and may drive some species to low levels (Ruscoe & Murphy 2005) and they will also prey on lizards and have been associated with suppression of lizard populations (Newman 1994). Another way in which both ship rats and house mice contribute to loss of native biodiversity is that they sustain populations of invasive apex predators such as stoats and cats that also prey on native species (O'Donnell & Phillipson 1996).

1.4.1 Ship rat management

Because of the known negative effects of ship rats on native biodiversity, this species is eradicated or sustainably managed where possible (Parkes & Murphy 2003). Eradication requires that likelihood of reinvasion is low, such as where the sea or pest-proof fencing acts as a barrier allowing eradication of ship rats from offshore islands and some mainland conservation areas (Towns & Broome 2003; Burns *et al.* 2011). Sustained control is the option taken where reinvasion cannot be prevented (Parkes & Murphy 2003). To maximise benefit for native species

(usually birds), but at the same time to minimise cost and effort, sustained control of ship rats often maintains low populations through spring and summer whilst birds are breeding and most vulnerable to predation, but ceases all control effort outside of this time (Parkes & Murphy 2003).

Methods used to eradicate or control ship rats include aerial or ground based distribution of toxic baits, or kill-trapping (Parkes & Murphy 2003; Towns & Broome 2003). Aerial baiting can cover large areas, including locations inaccessible on the ground. Some aerial baiting operations targeting another widespread mammalian pest, the brushtail possum (*Trichosurus vulpecula*), also affect ship rats (Innes *et al.* 1995). Ground based distribution of toxin involves placing bait in stations at intervals on a grid throughout the target area being managed (Thomas & Taylor 2002). Kill-traps are placed at intervals on a grid network. Kill trapping rodents is highly labour-intensive because these animals are often present at high densities and traps must be cleared and reset each time an animal is caught. For this reason toxic bait is usually the preferred method (Parkes & Murphy 2003).

To monitor ship rat populations the three main methods used are live-trapping, kill-trapping and tracking indices (Innes 2005b). All three methods can be used to generate indices of abundance. By marking live-trapped individuals, usually on grids or trapping webs, the minimum number of animals known to be alive (MNKA) can be calculated (Krebs 1966). Kill-trapping can be used to derive a trap success index by counting the number of animals captured per hundred trap-nights, correcting for traps that were triggered but did not catch (Innes *et al.* 1995; King *et al.* 1996c). Kill-traps are placed on lines or grids, and cleared daily (usually for three days). Tracking tunnels do not restrain animals, but measure their activity. Each tunnel contains a central inkpad flanked by paper so that animals walk through and leave prints which can be identified (King & Edgar 1977; Gillies & Williams 2007). Tunnels are usually set and baited for one night and the tracking index for, say, rats is the percentage of tunnels with rat prints detected in them. Tracking indices for ship rats have been found to correlate

with abundance estimated by other means (Brown *et al.* 1996; Innes *et al.* 2010b).

Abundance indices are a function of the number of animals present, but also the probability of detecting them (Slade & Blair 2000). Probability of detecting animals depends on how active they are and therefore how frequently they encounter devices (Stokes *et al.* 2001), and also how willing they are to interact with devices (Baker *et al.* 2001). These factors can vary between surveys, for example due to habitat type, food availability or weather (Stokes *et al.* 2001; King *et al.* 2003; Watkins *et al.* 2010b). Therefore as indices do not explicitly account for probability of detection, the relationship between the estimates generated and true abundance may vary by some unknown quantity, and different surveys may not be comparable (White 2005; Watkins *et al.* 2010b).

Live-trapping can be used to measure true abundance (or density) using closed-capture models which calculate the probability of detection (in this case the probability of capturing individuals) based on individual capture histories and incorporate this information to extrapolate to N (Efford 2004; White 2005). For example, using this type of analysis Wilson *et al*. (2007) found that densities of ship rats in mixed podocarp-broadleaf forest were 5 rats/ha and 9 rats/ha during autumn of two consecutive years. However, calculating true abundance requires reasonably large sample sizes and live-trapping can be labour intensive (McKelvey & Pearson 2001). Indices of abundance from kill-trapping and tracking are far easier to obtain and may provide adequate information for some monitoring purposes (Innes *et al.* 1995; King *et al.* 1996c; Blackwell *et al.* 1998; Watkins *et al.* 2010b).

1.4.2 Effects of ship rat management on house mice

The successful control or eradication of ship rats over recent years has drawn attention to the house mouse. After ship rat removal, house mice are often detected more frequently, even though the toxins and traps being used may also be harmful to house mice (Caut *et al.* 2007). This implies that some interaction between these species limits house mice when rats are present. For example

Innes *et al*. (1995) found that control of ship rats in podocarp-broadleaf forest of the North Island was associated with an increase in house mouse tracking rates 3-6 months after control began. Clout (1995) similarly detected mice following ship rat control when they had not been observed previously, and on islands, both off New Zealand and elsewhere in the world, ship rat eradications have been associated with increased house mouse abundance (Caut *et al.* 2007; Witmer *et al.* 2007).

This increase in mouse numbers may be yet another negative impact on native wildlife, and yet the science of managing house mouse populations is less advanced than for ship rats. Mice have been eradicated from some offshore islands but the success rate is lower than for rats (Howald *et al.* 2007; MacKay *et al.* 2007). The reasons for this are unclear, but as mice sometimes have small home ranges, they may survive operations where there are gaps in toxin distribution (MacKay *et al.* 2007). Toxic bait aversion or resistance may also be an issue (MacKay *et al.* 2007). Mice have been eradicated from some pest-proof fenced conservation areas, but remain a problem in others though it is unclear whether reinvading or residual animals are the cause (Burns *et al.* 2011).

Monitoring techniques used for house mice are the same as those used for ship rats. True abundance estimated using closed-capture models has been demonstrated to correlate well with the minimum number known alive (MNKA) index for house mice, but the relationship with footprint tracking indices is unclear (Ruscoe *et al.* 2001). In addition, ship rats may influence the activity and behaviour of mice making them less likely to be detected during field surveys (Brown *et al.* 1996; Harper & Cabrera 2010). Hence changes in house mouse detection rates following ship rat removal may be due to greater mouse abundance, but also higher probability of detection.

1.5 The relationship between house mice and ship rats

Exploitation competition, interference competition and predation have all been suggested as mechanisms underpinning the ship rat-house mouse relationship

(Clout *et al.* 1995; Innes *et al.* 1995; King *et al.* 1996c; Tompkins & Veltman 2006; Ruscoe *et al.* 2011). IG predation, as opposed to predation per se, is a more appropriate concept given that ship rats and house mice can be considered members of the same guild of terrestrial, omnivorous small mammals and therefore the relationship between them may have elements of both predation and competition. Here I review the information available and how it relates to different aspects of IG interactions.

1.5.1 Niche overlap

Ship rats and house mice are often present in the same habitat types but more abundant in different types (Miller & Miller 1995; King *et al.* 1996c). Hence, the fundamental niche of mice includes forest habitat in general, and therefore overlaps with that of ship rats at the broad scale. However, as mice increase in habitats dominated by ship rats once the rats are removed, it appears that their realised niche is constrained by rats at the local scale. Within forest habitat, ship rats are highly arboreal (Hooker & Innes 1995), which accounts for their impact on nesting birds given that they are able to access nests along very thin branches (Brown *et al.* 1998; Innes 2005b; Innes *et al.* 2010a). Despite also being excellent climbers, house mice are considered to be more terrestrial (Ruscoe & Murphy 2005). Ship rats therefore have access to a variety of resources that are unavailable to house mice. However, ship rats also spend time on the forest floor (Hooker & Innes 1995) and food items found amongst leaf litter are important to them much as they are house mice (Craddock 1997).

Plant matter consumed by ship rats and house mice is usually seeds and fruit, and animal matter is predominantly invertebrates (Innes 2005b; Ruscoe & Murphy 2005). Both species are opportunistic and flexible in terms of diet choice; however, they tend to rely on different items as the major component of their diet. The most common invertebrate item consumed by ship rats is usually weta (Orthoptera) (Innes 2005b), whilst mice are reported to eat lepidopteran larvae most frequently (Ruscoe & Murphy 2005). Ship rats and house mice may compete for the toxins, traps or tunnels used to control or monitor them, all of which exploit foraging behaviour by incorporating food lures.

1.5.2 The nature of direct interactions

Ship rats (average 120-160 g, Innes 2005b) are around eight times larger than house mice (average 15-20 g, Ruscoe & Murphy 2005) and prey on a range of invertebrates, but also on vertebrates such as birds (Brown *et al.* 1998; Innes *et al.* 2010a) and they scavenge dead conspecifics. Ship rats therefore show the general characteristics associated with IG predators (Polis *et al.* 1989). There are reports of ship rats killing house mice (Lidicker 1976; Granjon & Cheylan 1988), but these are mainly anecdotal and it is unknown whether this behaviour is frequent and if it is related to feeding. Few diet analysis studies of ship rats have found evidence of mouse remains. However, mouse DNA was detected in ship rat stomachs following a beech mast, when mice were at high density (McQueen & Lawrence 2008). Bramley (1999) found that mice were less active when housed near to a ship rat, indicating a fear response.

1.5.3 Effects on resource use

The effect of ship rats on the foraging behaviour of house mice has not been directly investigated. However, in the Galápagos Islands Harris and MacDonald (2007) found that at the population level house mice did not benefit from patchy food resources in the presence of ship rats, indicating that rats defended these food patches, or that house mice avoided them because of the presence of rats.

1.5.4 Impacts on fitness parameters and life history characteristics

King *et al*. (1996b) found that mouse populations in forest habitat dominated by ship rats were similar in reproductive rate but lower in recruitment rate than populations in habitat where ship rats were scarcer. A possible reason for this is that juvenile mice are particularly vulnerable to ship rats preying on nestlings or on juveniles emerging from the nest. Alternatively juvenile mice may be more susceptible to food shortage due to exploitation competition. In the Galápagos Islands, Harris and MacDonald (2007) found that house mice did not increase in body weight, reproductive activity or juvenile recruitment rate at sites where

ship rats were suppressed; instead, the abundance of mice increased due to immigration.

1.5.5 Population level effects

In New Zealand, Brown *et al*. (1996) found that a short-term removal of ship rats over just five nights resulted in a gradual increase in house mouse detection rates (Figure 1. 1). Similarly, in the Galápagos Harper and Cabrera (2010) found that during mouse specific trapping for four nights no animals were captured. However, once they began removing ship rats, they caught mice in increasing numbers, particularly after 13 days when the numbers of rats had declined substantially.

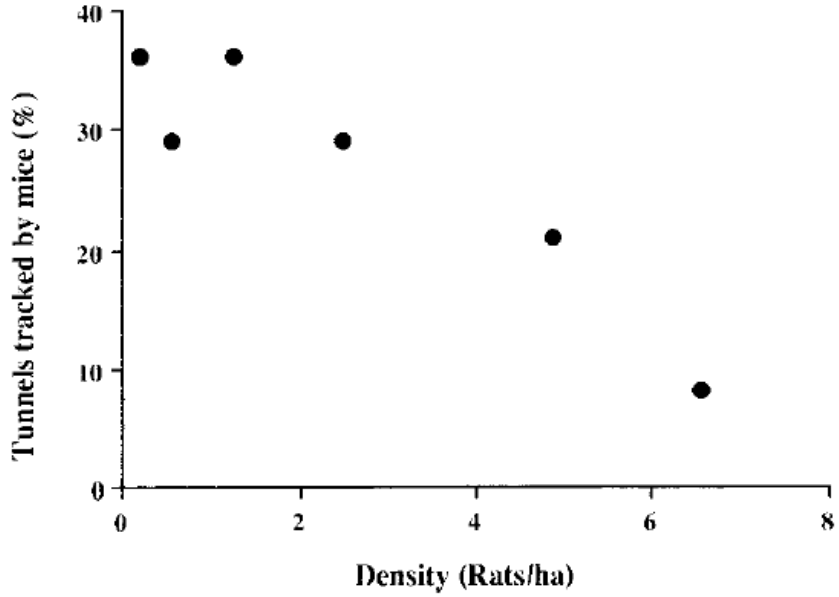


Figure 1. 1 Taken from Brown *et al*. (1996). Correlation between mouse tracking rates and density of ship rats still alive as removal trapping progressed over five nights.

Rapid increases in detection rates of mice during these pulse removal experiments indicate that the mice were suppressed by rats via some means other than indirect exploitation competition for food resources which take time to recover (Bender *et al.* 1984; Dickman 1991; Maitz & Dickman 2001). In addition increased survival as a result of release from mortality due to predation could not have achieved such a rapid response in the time. Instead, mice must

have been suppressed, either by interference by ship rats, or by the effects of avoiding them as predators. If so, it is unclear by what means the previously undetected mice could so rapidly appear. The two most obvious potential explanations are that (1) removal of rats creates a sink effect, allowing mice to immigrate into the area, possibly from refuge habitat; or (2) mice were present all along, but not detected because their activity was suppressed or they were unwilling to approach and interact with devices used to survey them, perhaps because of aversion to ship rat scent on devices (Brown *et al.* 1996).

Longer term press suppression of ship rats in New Zealand can be achieved by control operations, usually using toxins and often covering wide areas. Ruscoe *et al*. (2011) used closed capture models to analyse mark-recapture data for house mice and confirmed that abundance of mice did increase following removal of rats, however, where indices are used, changes in detection probability may contribute to some unknown extent to the observed differences in mouse detection rates. Several studies have found that mice are negatively affected by toxins used to control rats at first, but then increase over summer and to a peak in autumn when juveniles would be recruiting to the population (Innes *et al.* 1995; Miller & Miller 1995; Gillies *et al.* 2003b) (Figure 1. 2).

On Buck Island (USA Virgin Islands), Witmer *et al* (2007) observed an increase in house mouse abundance, or possibly also in activity, following eradication of ship rats. Prior to ship rat eradication house mice had not been detected. In the Galápagos, Harris and MacDonald (2007) found that press removal of rats resulted in greater abundance of mice due to immigration on to removal areas. They also found that food supplementation caused house mice to become more abundant, but only where food was broadly scattered, rather than patchily distributed. They reasoned that this was due to interference competition from ship rats which could monopolise food patches, but not defend scattered food.

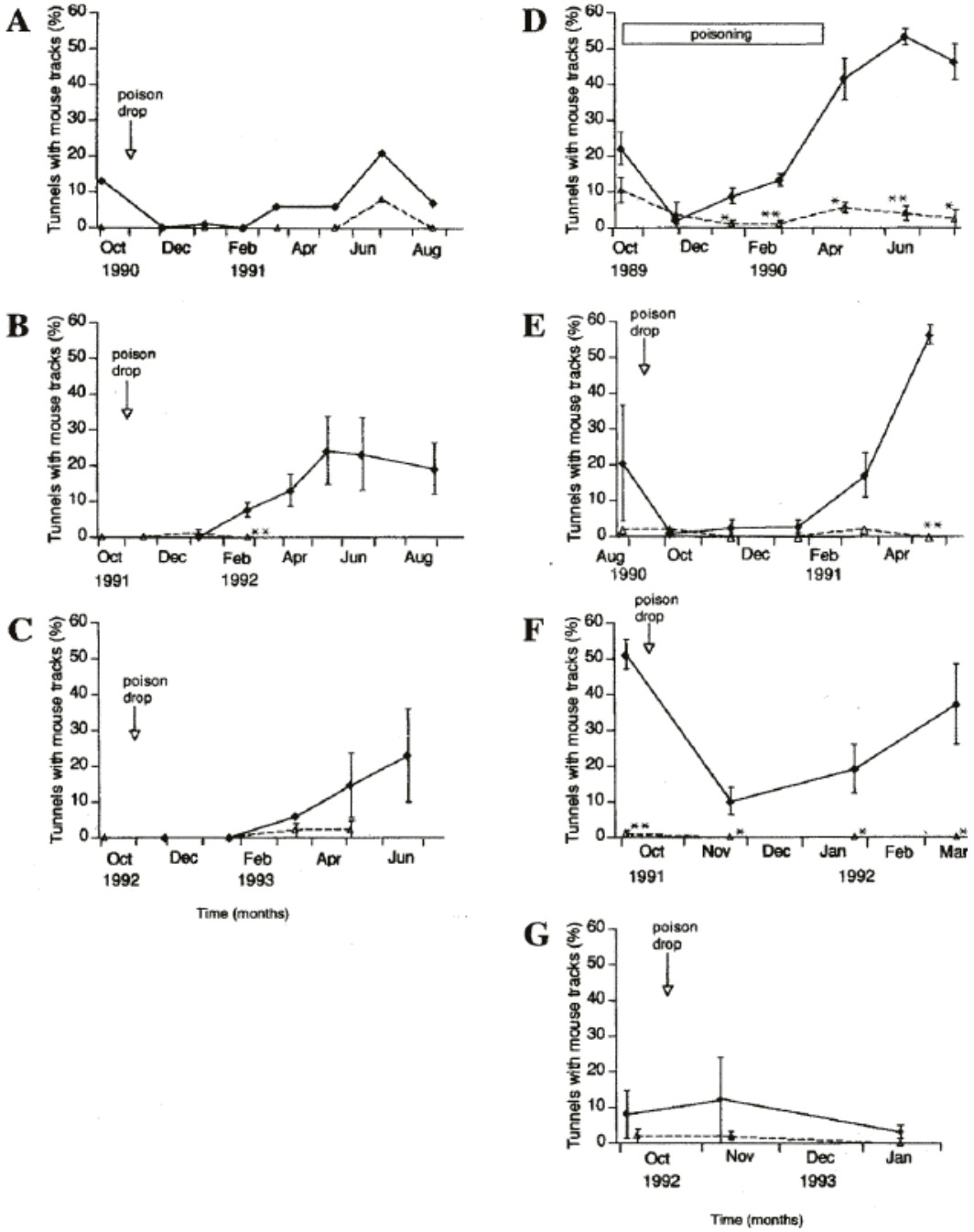


Figure 1. 2 Taken from Innes *et al*. (1995). Tracking frequencies of mice before and after poisoning at Kaharoa, 1990-91 (A), 1991-92 (B) and 1992-93 (C), and Mapara, 1989-90 (D), 1990-91 (E), 1991-92 (F) and 1992-93 (G). Bars are standard errors, and asterisks indicate significant difference (= P<0.01; * = P<0.05) between poison (solid diamond/solid line) and untreated (hollow triangle/dashed line) blocks.**

Table 1. 2 Studies providing information about ecological and behavioural attributes of the relationship between house mice and ship rats and whether, in aggregate for each category, this evidence supports, is consistent with or does not support a hypothesis of intraguild predation, interference competition or exploitation competition

				Direct mechanisms		Indirect mechanism
Attribute	**Evidence**	**Location**	**Reference**	**Intraguild predation**	**Interference competition**	**Exploitation competition**
Niche overlap	Ship rats and house mice can occupy many of the same habitat types, although they are most abundant in different types when both species are present	New Zealand	(King *et al.* 1996c)	Consistent with	Consistent with	Consistent with
	However, ship rats are arboreal, whilst house mice are more terrestrial	New Zealand	(Ruscoe & Murphy 2005)			
	Some overlap in diet, but uncertain what extent	New Zealand	(Ruscoe & Murphy 2005)			

Direct interactions	Ship rats exhibit traits that characterise intraguild predators	New Zealand	(Innes 2005b)	Support, but evidence anecdotal or circumstantial	Not supported, but evidence anecdotal or circumstantial	Not supported
	Some evidence that ship rats will kill house mice and eat them	France Australia	(Granjon & Cheylan 1988) (Lidicker 1976)			
	House mouse remains in ship rat stomachs	New Zealand	(McQueen & Lawrence 2008)			
	House mice were less active when in close proximity to ship rats	New Zealand	(Bramley 1999)			
Effects on resource use	Ship rats dominated patchy food resources by defending them against house mice or mice avoided them because rats were present	Galápagos Islands	(Harris & Macdonald 2007)	Consistent with	Consistent with	Not supported
Impacts on fitness parameters and life history characteristics	Ship rats may have suppressed mouse recruitment in forest habitat	New Zealand	(King *et al.* 1996b)	Consistent with	Consistent with	Not supported
	House mice immigrated on to sites where ship rats were removed, but survival, recruitment and body weight were unaffected	Galápagos Islands	(Harris & Macdonald 2007)			

Population level effects	Abundance of ship rats and house mice was spatially negatively correlated	New Zealand	(King *et al.* 1996c) (Miller & Miller 1995)	Consistent with	Consistent with	Not supported
	Pulse removal of ship rats resulted in increased abundance or activity	New Zealand Galápagos Islands	(Brown *et al.* 1996) (Harper & Cabrera 2010)			
	Press removal of ship rats resulted in increased abundance of house mice	New Zealand Galápagos Islands	(Ruscoe *et al.* 2011) (Harris & Macdonald 2007)			
	Press removal of ship rats resulted in increased activity or abundance of house mice	New Zealand USA Virgin Islands	(Gillies *et al.* 2003b) (Innes *et al.* 1995) (Miller & Miller 1995) (Witmer *et al.* 2007)			
	Supplementing food increased mouse abundance where it was distributed in a scattered regime, but not where it was patchily distributed	Galápagos Islands	(Harris & Macdonald 2007)			

1.6 Study aims

The aim of this thesis was to research interactions between house mice and ship rats in order to distinguish between exploitation competition, interference competition and IG predation as mechanisms underpinning the relationship between these species. The information from previous studies (summarised in Table 1. 2) indicates that although there is uncertainty about how much their diets overlap, ship rats and house mice have potential to compete for resources to some extent. However, exploitation competition may not be the main mechanism by which ship rats suppress house mice because there is also evidence of direct interactions. Ship rats may be predators of house mice, but much of the evidence for this is circumstantial or anecdotal. In addition there is little information about whether house mice avoid ship rats and if avoidance limits foraging.

Some of the information that has been collected overseas, such as that in the detailed and extensive experiments conducted by Harris and MacDonald (2007) may not be entirely relevant to rodents in New Zealand ship rat dominated habitats because differences in resource availability and habitat structure can influence characteristics of the relationship between species. Therefore certain aspects, such as the response of rodents to supplementary feeding and the effect of ship rat removal on life history characteristics and fitness parameters of house mice would benefit from further exploration in the New Zealand context. Pervading most previous studies of the population level effects of ship rat removal on house mice is uncertainty about the relative changes in abundance or activity and thus detection probability of mice, particularly for tracking tunnel indices.

The specific objectives, which comprise the chapters of this thesis, were therefore:

1. To review the numerous diet studies for ship rats and house mice and assess the extent to which they consume similar food items and therefore show diet overlap.

2. To observe encounters between ship rats and house mice and determine whether ship rats exhibit predatory behaviour.

3. To investigate whether house mice avoid ship rats and how this influences their foraging behaviour.

4. a) To compare the effects of ship rat control on house mouse abundance as measured by live-trapping and activity as measured using footprint tracking tunnels.

   b) To investigate the role of food availability in limiting house mouse abundance in ship rat dominated forest habitat.

As the chapters explore different aspects of the ship rat-house mouse relationship it seemed most appropriate to present each in the style of a separate research article although this inevitably leads to some repetition of background information.

All research components involving animals were approved by the University of Waikato Animal Ethics Committee, protocol numbers: 734, 735, 761 and 800.

2 A review of diet studies of ship rats and house mice: potential for competition?

2.1 Abstract

Ship rats (*Rattus rattus*) and house mice (*Mus musculus*) are the most widespread of the introduced rodents in New Zealand. The negative correlation in abundance and distribution of these species is often attributed to an interaction between them involving competition for food. However, despite having broadly similar niches, it is unclear the extent to which the diets of ship rats and house mice overlap. I reviewed studies that used stomach content analysis to determine the diets of ship rats and house mice in sympatry or isolation and occupying various habitat types. I compared the overall frequency of plant, animal or fungal matter eaten by ship rats and house mice and I investigated animal matter in more detail because it appears to be an important component of the diet of both species and detailed information was available. The diet of ship rats was dominated overall by plant matter in some studies and animal matter (predominantly invertebrates) in others whilst house mice primarily consumed animal matter in all studies. The most frequently reported invertebrate diet item for mice was lepidopteran larvae whilst for rats it was weta (Orthoptera). There was however overlap in the range and size of invertebrates consumed by rats and mice and cases in which the same food item was the major diet component when the species were in sympatry. There is potential for these species to compete for food. However, resource limitation must be demonstrated and house mice may be primarily influenced by interference competition or intraguild predation from ship rats, which can affect mice even when resources are plentiful.

2.2 Introduction

Where species use similar resources, their niches are described as overlapping and there is potential for competition between them. This is because resources depleted by individuals of one species are unavailable to those of another. If any of those resources are limited, the fecundity, survivorship or growth of either or both species may be negatively affected (Begon *et al.* 2006). Determining the resource use and degree of overlap between two species does not therefore predict that they will be competitors because the particular resources that overlap may not be limiting (Abrams 1980). However, it is one aspect of understanding the relationship between them (MacNally 1983).

The ship rat (*Rattus rattus*) and house mouse (*Mus musculus*) are introduced rodents in New Zealand as well as many other locations around the world (Innes 2005b; Ruscoe & Murphy 2005). They are the most widely distributed rodent species on the New Zealand mainland and often coexist, although they are more abundant in different habitat types (King *et al.* 1996c). Ship rats are more arboreal than mice and are associated with structurally complex forest, whilst house mice more frequently inhabit areas with dense ground cover (King *et al.* 1996c). Other introduced rodents in New Zealand are the Norway rat (*Rattus norvegicus*) and Polynesian rat or kiore (*Rattus exulans*), but they have a more limited distribution (Atkinson & Towns 2005; Innes 2005a). No native rodents exist in New Zealand, indeed the only native terrestrial mammals are two species of bat (King 2005).

Ship rats limit the abundance and distribution of house mice in rat-dominated habitat types in New Zealand, as demonstrated by increased mouse detections following removal of ship rats (Innes *et al.* 1995; Brown *et al.* 1996; Ruscoe *et al.* 2011). The same effect has also been observed in other parts of the world (Harris & Macdonald 2007; Witmer *et al.* 2007; Harper & Cabrera 2010). Competition has been suggested as a mechanism by which these species interact, and the obvious limiting resource is food.

In New Zealand, ship rat and house mouse populations are likely to be limited by food resources, particularly during winter (Fitzgerald *et al.* 1981; 1996; Ruscoe & Murphy 2005; Ruscoe *et al.* 2011). Numerous studies that have analysed the stomach contents of mice and rats have revealed that both species have opportunistic, omnivorous diets, with the bulk consisting of invertebrates and seeds or fruit (reviewed by Innes 2005b; Ruscoe & Murphy 2005). Some degree of resource overlap between ship rats and house mice has been proposed, however, to my knowledge there is no review of the results of these studies in the context of considering competition.

I reviewed studies where the diet of either or both species was examined and collated the results to compare the items consumed. The advantage of comparing information from multiple studies is that diet has been analysed for ship rats and house mice from a range of habitats, either in isolation from each other or in sympatry. Studies that examine species only in sympatry risk the possibility that only the realised niches of the animals are measured, because their resource use is limited by competition.

2.3 Methods

I searched for published studies of the diets of house mice and ship rats within New Zealand and I also included the results of MSc and PhD theses. I used the comprehensive reviews of Innes (2005b) and Ruscoe and Murphy (2005) as the basis for my search and also used internet search engines to find any further studies related to ‘mus’, ‘rattus’, ‘mouse’, ‘rat’, ‘diet’, ‘New Zealand’. I included one study from outside of New Zealand, that of Copson (1986) which took place on Subantarctic Macquarie Island. This Island is in the New Zealand biogeographic region and shares some similarities with New Zealand in terms of flora and fauna. The study was of particular interest because it looked at the diet of both species in sympatry.

I summarised the qualitative information provided in each study and I collated and graphically presented the quantitative information and measured niche overlap for a subsection of the data. Occurrence of food items in the diet of

animals was usually stated as frequency (percentage of animals within the sample that contained the item in their stomach), but was occasionally provided as the average percentage of the stomach volume, so I have indicated this in figures and excluded data provided as average percentage by volume from the niche overlap calculation.

Amongst studies, diet items were sometimes identified to genus or species, but usually only to Order and often items were grouped more broadly such as vertebrate meat or sign (e.g. hair or feathers). Several of the studies focused specifically on the invertebrate component of the diet, and only a small number of studies presented detailed information about the plant component, especially for mice. For this reason, to graph data, I summarised total frequencies of plant, animal and fungi matter in the diets of ship rats and house mice from studies where this information was provided. Where more detailed information was available I then divided the animal matter by Order for invertebrates and into vertebrate meat or vertebrate sign. I split some orders where necessary if the data available indicated a particular life stage (e.g. adult and larvae). If a genus or species was mentioned as being significant within the diet I have stated this amongst the qualitative information.

It was not possible to measure niche overlap for the plant and fungi component of the diets of ship rats and house mice because there was insufficient information at a consistent and ecologically relevant level (Greene & Jaksić 1983). For example some studies provided total frequency of all plant matter combined whilst others separated seeds and fruits and a few listed species. Because animal matter, specifically invertebrates, appears to be an important component of the diets of ship rats and house mice, particularly for reproduction (Miller & Webb 2001; Sweetapple & Nugent 2007) I deemed it useful, for descriptive purposes (Abrams 1980; Krebs 1999) to calculate overlap for this aspect of their niche. I calculated the mean frequency of occurrence for each diet item (from the studies where sufficient detailed information was provided see Appendix 1 and Appendix 2) weighted by sample size and used Pianka's index (Pianka 1973) in R (R Development Core Team. 2011) (package = pgirmess,

function = piankabio) to determine overlap. This method gives an index O_{jk} of between 0 (no overlap) and 1 (complete overlap) calculated as:

$$O_{jk} = \frac{\sum P_{ij} P_{ik}}{\sum P_{ij}^2 \sum P_{ik}^2}$$

where P_{ij} = frequency of resource category i of the total resources used by species j and P_{ik} = frequency of resource category i of the total resources used by species k.

2.4 Results

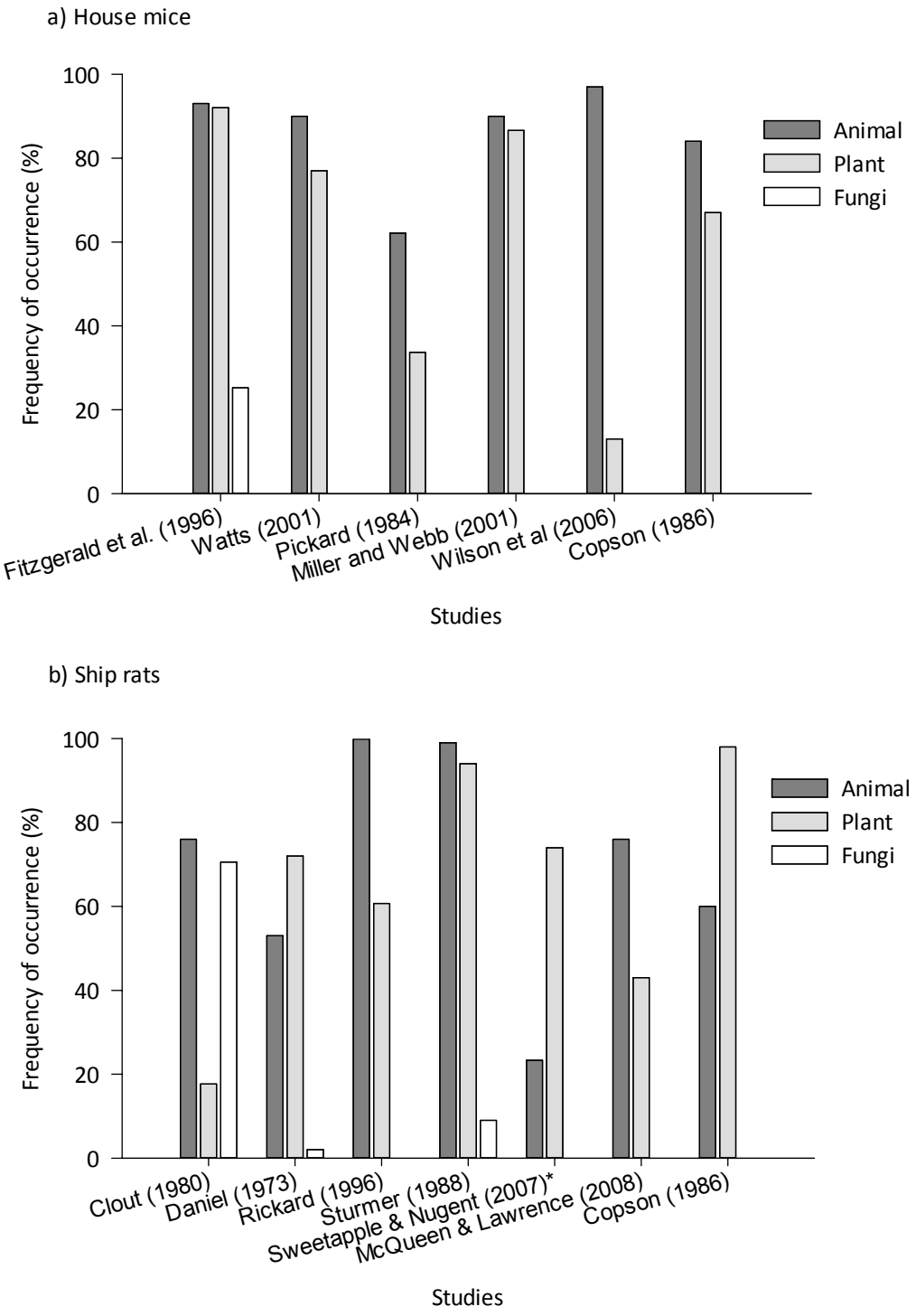
2.4.1 Total plant, animal and fungi diet components

All studies showed that ship rats and house mice were omnivorous. Their diets contained plant matter, usually seeds or fruit; animal matter, which consisted mainly of invertebrates; and in some cases fungi, including the fruiting body and spores (Figure 2. 1, Table 2. 1, Table 2. 2). Animal matter always featured most frequently overall in the diets of house mice in a range of habitat types (Figure 2. 1.a, Table 2. 1), though there could be seasonal differences (Fitzgerald *et al.* 1996). In some studies plant matter was found almost as often as animal matter (Fitzgerald *et al.* 1996; Miller & Webb 2001) whilst in others it was a much less frequent item (Wilson *et al.* 2006). Fitzgerald *et al*. (1996) found fungi in 25 % of mice and Baden (1986) also found that it was present in 4-16% of samples, but it was not detected in other studies.

The diet of ship rats was dominated by plant matter in some studies (e.g. Daniel 1973; Copson 1986; Sweetapple & Nugent 2007) and animal matter in others (e.g. Clout 1980; Rickard 1996; McQueen & Lawrence 2008) (Figure 2. 1.b, Table 2. 2). This could vary throughout the year, for example, Innes (1979) found that animal matter dominated the diet of ship rats overall, but plant matter was more prevalent in autumn and winter. The difference in prevalence of animal or plant matter did not appear to be related to broad habitat type because studies from forest described as podocarp-broadleaf showed variation (Daniel 1973; Innes 1979; Sweetapple & Nugent 2007). Fungi was not present or not detected in

most studies, but was a common item in the diet for ship rats sampled in pine forest where it was found in 71% of samples (Clout 1980) and was present to a lesser degree in podocarp-broadleaf forest (2%, Daniel 1973; 9%, Sturmer 1988).

Copson (1986) studied both ship rats and house mice in sympatry on Macquarie Island. He remarked that their diets were qualitatively similar, but had considerable quantitative differences in terms of the plant versus animal components: “The house mouse's diet consists mainly of invertebrates, some seed and plant material and occasional vertebrate flesh; the ship rat's diet is mainly plant matter supplemented by invertebrates and vertebrate material.” Copson reported that mice appeared to preferentially prey on invertebrate items because plant items were also available to them through the year, but were not eaten frequently.



*Data are percentage by volume instead of frequency

Figure 2. 1. Occurrence of animal or plant food items in the diet of house mice (a) and ship rats (b) as determined by stomach content analysis. Data are from studies that have taken place in New Zealand and in which totals for these categories were presented. One exception is Copson (1986), which took place on Subantarctic Macquarie Island, but provides information about both species in the same location. More information about studies including habitat type and sample size is presented in Table 2. 1 and Table 2. 2.

Table 2. 1. Diet studies for house mice in a range of habitats and in the presence or absence of ship rats. All data are from New Zealand except the study by Copson (1986) which took place on Macquarie Island

Reference	Location	Habitat	N	Summary of results	Ship rat diet and abundance (same site)
Badan (1986) 1.	Woodhill State Forest, near Auckland, North Island	Young pine (*Pinus radiata*) forest	260	Data presented in Figure 2. 2.a. Lepidopteran larvae dominated the diet, predominantly variable-bell moth (*Pyrogotis semiferana* Walker) larvae, but also Kowhai moth (*Uresiphita polygonalis maorialis* Felder) larvae Seeds (Inkweed and smooth fleabane (*Erigeron pusillus* Nutt.) featured except in December	Diet not sampled Abundance not mentioned
Badan (1986) 2.	Same as Badan (1986) 1.	Mature pine (*Pinus radiata*) forest	334	Same as Badan (1986) 1.	Diet not sampled Abundance not mentioned
Badan (1986) 3.	The Hunua Ranges, North Island	Kauri (*Agathis australis Salisb.*) forest with beech (*Nothofagus truncata Col.*)	117	Data presented in Figure 2. 2.a. Lepidopteran larvae made a smaller contribution than in Badan (1986) 1. And 2. Kauri seeds eaten	Diet not sampled Abundance not mentioned

Copson (1986)	Subantarctic Macquarie Island	Grassland, herbfield and fen	108	Data presented in Figure 2. 1.a. Invertebrates were the major diet component with spiders (Aranaea) and lepidopteran larvae most common Plant material was mainly seeds including *Callitriche antarctica*	Diet sampled, see Table 2. 2
Craddock (1997)	Wenderholm Regional Park and Heaton's farm, near to Auckland, North Island	Native broadleaf coastal forest	221	Plant component not studied Lepidoptera larvae were the major invertebrate component of the diet and spiders (Araneae) also featured frequently Cave weta (Orthoptera, *Rhaphidophoridae*) and tree weta (Orthoptera *Stenopelmatidae*) were also eaten, but were a smaller component Mice preferred prey in the range 3-12 mm	Diet sampled, see Table 2. 2 Present at variable abundance (controlled in some areas)
Fitzgerald *et al*. (1996)	Orongorongo Valley, near Wellington, North Island	Beech (*Nothofagus truncata*) and podocarp-broadleaf forest Mice equally numerous in both habitats and no diet differences noted	830	Data presented in Figure 2. 1.a. and Figure 2. 2.a. Invertebrate and plant items were both frequently found Seed was the most common plant item Lepidoptera larvae were the most common invertebrates followed by spiders (Aranaea)	Diet not sampled Present at variable abundance, mainly scarce in beech forest

Jones and Toft (2006)	Boundary Stream Mainland Island, Hawkes Bay, North Island	Mixed beech, tawa and podocarp forest	66	Data presented in Figure 2. 2.a. Invertebrates were the major diet component with Lepidoptera larvae (particularly *Cryptaspasma querula*) most prevalent followed by spiders (Aranaea)	Diet not sampled Present at low abundance
Miller and Miller (1995)	Rangitoto Island, Hauraki Golf	Coastal vegetation Open scoria and kanuka (*Kunzea ericoides*) forest	179	Invertebrates were the major diet component with tree weta (Orthoptera, *Hemideina thoracica*) most common Spiders (Aranaea), cockroaches (Blattodea) and centipedes (Chilopoda) were also present *Collospermum hastum* seeds were found	Diet sampled, see Table 2. 2 More common in forested areas
Miller and Webb (2001)	Ocean View Recreational Reserve, Otago, South Island	Coastal sand dunes, vegetation dominated by marram grass (*Ammophila arenaria*)	102	Data presented in Figure 2. 1.a. and Figure 2. 2.a. Invertebrates were the major diet component, mainly lepidopteran larvae followed by beetles (Coleoptera) Plant material was also found frequently	Diet not sampled Not detected
Pickard (1984)	Mana Island	Grassland/scrub	282	Data presented in Figure 2. 1.a. and Figure 2. 2.a. Invertebrates were the major diet component	Not present

Watts (2001)	Rotoiti Nature Recovery Project, Nelson Lakes National Parks, South Island	Beech forest	30	Data presented in Figure 2. 1.a. and Figure 2. 2.a. Invertebrates were the major diet component, mainly Lepidopteran larvae, spiders (Araneae) and beetles (Coleoptera) Plant material was mainly seed	Diet not sampled Not usually prevalent in beech forest
Wilson *et al*. (2006)	Mount Burns, Fiordland National Park, South Island	Alpine tussock grassland and beech forest	67	Data presented in Figure 2. 1.a. and Figure 2. 2.a. Invertebrates were the major diet component (61% by volume of the stomach contents, with bait making up the bulk of the remainder) Weta (Orthoptera) dominated the diet along with spiders (Aranaea) and lepidopteran larvae Plant material consisted mainly of seed	Diet not sampled Not detected

Table 2. 2. Diet studies for ship rats in a range of habitats and in the presence or absence of house mice. All data are from New Zealand except the study by Copson (1986) which took place on Macquarie Island

Reference	Location	Habitat	N	Summary of results	House mouse diet and abundance (same site)
Blackwell (2000) 1.	Lake Waikaremoana, Te Urewera National Park, North Island	Mixed podocarp-broadleaf and beech forest	49	Data presented in Figure 2. 2.b. Invertebrates were the major diet component particularly weta (Orthoptera), and coleopteran and lepidopteran larvae also featured	Diet not sampled Usually at very low abundance
Blackwell (2000) 2.	Same as Blackwell (2000) 1.	Mixed podocarp-broadleaf and beech forest	121	Same as Blackwell (2000) 1.	Diet not sampled Usually at very low abundance
Clout (1980)	East of Tokoroa in the central North Island	Pine (*Pinus radiata*) plantation	17	Data presented in Figure 2. 1.b. and Figure 2. 2.b. Invertebrates were the major component of the diet with lepidopteran larvae and weta (Orthoptera) featuring most frequently Pselaphinae (beetles <2.5 mm long) were present Plant material included moss and pine needle fragments. No seed or fruit was detected.	Diet not sampled Not detected

Copson (1986)	Subantarctic Macquarie Island	Grassland, herbfield and fen	95	Plant matter was the major diet component including *Callitriche antartica* seeds and *Poa* sp, Invertebrates also featured, particularly spiders (Araneae) and lepidopteran larvae	Diet sampled see Table 2. 1
Craddock (1997)	Wenderholm Regional Park and Heaton's farm, near to Auckland, North Island	Broadleaf coastal forest	103	Plant component not studied Lepidopteran larvae dominated the invertebrate component of the diet and cave weta (Orthoptera, *Rhaphidophoridae*), tree weta (Orthoptera *Stenopelmatidae*) and beetles (Coleoptera) also featured prominently Rats targeted invertebrates that were >3 mm in size although they did eat some that were <3 mm >50% of the invertebrates consumed in both areas were <12 mm	Diet Sampled see Table 2. 1 Present in variable abundance
Daniel (1973)	Orongorongo Valley, Wellington, North Island	Podocarp- broadleaf forest	173	Data presented in Figure 2. 1.b. and Figure 2. 2.b. Plant matter dominated the diet, mainly comprising unidentified pericarp or endosperm material, which probably comprised kernels or endosperm of hinau, mira or nikau palm nuts Of the invertebrate component, tree weta (Orthoptera) were particularly prominent.	Diet not sampled Usually scarce in this habitat type when rats are present

Innes (1979)	Tiritea Catchment Reserve, Northern Tararuas, North Island	Podocarp-broadleaf forest	180	Data presented in Figure 2. 2.b. Invertebrates were the major diet component, particularly weta (Orthoptera, *Hemideina*) Arthropods eaten included beetles (Coleoptera), spiders (Araneae), ants (Hymenoptera), moths (Lepidoptera), centipedes (Chilopoda) and nymphal cicadas (Hemiptera) Plant foods predominated in autumn and winter particularly Kawakawa (*Macropiper excelsum*) and Kiekie (*Freycinetia banksii*) seed	Diet not sampled Very low abundance
McQueen and Lawrence (2008)	The Dart Valley, South Island	Beech (mostly *Nothofagus fusca and N. menziesii*)	98	Data presented in Figure 2. 1.b. Invertebrates were the largest diet component Plant material also featured, mainly beech seed Hairs featured in 46% of animals and skin with hairs attached in 12%. Mouse DNA found in 6/10 stomachs sampled for it and rat DNA in 8/10	Diet not sampled Very high abundance
Miller and Miller (1995)	Rangitoto Island, Hauraki Golf, North Island	Coastal vegetation, open scoria and kanuka (*Kunzea ericoides*) forest	26	Inverts were the major diet component and tree weta (Orthoptera, *Hemideina thoracica*) were most common Slugs (Gastropoda) and cockroaches (Blattodea) also featured Karo (*Pittosporum crassifolum*) seeds were found	Diet Sampled see Table 2. 1 Abundant at times, trapped most often on open scoria

Rickard (1996)	Okarito Forest, Westland National Park, South Island	Lowland podocarp forest	28	Data presented in Figure 2. 1.b. and Figure 2. 2.b. Invertebrates were the major diet component with weta (Orthoptera, *Hemideina crassiden & Hemiandrus sp*) most common and spiders (Aranaea) and beetles (Coleoptera) also featuring No beetles with a length <8 mm were found Plant material was seed or fruit	Diet not sampled Abundance undetermined
Sturmer (1988)	Stewart Island	Mixed podocarp and silver-pine forest	415	Data presented in Figure 2. 1.b. and Figure 2. 2.b. Invertebrates were a major component of the diet, but plant material also featured frequently Weta (Orthoptera) were the most frequently eaten food item Miro (*Prumnopitys ferruginea*) fruit was most common plant item followed by dwarf mistletoe (*Korthalsella salicornioides*) and rimu fruit (*Dacridydium cupressinum*)	Not present
Sweetapple and Nugent (2007)	Hauhungaroa Range, Pureora Forest Park, North Island,	Podocarp-broadleaf forest	218	Data presented in Figure 2. 1.b. Plant matter was the major component of the diet, particularly seed of miro (*Prumnopitys ferruginea*) and toro (*Myrsine salicina*) and fruit of pokaka (*Elaeocarpus hookerianus*) and pepper tree (*Pseudowintera colorata*)	Diet not sampled Scarce when rat trapping for diet analysis took place

2.4.2 Animal matter in more detail

Lepidopteran larvae were consistently mentioned as the most frequent item in the diet of house mice in almost all studies across a range of habitat types and in the presence and absence of ship rats (Table 2. 1, Figure 2. 2.a). Spiders (Aranaea) were frequently found and beetles (Coleoptera) featured prominently in several studies. Weta (Orthoptera) were also mentioned (Table 2. 1, Figure 2. 2.a) and in two studies weta dominated the diet (Miller & Miller 1995; Wilson *et al.* 2006).

In most studies, weta (Orthoptera) were the most frequently found item in the diet of ship rats (Table 2. 2, Figure 2. 2.b). Daniel (1973) noted that rats with weta in their stomachs often also had finely masticated green leaf material, which he suggested was present having been eaten by the weta. In two studies lepidopteran larvae were the most frequently found item (Clout 1980; Craddock 1997). On Macquarie Island, where weta are not present (Marris 2000), Copson (1986) reported that spiders (Aranaea) featured most prominently in ship rat stomachs. Pianka's index of dietary overlap between ship rats and house mice for the invertebrate component of the diet was 0.407.

Rickard (1996) found that ship rats preferentially preyed upon beetles >8 mm in length. Craddock (1997) found that rats targeted invertebrates that were >3 mm in size, but did eat some that were <3 mm. He also noted that >50% of the invertebrates consumed in both areas were <12 mm indicating that relatively small prey items were important to ship rats. Craddock also studied mice in the same areas and reported that they preferentially ate items in the range 3-12 mm, but also sometimes took items >12 mm. In other studies ship rats were also recorded consuming small items such as ants (Innes 1979) and Pselaphinae (small beetles < 2.5 mm) (Clout 1980) although these did not constitute major components of the diet.

Miller and Miller (1995) studied ship rats and house mice on Rangitoto Island and found that the diets of both were dominated by tree weta of the species

Hemideina thoracica. Rats and mice therefore relied on the same species as a major component of their diets.

Craddock (1997) reported that in broadleaf coastal forest there was potential for ship rats and house mice to compete for the lepidopteran larvae that was a major feature of both their diets. However, he also found that there were notable differences in the diets of the species with ship rats consuming a greater variety of invertebrates as their diet featured groups (Blattodea, Hymenoptera, Isopoda, and Collembola) that were not eaten by mice. In addition, whilst both species predominantly ate prey that could be found on the forest floor, ship rats also consumed arboreal species (Craddock 1997). Consumption of arboreal species by ship rats was also described by Blackwell (2000).

Several studies linked invertebrate consumption to important life stages requiring high energetic demands. For example, Miller and Webb (2001) found the remains of spiders (Aranaea) more often in reproductively active mice of both sexes than in non-reproductive mice in summer; and Sweetapple and Nugent (2007) found that ship rat fecundity was closely correlated with invertebrate consumption.

More studies recorded vertebrate remains for ship rats than for house mice (Figure 2. 2.b). Bird feathers and remains of lizards were found in mouse stomachs only on Mana Island (Pickard 1984). Four studies found bird feather in the stomachs of ship rats (Daniel 1973; Innes 1979; Clout 1980; McQueen & Lawrence 2008). Vertebrate remains were usually infrequently found (<6% frequency of occurrence) except in McQueen and Lawrence's (2008) study of ship rats during a mouse plague which followed a masting event in beech forest where vertebrate remains of house mice, ship rats and birds were common in stomachs of ship rats (hairs in 46%, skin with hairs attached in 12% and feathers in 8%).

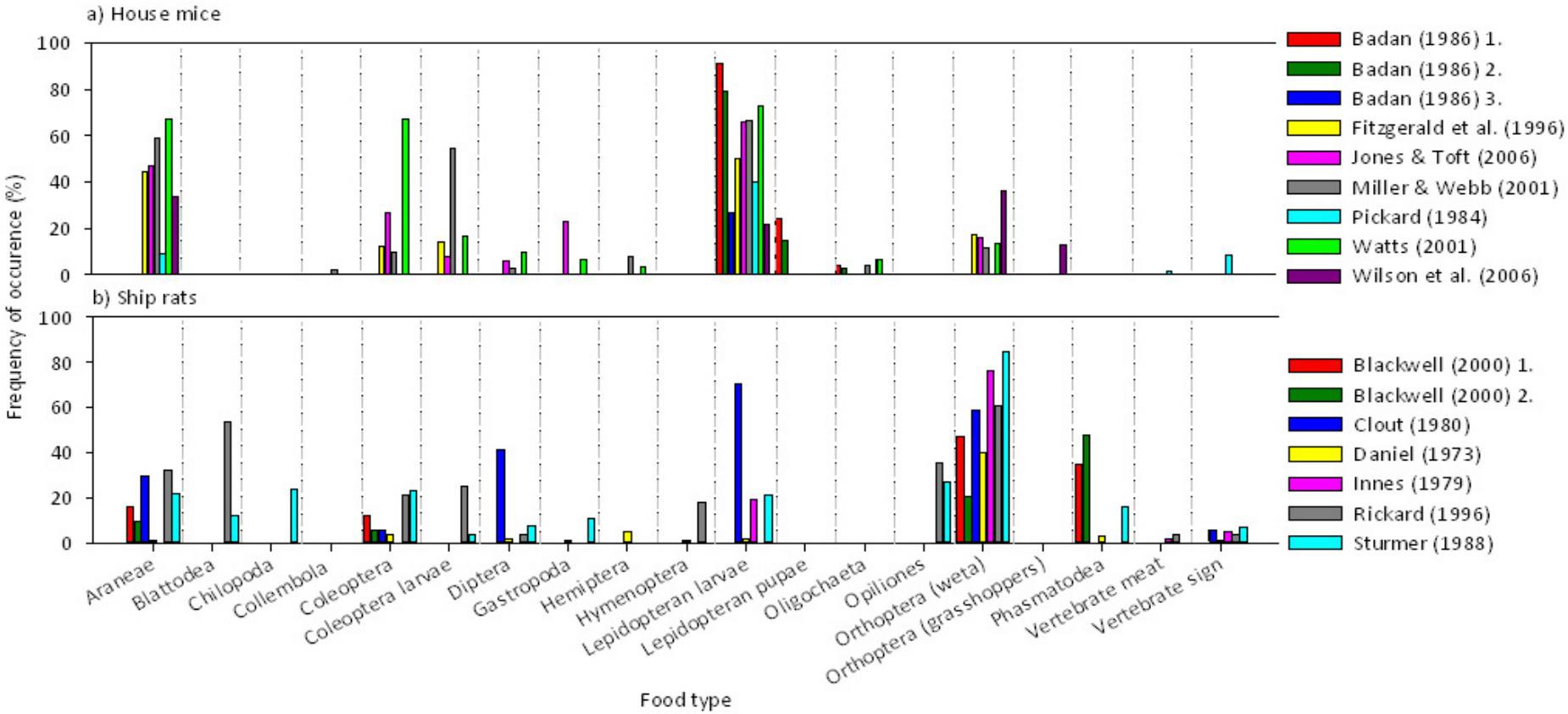


Figure 2. 2. Breakdown of the animal component of the diets of house mice (a) and ship rats (b). Data are from studies in New Zealand. Table 2. 1 and Table 2. 2 give further details of the studies including habitat information and sample size.

2.5 Discussion

Ship rats and house mice exhibit opportunistic, omnivorous feeding habits and these attributes have played a prominent part in enabling them to invade many different locations and habitat types around the globe (Landry 1970; Howald *et al.* 2007; St Clair 2011). In this review focused on diet studies of ship rats and house mice in New Zealand, these characteristics were evident as both species consumed a broad range of food items. Some authors also commented on the opportunistic and flexible nature of their study species' diets (Sturmer 1988; Blackwell 2000).

Overall, animal matter, primarily invertebrates, dominated the diet of house mice in all studies. The diet of ship rats was also dominated by animal matter in some studies, showing similarity with house mice. However, in others ship rats differed from house mice in that plant matter was most frequently observed in stomachs. Predominance of plant matter in the diet of ship rats is usual in locations outside of New Zealand. Either exceptional availability of invertebrates (notably weta) or scarcity of fruit could explain why ship rats are often found to consume more animal matter in New Zealand (Innes 2005b).

Despite the prevalence of plant compared to animal matter in the diet of ship rats in some studies, consumption of animal matter, predominantly invertebrates, was linked to fecundity of both species (Miller & Webb 2001; Sweetapple & Nugent 2007) indicating that it is an important component. Pianka's index of dietary overlap was moderate for the invertebrate component of the diet of house mice and ship rats. This reflects overlap in many of the invertebrate types consumed by both species, but also quantitative differences in the main component of the diet with the most frequently reported major invertebrate diet item being lepidopteran larvae for mice and weta (Orthoptera) for rats. However, there were examples of both species in sympatry consuming the same food item as the main component of their diet (Miller & Miller 1995; Craddock 1997), which would cause greater overlap and more potential for competition if that resource was limiting.

As ship rats are considerably larger (approximately eight-times) than house mice, it is possible that they eat similar groups of invertebrates at the Order level, but consume species of different sizes. Differentiation in the species consumed would reduce competition. However, there was evidence of overlap in the size range of invertebrate species consumed by ship rats and house mice (Craddock 1997). In addition, where they both predominantly consume the same species of invertebrate (Miller & Miller 1995), even if they consume different size classes they may still influence the availability of prey for one another because small invertebrates are consumed before they can become adults and adults are consumed and unable to reproduce.

One specific part of the diet which differs for ship rats compared to house mice is consumption of arboreal invertebrates. House mice can climb well, but are not known to be arboreal as ship rats are (Ruscoe & Murphy 2005), therefore mice do not have access to this resource, which was observed to be relatively important for ship rats in some studies (Craddock 1997; Blackwell 2000). Ship rats were also reported to consume vertebrate matter in more studies than house mice were, though it was usually only a minor part of the diet (but see McQueen & Lawrence 2008). This is unlikely to reflect food preferences of the two species because house mice will consume vertebrate meat when they get the opportunity (Cuthbert & Hilton 2004). Instead, the greater size of ship rats probably allows them to attack vertebrate prey and their arboreal habits enable them to access bird nests (Brown *et al.* 1998; Innes *et al.* 2010a).

Given the link between invertebrate consumption and fecundity of house mice and ship rats it is conceivable that there may be greater diet overlap and potentially more intense competition during peak breeding times, which are usually in spring and summer (Innes 2005b; Ruscoe & Murphy 2005). However, winter may also be a crucial period when food shortage coupled with colder weather causes most rodent populations to decline, therefore competition for scarce resources could be significant (Innes 2005b; Ruscoe & Murphy 2005).

2.5.1 Conclusions

Ship rats and house mice both exhibit flexible and opportunistic diets. Whilst some aspects of the diets of the two species differ, they also show overlap in the range and size of food items they will consume and may rely on the same major diet component in some environments. This means there is potential for these species to compete for food and for removal of one to result in an increase in the resources available to the other. However, demonstrating that lack of resources limits house mice in the presence of ship rats in New Zealand requires experimental manipulations and evidence that the shared resources are limited. Furthermore, the effects of interference competition or intraguild predation from ship rats, which may be evident even when resources are plentiful, may be more important.

3 Do ship rats exhibit predatory behaviour towards house mice?

3.1 Abstract

Evidence suggests that ship rats (*Rattus rattus*) influence the abundance and distribution of house mice (*Mus musculus*) through aggressive behaviour which may include killing. However, there are few observations of ship rats and house mice encountering each other to confirm this behaviour. In addition, there is uncertainty about whether aggressive behaviour towards house mice by ship rats is predatory in which case it would lack threat and display features associated with other forms of aggression, such as that exhibited during intraspecific fighting, and would be associated with feeding. To investigate these issues, but avoid animals suffering injuries, I observed interactions between paired conspecific and heterospecific rodents either side of a wire mesh screen. I found that the majority (58 - 75 %) of ship rats exhibited aggressive behaviour towards mice which was very rarely reciprocated. Encounters with house mice lacked the threat and display behaviour exhibited during intraspecific encounters and were more aggressive. To determine whether aggression of ship rats towards house mice is associated with feeding I used a euthanased mouse, moved via a line, as a model and presented this to ship rats that were fed a restricted or unrestricted diet. Most rats of both groups interacted with the euthanased mouse and showed attacking and restraining behaviour. All rats that interacted with the mouse ate at least part of it, though food restricted rats tended to eat more. As the aggressive behaviour of ship rats towards house mice lacked threat and display features and was related to feeding, I conclude that it can be described as predatory.

3.2 Introduction

Intraguild (IG) predation describes a relationship between species which have overlapping resource requirements, and are thus potential competitors, but which also kill and eat one another (Polis *et al.* 1989). IG predation may be primarily a mechanism to reduce competition, in which case it can be considered as an extreme form of interference competition involving territorial aggression or resource defence (Polis *et al.* 1989; Sunde *et al.* 1999). Alternatively, reduced competition may be an incidental consequence of opportunistic feeding behaviour in which case aggression is predatory (Polis *et al.* 1989; Stapp 1997). Identifying IG predation and distinguishing between these motives can be complex, particularly for small, elusive species, however such information allows a better understanding of the dynamics of interspecific relationships (Stapp 1997).

IG predation is observed most frequently among generalist predators (Polis *et al.* 1989). Within Rodentia, most species are granivorous or herbivorous, however, a number of diverse species have a more varied omnivorous diet (Landry 1970; Stapp 1997). Some of the most notorious, adaptable omnivores are the invasive rodents including the ship rat (*Rattus rattus*) and house mouse (*Mus musculus*). Due to their commensal association with humans, these species have been widely distributed beyond their natural ranges including in New Zealand (Towns *et al.* 2006).

Evidence suggests that interactions with ship rats influence the abundance and distribution of house mice (Innes *et al.* 1995; King *et al.* 1996c; Harris & Macdonald 2007). Though difficult to demonstrate, competition between ship rats and house mice is possible because their diets overlap (Chapter 2). However, indirect exploitation competition for resources alone is unlikely to underpin the relationship between these species, as there is also evidence that ship rats negatively influence the behaviour of house mice through some means of direct interaction (Brown *et al.* 1996; Harris & Macdonald 2007; Harper & Cabrera 2010).

As well as potential competitors, ship rats may also be predators of house mice. Some evidence that rats kill mice has been observed (Lidicker 1976; Granjon & Cheylan 1988) and gut content analysis has occasionally found house mouse remains in ship rat stomachs (McQueen & Lawrence 2008). It is not clear how common aggression and killing of mice is amongst ship rats, or whether it is primarily an extreme form of interference competition or simple predatory aggression. The ship rat-house mouse relationship is of particular interest to wildlife management and conservation because interactions between these pest species hinder monitoring and control of populations (Innes *et al.* 1995; Tompkins & Veltman 2006; Caut *et al.* 2007; Harris & Macdonald 2007; Witmer *et al.* 2007; Harper & Cabrera 2010). The dynamics of the relationship may also shed light on the otherwise unknown mechanisms for how ship rats have negatively influenced native small mammal species similar in size and behaviour to the house mouse (Harris 2009).

Mouse killing behaviour ('muricide') has been demonstrated and studied intensively in Norway rats (*Rattus norvegicus*). Karli (1956) found that this behaviour was exhibited by 70% of wild-caught animals in laboratory trials. In Norway rats, muricide is considered predatory in nature rather than related to other forms of aggressive behaviour such as territorial aggression (O'Boyle 1974). This is for two main reasons: 1) Muricide lacks characteristics such as threat and display postures that typify territorial aggression. By comparison Norway rats do exhibit threat and display behaviours during intraspecific antagonistic encounters, and also when killing ship rats, which Takahashi and Blanchard (1982) described as "an admixture of predation and intraspecific attack". 2) Muricide is associated with feeding, as Norway rats usually at least partially consume the mice they kill, and they are more likely to be mouse killers if they are hungry (Karli 1956; Paul 1972; O'Boyle 1974).

In comparison to Norway rats (average 200-400g, Innes 2005a), ship rats (average 120-160g, Innes 2005b) are generally smaller and considered less aggressive (King *et al.* 2011a). Ship rats dominated, but did not kill Polynesian rats (*Rattus exulans*) (average 60-80g, Atkinson & Towns 2005) in captive trials

(McCartney & Marks 1973). House mice (average 15-20g, Ruscoe & Murphy 2005) are much smaller than both ship rats and Polynesian rats so logic, as well as information from field studies, predicts that ship rats would dominate encounters. The aim of my study was to test this and to investigate whether behaviour of ship rats towards house mice shows features similar to that of Norway rats, and hence is predatory.

Modern ethical constraints prevent experiments in which one animal could harm another, so I developed indirect methods to study behaviour. In the first of three experiments, I determined the dynamics of interspecific encounters by observing the response of animals towards each other either side of a wire mesh screen, which allowed close but not direct contact, to study aggression. I also investigated any sex-related, and for house mice age-related, differences in behaviour. There is some evidence that juvenile mice may be more vulnerable to the effects of ship rats (King *et al.* 1996b) than adults and this could be because they exhibit risky behaviour during encounters. In experiment 2, I compared interspecific and intraspecific encounters to determine whether there are differences in behaviour exhibited.

The third experiment was designed to investigate feeding, by using an animated euthanased mouse as a model. By animating the dead mouse, I could distinguish between predatory behaviour and scavenging. I studied the response of rats on different feeding regimes to the mouse model and to live house mouse and conspecific opponents.

3.3 Methods

3.3.1 Trapping and housing of animals

I live-trapped wild house mice and ship rats at various sites within the Water Treatment reserve, Te Miro (30 minutes outside of Hamilton in the Waikato region, North Island) and also on other privately owned land in the Waikato area in spring and summer at intervals between 2008 and 2011. Trapping sites for mice were separated by at least 300 m and for rats by 600 m, which exceeds home range length for these animals (Innes 2005b; Ruscoe & Murphy 2005). This

allowed me to pair animals that were likely to be unfamiliar with each other for trials.

To capture mice I set groups of 10-40 Longworth live-capture small mammal traps in areas of scrub, or rank grassland at each site. Traps contained polyester fibre for insulation and were spaced approximately 10 m apart. For the capture of ship rats, I set wire cage traps (generic make, 200x200x300 mm) within native forest and pine forest at approximately 20 m spacing. Cage traps each had a tin can wired inside to provide shelter, but I did not add bedding because rats can become tangled in it. I baited all traps with carrot and peanut butter and checked them daily. I weighed and examined captured animals, placed them in secure containers and transported them to the University of Waikato animal house facility.

I housed mice individually in laboratory-style mouse cages (300x200x200 mm) with plastic bases and wire lids. I provided them with pine shavings and shredded newspaper for bedding. I housed ship rats individually in wire cages (600x800x4000 mm) and provided them with nest tubes containing shredded newspaper. I kept house mice and ship rats in separate rooms and I also divided intraspecific subjects and opponents into different rooms (ship rats) or separate parts of the same room (house mice).

I fed all animals on a mixture of rodent lab pellets, oats, crisped rice, wild birdseed, pumpkin seeds, sunflower seeds, raisins, peanuts, cat biscuits and fresh carrot. Fresh water was available at all times. I kept all animals for a two-week habituation period prior to beginning trials. Following this, I reweighed and examined them to ensure they were healthy. None lost weight, except females who were caught whilst pregnant and gave birth. Either I excluded these females from trials, or I used them once I had humanely euthanased their offspring and given them a further period of two weeks to recover and maintain steady weight.

3.3.2 Experiment 1

3.3.2.1 Procedure

Encounters took place in a glass aquarium (600x300x300 mm), which I modified by securing a fine, wire mesh divider (20x6 mm mesh gap) across the centre bisecting it. I placed a wood and wire mesh lid on top. A thin substrate of sawdust covered the base of the aquarium and each half contained a source of water. I ran trials in a quiet room, after dark when mice and ship rats would be active and I used a near infrared (NIR) video camera and light to record footage.

I introduced an animal of each species to either half of the aquarium. A solid partition alongside the wire divider prevented them coming into contact straight away. I left the room and gave animals a 30 minute period to adjust to their new surroundings. Following this, I returned to the room and removed the solid partition so that animals could interact for the following 30 minutes. This constituted Phase 1 of the trial. In phase 2 I returned to the room and put the partition in place again for a 30-minute rest period without contact before removing it once more for a second 30-minute encounter time. At the end of trials I returned animals to their cages, cleaned the aquarium, and applied fresh substrate.

I used eighteen house mice for trials (six adult females, six adult males and six juveniles of either sex). I classed juveniles as those mice that weighed ≤13.5 g at the time of trials, in accordance with King *et al*. (1996b). Mice took part in one trial each. I used twelve ship rats, six adult males and six adult females. I used half the ship rats in two trials each. I randomly paired ship rats with house mice.

3.3.2.2 Analyses

I reviewed videoed behaviour in slow-motion playback and implemented behaviour sampling and time interval sampling (Martin & Bateson 2007). I used behaviour sampling to record instances when animals interacted, defined as any occasion in which animals came so close together on either side of the wire divider that, if it had not been in place, they could have made contact. For clarity, I refer to ‘interactions’ as these moments of close (but not direct) contact, and

'encounters' as the entire period when animals were exposed to each other and interactions could potentially take place.

In accordance with (Blaustein 1980), I recorded the identity of the animal that initiated each interaction by approaching the opponent, and the identity of the animal that retreated. I also recorded whether interactions were aggressive. I defined aggression as any biting or clawing of the wire screen that was directed at the opponent. I summarised these results and compared the number of interactions and aggressive interactions between the sexes for both species, and age groups for house mice, using ANOVA following $\log_{10}(1+x)$ transformation of the data to correct for non-normal distribution.

I used time interval sampling to record the activity of the animals at every one-minute interval during trials. I then classified these activities as moving, motionless or other for analysis. If I observed no movement, I described animals as 'motionless'. I defined 'moving' as travelling from one point to another around the aquarium. In the category 'other' I included activities that did not involve either complete stillness or conspicuous travelling such as grooming and sniffing the air (see Appendix 3 behaviour classification).

I modelled the percentage of time spent moving, motionless or other for rats and mice using linear mixed effects models. Data were $\log_{10}(1+x)$ transformed where necessary to address non-normal distribution of residuals. In each model I included 'partition' (in or out) and 'phase' (one or two) as fixed effects to compare activity during the four 30 minute stages of the experiment, and animal ID as the random effect to account for repeated observations of animals in each stage.

In mouse models I included mouse 'type' (male, female or juvenile) as an additional fixed effect and 'rat movement' (percentage of time intervals rats spent moving during the same period), to investigate any behavioural response of mice to rat activity. For rat models, I used only data collected during the first trial for rats that were used more than once, and I included sex as a fixed effect. All interaction terms were included in models. I used maximum likelihood

estimation to model data and I carried out backwards removal of non-significant terms until the most parsimonious models were achieved. All analyses were performed using R (R Development Core Team. 2011) and for mixed effects models I used the lme4 package.

3.3.3 Experiment 2A

3.3.3.1 Procedure

For the second experiment, I placed animals on a switched light/dark cycle (21:00/09:00) for greater convenience for running trials. I used the same procedure as in experiment 1 for experiment 2, except that I replaced the wire mesh lid of the aquarium with a solid lid to prevent mice from climbing upside down from it, which occasionally made them difficult to observe.

Subjects were eight ship rats and eight house mice (with even sex ratio). I randomly paired same-sex animals from this group for interspecific trials. For intraspecific trials, I paired each subject animal with a same-sex, unfamiliar conspecific from a separate group (eight mice and eight rats) known as opponents. Each subject therefore took part in two trials, which were presented in a random order and in total these comprised eight interspecific trials, eight intraspecific ship rat trials and eight intraspecific house mouse trials.

3.3.3.2 Analyses

I analysed video footage using the same procedure as for experiment 1, except that I omitted retreat and advance behaviours. I compared the number of interactions and the number and proportion of aggressive interactions for animals in intra-specific vs. interspecific trials using a paired t-test. For analysing activity patterns I used the same modelling procedure as in experiment 1 with the addition of the fixed effect ‘opponent species’ to describe whether data were collected during inter- or intraspecific trials. I included the interaction terms ‘opponent species*partition*phase’ and ‘opponent species*sex’ to investigate how encountering a conspecific or heterospecific influenced the behaviour of animals of each sex during the four stages of the experiment and carried out backward removal of non-significant terms.

3.3.4 Experiment 2B

3.3.4.1 Procedure

Using the same apparatus as in experiments 1 and 2, I tested the response of four previously unused ship rats to an animated euthanased mouse model. For the first hour, trials proceeded as they had previously, with a live mouse presented in the opposite half of the aquarium to the rat. However, when I put the partition in place for the rest period of phase 2, I removed the mouse, euthanased it with CO_2 and attached it to a length of fishing line secured around the neck.

As I removed the partition for the final stage of the experiment, I also removed a square section (80 mm x 80 mm) from the centre of the wire mesh screen. I placed the dead mouse in the aquarium and aligned the fishing line so that I could move the mouse up and down the wire and over the missing section. I then retreated and watched via closed circuit television (cctv) from a separate room. I pulled the fishing line so that the mouse moved repeatedly up and down the mesh screen. Once the rat made contact with the mouse, I stopped pulling the line and left the mouse with the rat for the remainder of the 30-minute period.

3.3.5 Experiment 3

3.3.5.1 Procedure

For experiment 3, I designed and built a new enclosure to allow me to present a resident subject rat with a dead mouse, live mouse and live conspecific, and to video the subject's behaviour using a near infrared (NIR) video camera and lighting (Figure 3. 1). This time a double screen (creating 6 mm x 6 mm mesh gap) separated subject rats from live opponents because mice tended to spend more time climbing on the mesh screen in this apparatus, and one mouse was bitten through the mesh during a trial. This never occurred during the 26 interspecific trials performed in the aquarium.

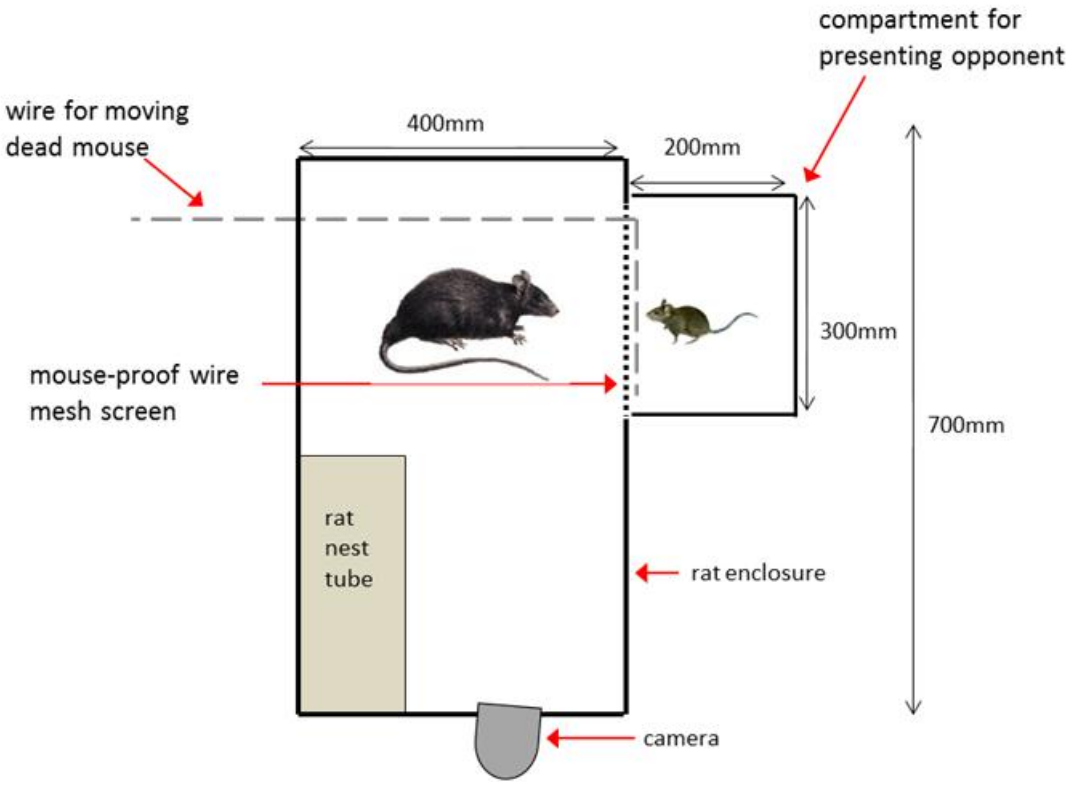


Figure 3. 1. Floor plan of the enclosure design for experiment 3.

Twelve adult ship rats were used in trials, five females and seven males. None had been used in any previous experiments and all had been kept on a 12-hour switched light/dark cycle (2100/09:00) since capture. Animals were introduced to the enclosure and allowed four nights to become habituated to their new environment. During this time they were given a constant supply of mashed rodent pellets soaked in a little water. Lab pellets provide a nutritionally balanced diet for rodents (see Appendix 4 for nutritional content), and all animals had been fed on them prior to trials. The purpose of mashing and soaking pellets was to discourage rats from cacheing them in their nest tubes.

I continued to provide six of the rats with a constant supply of food for the remainder of the experiment. The other six I placed on a restricted diet. Pilot trials revealed that rats ate almost immediately on emerging from their nest tube at the start of the night, indicating that they were hungry and motivated to eat at this point. Rats in the restricted group had their food removed towards the end (approximately 18:00) of the fourth habituation night and each night thereafter.

Food was not returned until after trials, which took place early the following night (approximately 10:30). Each food restricted rat was given an amount of mashed pellets (weighed when dry) equivalent to 10% of their body weight. This amount constitutes their average daily requirement (Bhardwaj & Khan 1974). The aim of this regime was to ensure that animals were hungry and motivated to feed during trials each day, but they had access to sufficient food for their daily requirements.

I presented each rat with a live conspecific, a live mouse and a model mouse opponent in a counterbalanced random order on separate nights. Opponents were placed in the compartment designed for them (Figure 3. 1). Once I left the room I allowed subject rats 1 hour and 40 minutes to emerge from their nest tube and begin interacting. A time limit was necessary so that live opponent animals were not detained in a stressful environment for too long. I defined any occasion when animals came close together either side of the wire divider as an interaction, and interactions as aggressive if they consisted of biting or clawing at the divider, directed at the opponent. After the first interaction I allowed 10 minutes of time with live opponents before ending the experiment and returning opponents to their cages.

I began moving dead mice when subject rats emerged from their nest tubes. I pulled the fishing line steadily from outside of the room the enclosure was in and observed the subject via cctv. Dead mice were dragged horizontally along the base of the wire mesh screen and entered the subject rat's enclosure by means of a hole in the screen. An interaction was recorded if the rat made contact with the dead mouse. Rats that chased and grabbed the moving mouse were classed as having 'attacked' it. If rats took fright and did not attack the moving mouse, I allowed them the opportunity to approach the mouse whilst not moving. Once rats took hold of the mouse I pulled it more to simulate the mouse attempting to escape. Rats that held on to the mouse without letting go were classed as having 'restrained' it. I allowed rats 20 minutes with the dead mouse after the initial interaction to observe any feeding behaviour.

I weighed dead mice before and after trials to determine the amount of mouse body consumed. I measured the latency to interact with all opponent types, and the latency to begin eating the dead mouse once contact had been made.

3.3.5.2 Analyses

To assess response of rats to the dead mouse I gave each animal an interaction score for its behavior (Table 3. 1). For each rat within the restricted or unrestricted diet groups, I graphed the results of interactions with the three opponent types to examine any consistency in behavior, and used a linear mixed effects model to assess whether diet or opponent type influenced the latency to interact. I compared the quantity of mouse eaten by the rats on different feeding regimes using a student's t-test to determine whether food-restricted rats ate more. I compared the total number of interactions and of aggressive interactions made towards live conspecific or mouse opponents using a paired t-test.

Table 3. 1. Interaction scores used to describe behaviour of ship rats towards animated euthanased house mice

Interaction score	Description
0	No interaction
1	Mouse eaten, but not restrained or attacked
2	Mouse restrained and eaten, but not attacked
3	Mouse attacked, restrained and eaten

3.4 Results

3.4.1 Experiment 1

During the 18 trials, ship rats and house mice interacted on 181 occasions. All paired animals interacted at least once. Ship rats seemed attracted and stimulated by the movement of house mice, and in most cases ship rats initiated interactions by approaching house mice (131/181 interactions). In response to any sudden movement made by rats, mice often jumped erratically around the aquarium. On some occasions, house mice jumped at the wire mesh screen, and in doing so encountered the ship rat waiting there. This behaviour accounted for most of the 50/181 interactions that were initiated by house mice. On almost all occasions, house mice retreated from interactions (173/181 interactions).

Of the 181 interactions 67 (37 %) were considered to be aggressive. Eight (66.7%) of the twelve ship rats displayed this behaviour, which involved lunging at mice and biting at the wire screen when in close proximity to them (e.g. Figure 3. 2). Chasing the mouse as it climbed on the wire mesh screen often preceded or followed aggressive behaviour. Non-aggressive rats that interacted with mice sniffed and even licked them, but did not attempt to bite (e.g. Figure 3. 3). I observed no aggression from mice.

When I removed the partition during encounters, mice spent significantly more time motionless and less time moving or engaged in ‘other’ activities (Table 3. 2, Figure 3. 4). They exhibited even less movement when I removed the partition for the second time. Juvenile mice spent significantly less time motionless and more time engaged in ‘other’ activities than adult female mice, whilst adult males were intermediate (Table 3. 2, Figure 3. 4). Both juvenile and adult male mice spent significantly more time moving than adult female mice did, but this difference was apparent only when the partition was in (Table 3. 2, Figure 3. 4). Despite differences in activity according to mouse type, there were no significant differences in the number of interactions or aggressive interactions. There was no significant relationship between movement of rats and behaviour of mice.

Ship rats spent more time motionless in the second phase of the trials than the first (Table 3. 2, Figure 3. 5), with a consequential reduction in movement activity, mainly when the partition was in. Ship rats moved about significantly more when the partition was out and they could interact with house mice (Table 3. 2, Figure 3. 5). No differences in behaviour between sexes of ship rats were apparent.

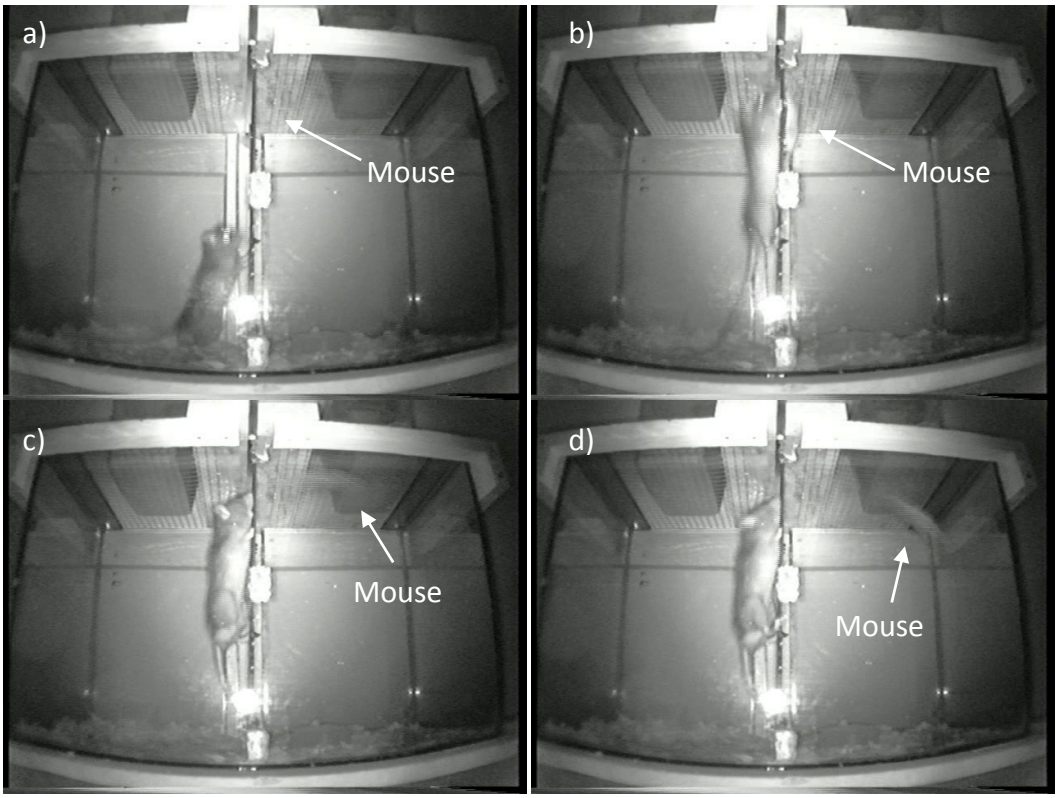


Figure 3. 2. Images of a ship rat interacting aggressively with a house mouse behind a wire screen which prevents the rat from harming the mouse. Ordered from a to d, the rat climbs the wire screen in pursuit of the mouse and bites at the screen causing the mouse to leap away.

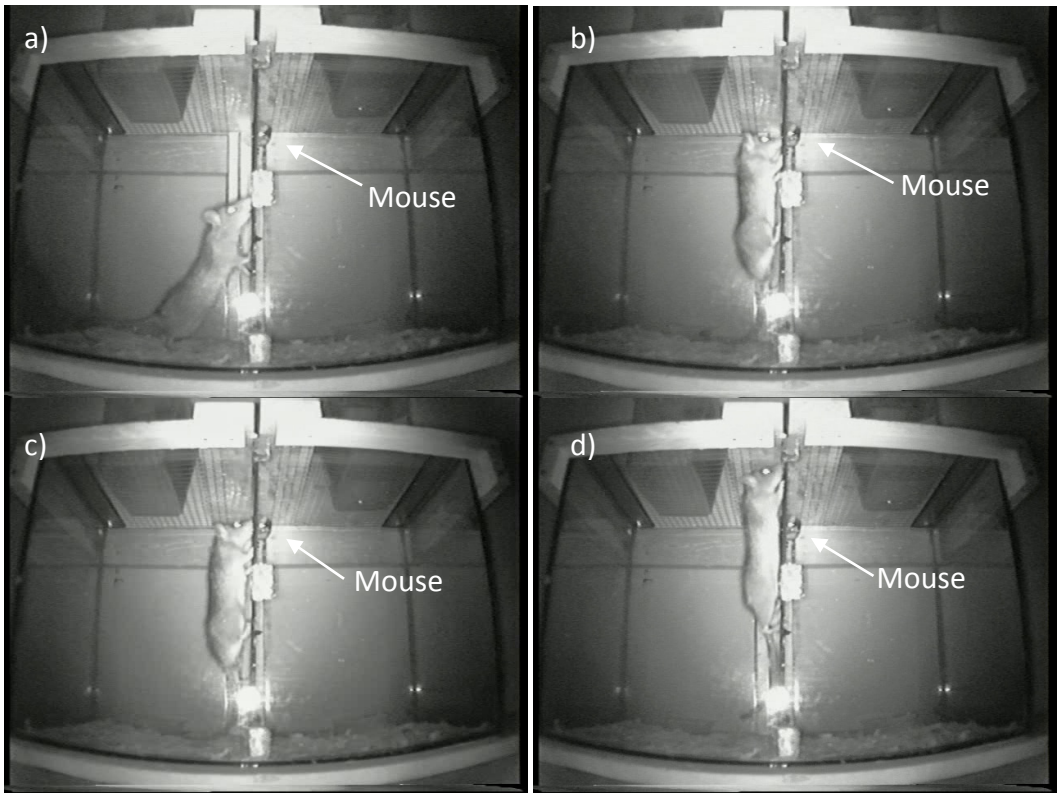


Figure 3. 3. Images of a non-aggressive ship rat interacting with a house mouse behind a wire screen. Ordered from a to d, the rat climbs the wire screen and encounters the mouse, which remains perfectly still whilst the rat sniffs and licks it and then continues climbing.

Table 3. 2.Results of linear mixed effects models of activity (motionless, moving or other) for house mice and ship rats during encounters in an aquarium with a central wire screen to prevent direct contact. The random effect in all models was the individual animal ID to account for repeated data collection from the same animals in different stages of the experiment. 'Partition' refers to the presence or absence of a wooden partition that blocked the animals from interacting through the wire mesh screen for the first and third stage (stage = 30 minutes) of each two hour trial. Phase refers to the first or second half of the trial. For house mice n = 18 (6 adult female, 6 adult male, 6 juvenile of either sex: 'mouse type') with 71 observations (18 mice x four partition:phase combinations, with one observation lost due to video failure in the last phase of a trial). For ship rats n = 12 (6 female, 6 male) with 48 observations (12 rats x four partition:phase combinations). Non-significant terms were removed from the fully saturated models until the most parsimonious form was reached

Species	Behaviour	Model	Model terms	F value	d.f.	P value
House mouse	Motionless	Partion + Mouse type	Partition	249.488	1,	< 0.001
			Mouse type	5.461	2	0.006
	Moving	Partition*Phase+Partition*Mouse type	Partition	149.688	1	< 0.001
			Phase	0.818	1	NS
			Mouse type	1.766	2	NS
			Partition*Phase	4.905	1	0.030
			Partition*Mouse type	4.339	2	0.017
	Other	Partition + Mouse type	Partition	106.696	1	< 0.001
			Mouse type	4.320	2	0.017
Ship rat	Motionless	Phase	Phase	11.279	1	0.002
	Moving	Partition*Phase	Partition	12.426	1	< 0.001
			Phase	7.6373	1	NS
			Partition*Phase	4.706	1	0.035
	Other	NS				

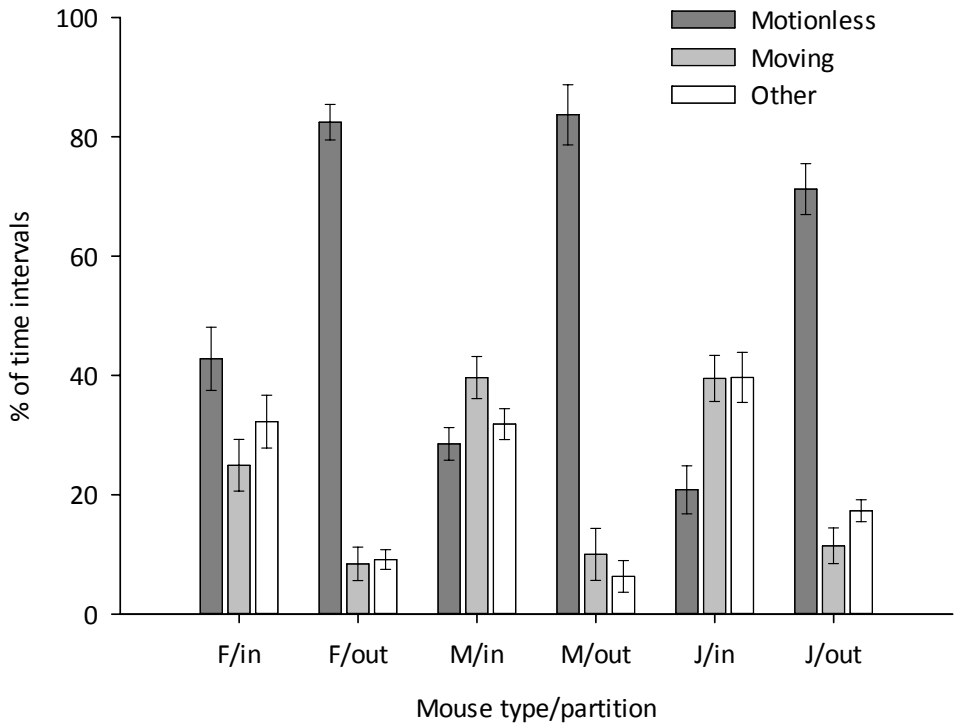


Figure 3. 4. Percentage of time intervals where the activity states of house mice (n=18: adult female, 'F', n=6; adult male, 'M', n=6; juvenile of either sex, 'J', n=6) were classed as motionless, moving or 'other'. Data are from encounters with a ship rat in a modified aquarium. During each two-hour trial, a wooden partition prevented animals from interacting for the first and third 30 minute stages ('in') to allow a period of habituation and rest. The partition was removed for the second and fourth stages ('out') so that animals could come into close, but not direct contact either side of a wire mesh screen. Data are means, error bars are ± 1 standard error.

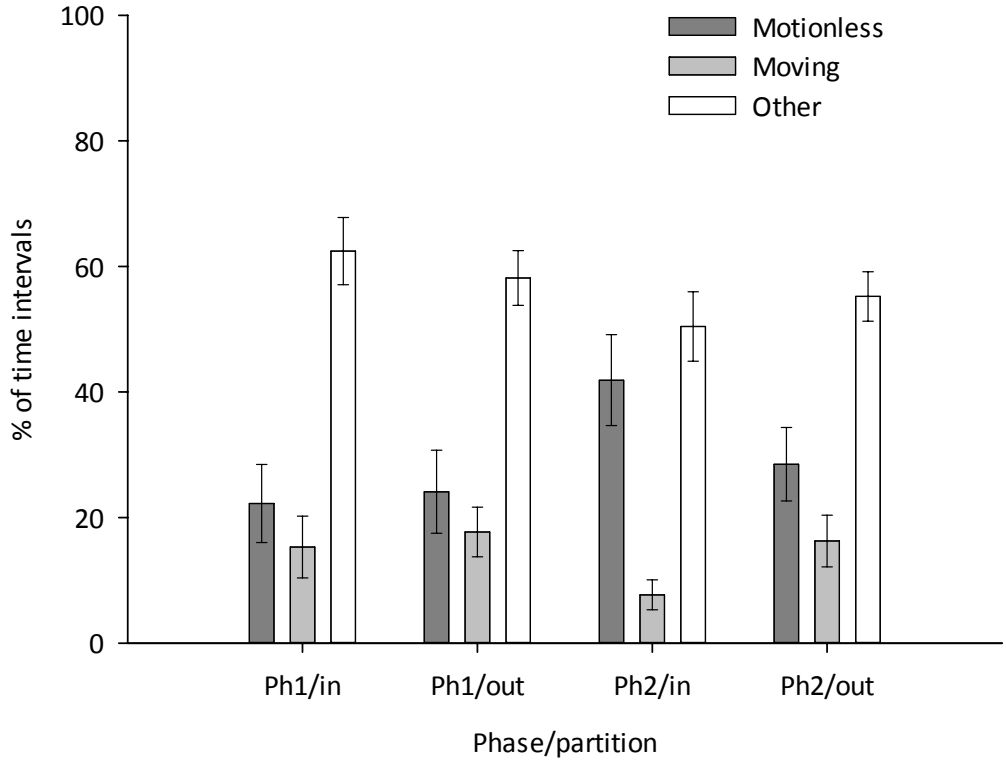


Figure 3. 5. Percentage of time intervals where the activity states of ship rats (n=12) were classed as motionless, moving or 'other'. Data are from encounters with a house mouse in a modified aquarium. Each two-hour trial was divided into a first ('Ph1') and second ('Ph2') one-hour phase. A wooden partition prevented animals from interacting for the first 30 minute of each phase ('in'). The partition was removed for the second 30 minutes ('out') so that animals could come into close, but not direct contact either side of a wire mesh screen. Data are means, error bars are ± 1 standard error.

3.4.2 Experiment 2A

All ship rats interacted willingly and frequently with conspecifics (Table 3. 3). Subjects and opponents often approached each other simultaneously and sat together either side of the wire mesh screen (e.g. Figure 3. 6.a). Rats interacted more during intraspecific trials compared to interspecific trials (Table 3. 3), but a higher number and proportion of interactions were aggressive during interspecific trials (Table 3. 3) (e.g. Figure 3. 7). The proportion of interspecific interactions classed as aggressive was higher than for experiment 1. Some ship rats exhibited raised hackles, lateral display movement (sideling or 'crab walking') (Scott 1966; O'Boyle 1974; Blanchard *et al.* 1975) and hip throwing

(presenting hindquarters to opponent broadside) (Scott 1966; O'Boyle 1974; Price & Belanger 1977) in response to exposure to a conspecific (e.g. Figure 3. 6.b). I never observed ship rats exhibit this behaviour in response to a mouse.

House mice did not interact with conspecifics as frequently as ship rats did (Table 3. 3). Generally, interactions were non-aggressive (e.g. Figure 3. 8.a) though mice often appeared nervous of each other. Occasional low level aggression was exhibited by subject or opponent mice, which involved one mouse lunging and usually resulted in the other mouse jumping away (e.g. Figure 3. 8.b). On one occasion, 'tail rattling' (John 1973) was exhibited. I observed one incident of mouse aggression towards a rat. This involved the mouse biting once at the wire mesh when a rat was in close proximity. This was the only observation of a mouse showing any aggression towards a rat in any of the experiments.

Table 3. 3. Interactions between ship rats and house mice during two 30-minute encounters. Data are the total number of interactions (defined as close contact between animals either side of a wire mesh screen) and the number of aggressive interactions (those that involved biting or clawing). Each rat and mouse experienced an intraspecifc encounter and an interspecific encounter so paired t-tests were used to compare data. Animals that did not exhibit aggression were excluded from the comparison of proportions. Data were too sparse to statistically compare aggression for house mice (NA). NS = non-significant, * = only one incident

		Opponent				
Subject	**Response**	**Ship rat**	**House mouse**	**t value**	**d.f.**	**P value**
Ship rat	Total no. of interactions	414	63			
	No. of animals that interacted (%)	8 (100)	6 (75)			
	Mean no. of interactions per trial (± SD)	51.8 (± 38.3)	7.9 (± 6.6)	-3.624	7	0.008
	Total no. of aggressive interactions (%)	15 (3.6)	39 (61.9)			
	No. of animals that exhibited any aggression (%)	3 (37.5)	6 (75)			
	Mean no. of aggressive interactions per trial (± SD)	1.9 (± 2.9)	5 (± 4.7)	2.739	7	0.014
	Mean proportion of interactions that were aggressive per trial (± SD)	3.7 (± 7.5)	58.6 (± 18.1)	7.916	5	<0.001
House mouse	Total no. of interactions	63	64			
	No. of animals that interacted (%)	6 (75)	7 (87.5)			
	Mean no. of interactions per trial (± SD)	7.9 (± 6.6)	8 (± 7.1)	0.074	7	NS
	Total no. of aggressive interactions (%)	1 (1.6)	8 (12.5)			
	No. of animals that exhibited any aggression (%)	1 *(12.5)	2 (25)			
	Mean no. of aggressive interactions per trial (± SD)	0.01 (± 0.4)	1 (± 2.1)	NA		
	Mean proportion of interactions that were aggressive per trial (± SD)	1.1 ((± 2.7)	6.9 (± 12.1)	NA		

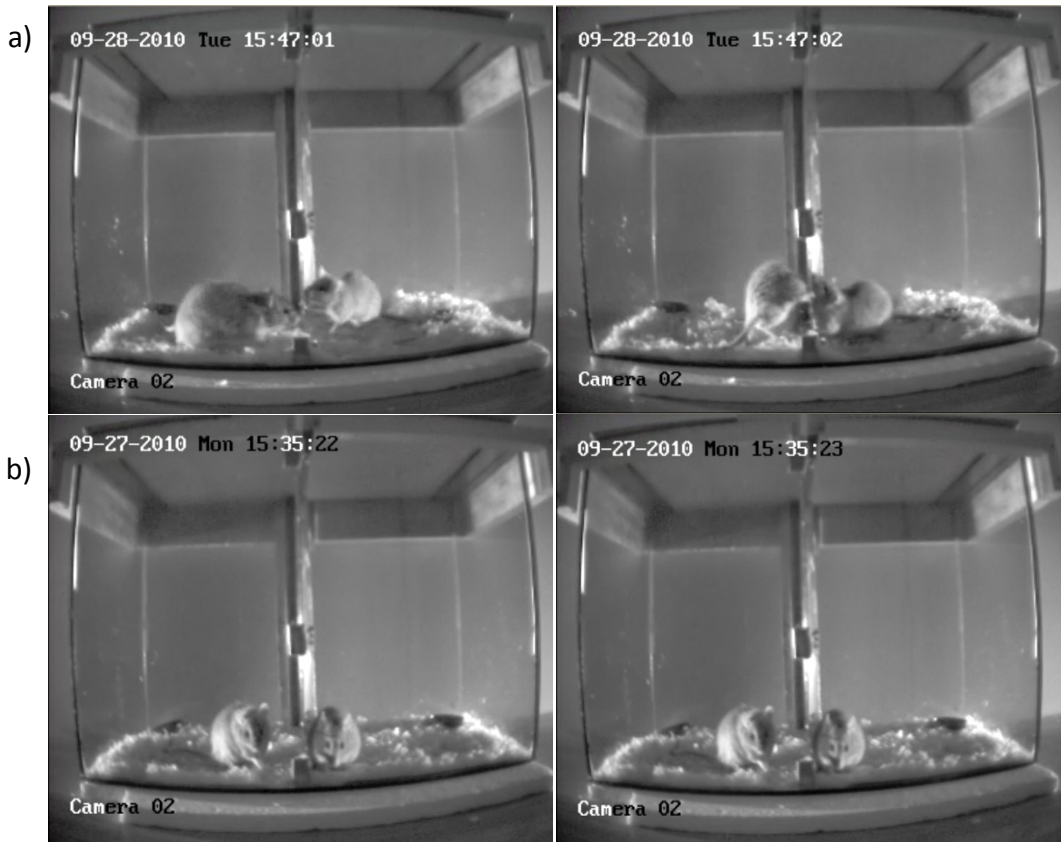


Figure 3. 6. Paired images of ship rats during encounters either side of a wire mesh screen in a modified aquarium. In a) the rat on the left exhibits hip throwing behaviour and the rat on the right responds aggressively by biting at the wire screen. In b) rats sit quietly in close proximity without aggression.

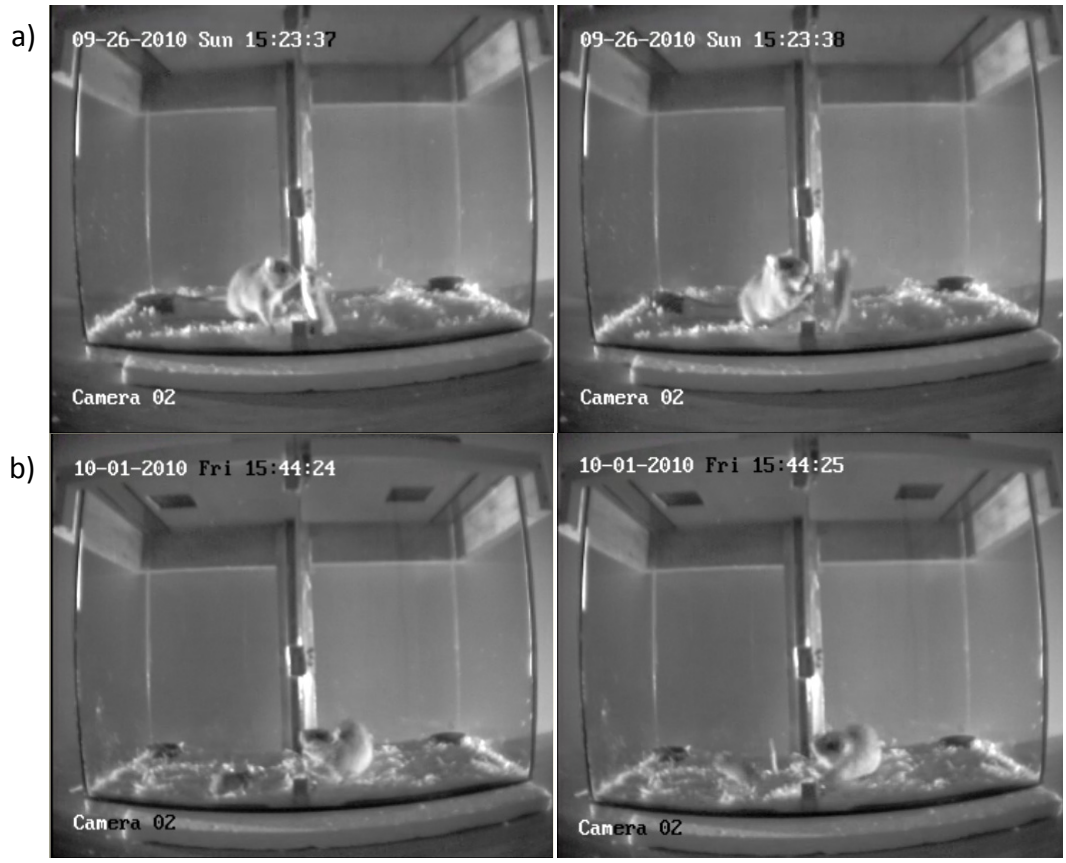


Figure 3. 7. Paired images of ship rats interacting with house mice through a wire mesh screen, which prevents them from harming each other. In both a) and b) ship rats act aggressively by biting at the wire mesh screen and house mice retreat by jumping away.

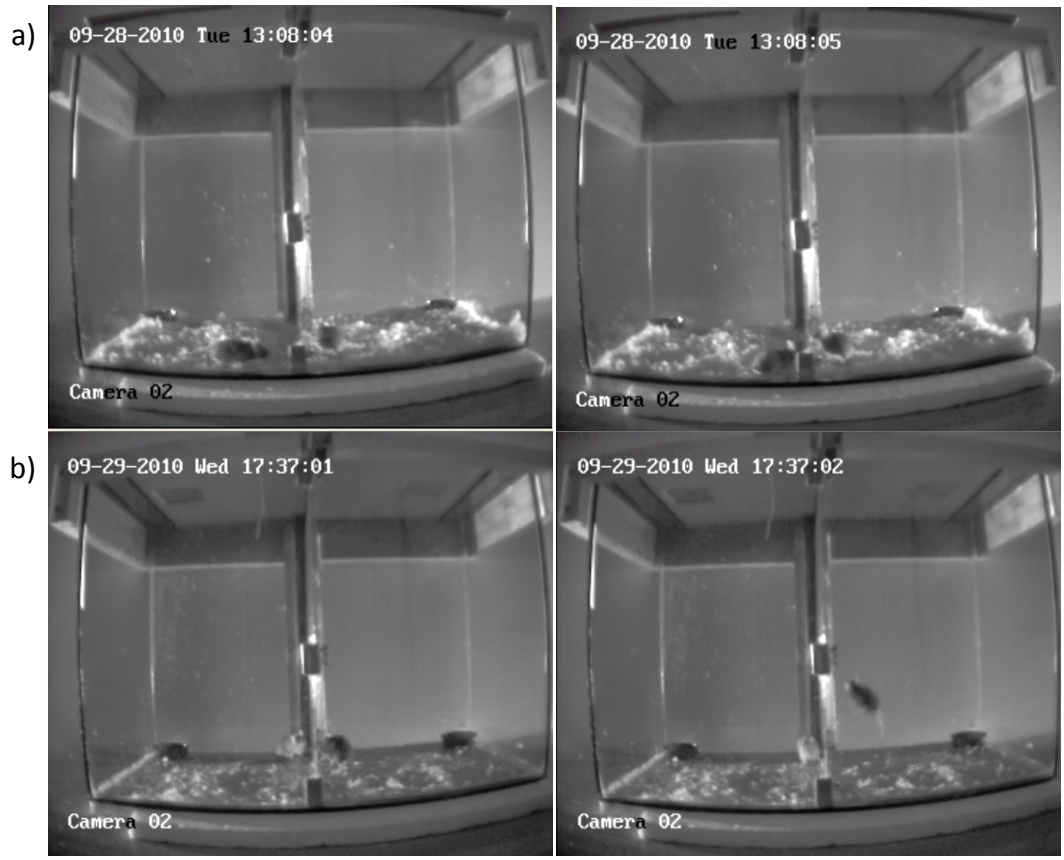


Figure 3. 8. Paired images of house mice interacting either side of a wire mesh screen in a modified aquarium. In a) the mouse on the left approaches the mouse on the right and they interact without aggression. In b) the mouse on the left lunges at the mouse on the right causing it to leap in the air.

Mice spent significantly more time motionless during encounters with a ship rat compared to a same-sex conspecific, and significantly less time engaged in conspicuous movement around the aquarium and in 'other' activities (Table 3. 4, Figure 3. 9.a). In both interspecific and intraspecific trials, removal of the partition caused mice to become motionless for a greater proportion of time, with a consequent decrease in both movement activity and 'other' activity (Table 3. 4, Figure 3. 9.a). However, this difference was greater in interspecific trials compared to intraspecific trials. Mice maintained similar proportions of motionless behaviour in phase 1 and phase 2 when encountering a rat, however, when encountering a conspecific they spent more time motionless in phase 2 compared to phase 1 (Table 3. 4). Male mice were significantly more active than females, and reduced their time spent engaged in 'other' activities less when the partition was out during encounters with a rat than females did (Table 3. 4).

Although sample sizes were small, (four animals of each sex), these findings are consistent with those of experiment 1. Mice spent less time moving and more time engaged in other activities in experiment 2 compared to experiment 1 although time spent motionless was comparable (Figure 3. 4, Figure 3. 9.a).

Ship rats spent significantly less time remaining motionless when encountering another rat compared to when encountering a mouse, and significantly more time engaged in other activities, mainly sniffing and grooming (Table 3. 4, Figure 3. 9.b). In both interspecific and intraspecific trials, ship rats spent less time motionless when the partition was out compared to in and more time engaged in other activities (Table 3. 4, Figure 3. 9.b). They spent more time motionless in the second compared to first phase of the trials with a reduction in time spent moving. However, this difference was greater in the intraspecific compared to interspecific trial (Table 3. 4, Figure 3. 9.b). No differences were apparent between the sexes for ship rats, in accordance with experiment 1.

Table 3. 4. Results of linear mixed effects models of activity (motionless, moving or other) for house mice and ship rats during intraspecific and interspecific encounters allowing close but not direct contact (random effect = animal ID). 'Partition' refers to the presence or absence of a wooden screen that blocked interactions for the first and third stage (30 minutes) of each two-hour trial. Phase refers to the first or second half of each trial. For each species n = 8 (4 female, 4 male) with 64 observations (8 animals x 2 trials x 4 stages)

Species	Behaviour	Model	Model terms	F value	d.f.	P value
House mouse	Motionless	Opponent species*Partition+Opponent species*Phase	Opponent species	68.500	1,58	<0.001
			Partition	68.500	1,58	<0.001
			Phase	2.917	1,58	NS
			Opponent species*Partition	14.177	1,58	<0.001
			Opponent species*Phase	5.073	1,58	0.028
	Moving	Opponent species+Partition+Sex	Opponent species	22.491	1,60	<0.001
			Partition	7.219	1,60	0.009
			Sex	6.539	1,60	0.013
	Other	Opponent.species*Partition+Opponent.species*Sex	Opponent species	25.730	1,58	<0.001
			Partition	54.170	1,58	<0.001
			Sex	0.0190	1,58	NS
			Opponent species*Partition	6.968	1,58	0.010
			Opponent species*Sex	4.481	1,58	0.039
Ship rat	Motionless	Opponent species+Partition+Phase	Opponent species	14.921	1,60	<0.001
			Partition	5.136	1,60	0.027
			Phase	5.606	1,60	0.021
	Moving	Opponent species*Phase	Opponent species	0.017	1,60	NS
			Phase	4.673	1,60	0.035
			Opponent species*Phase	5.105	1,60	0.028
	Other	Opponent species+Partition	Opponent species	17.720	1,61	<0.001
			Partition	5.1672	1,61	0.027

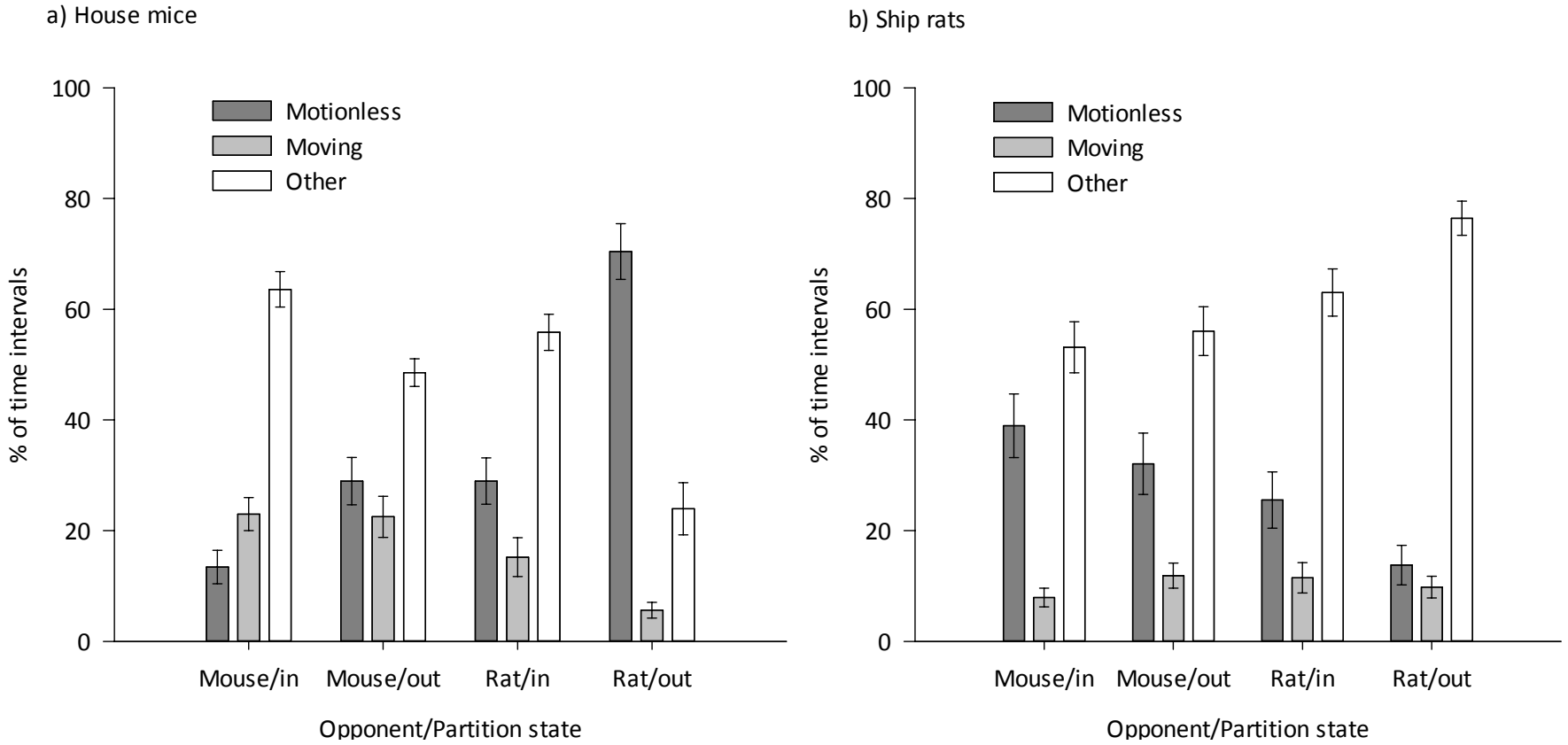


Figure 3. 9. Percentage of time intervals where the activity state of house mice (a) and ship rats (b) (n=8 with repeated measures in both cases) was classed as motionless, moving or 'other' during an encounter with a same-sex conspecific or heterospecific ('Rat' or 'Mouse'). During each two-hour trial, a wooden partition prevented animals from interacting for the first and third 30 minute stages ('in') to allow a period of habituation and rest. The partition was removed for the second and fourth stages ('out') so that animals could come into close, but not direct contact either side of a wire mesh screen. Data are means, error bars are ± 1 standard error.

3.4.3 Experiment 2B

All four rats that experienced encounters with an animated, euthanased mouse interacted with it. Rat 1 initially showed interest in the dead mouse, but did not bite it. The rat spent time exploring the other half of the aquarium that it had entered via the hole in the mesh. It grabbed hold of the mouse after seven minutes, restrained it and began eating. It ate at intervals from the face of the mouse for the remainder of the trial. Rat 2 chased and bit at the dead mouse eight minutes after it was placed within the aquarium. After approximately 40 seconds of chasing, rat 2 grabbed the dead mouse through the hole in the wire, bit it repeatedly and dragged it to the base of the wire screen where it ate a small part of a leg before losing interest and exploring the aquarium. Rat 3 chased and bit at the dead mouse immediately after it was placed in the aquarium and grabbed it through the hole in the wire screen after 15 seconds, biting it repeatedly. Rat 3 became disinterested after grabbing the mouse and began exploring the aquarium, but returned to the mouse three times to bite and paw at it, but only ate one eyeball. Rat 4 grabbed the mouse enthusiastically straight away (Figure 3. 10), but lost interest afterwards and ate only the eyes of the mouse.

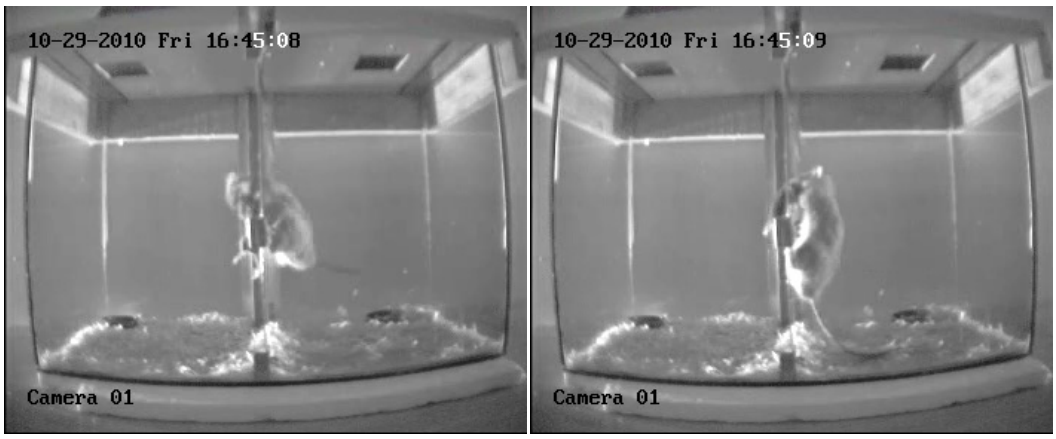


Figure 3. 10. A ship rat lunges and grasps a freshly euthanased house mouse in its teeth and forepaws. The mouse has been attached to fishing line so that it can be animated to simulate movement of a live mouse.

3.4.4 Experiment 3

Nine of the subject ship rats interacted with the dead mouse in some way (Figure 3. 11). Five rats showed behaviour classed as 'attacking'. They chased the moving mouse and grabbed it with teeth and forepaws (e.g. Figure 3. 12.a and b). They then bit and pawed it repeatedly and also held it and turned it in their paws. The four rats that interacted, but did not attack, appeared nervous of the dead mouse when it was moving and only interacted with it when it was still. Once they had grasped it, in all but one case they restrained it when it was pulled from them.

All rats that interacted with dead mice ate at least a small part of them (e.g. Figure 3. 12.c). Food restricted rats began eating within six seconds, but rats in the ad lib group took longer (Table 3. 5). There was a lot of individual variation, but overall, food restricted rats ate significantly more of the dead mouse than the rats fed an ad lib diet ($t = 1.875$, d.f = 10, $P = 0.045$). Pattern of eating varied, but soft tissue of the eyeballs, was often a focus (Table 3. 5).

The three rats (two from the ad lib food group and one from the restricted group) that did not interact with the dead mouse showed little interaction with and were not aggressive towards the live mouse either. However, they also interacted little with conspecific opponents (Figure 3. 11). There was no significant difference in latency to interact with the dead mouse compared to the live mouse, but latency to interact with a conspecific was significantly lower ($F = 5.459_{[2, 26]}$, $P = 0.010$). Feeding regime did not influence latency to interact with any of the opponents.

In accordance with experiment 2A, ship rats were aggressive significantly more often during interactions with house mice than with conspecifics ($t = 3.453$, d.f. = 11, $P = 0.005$) (Figure 3. 11). Nine (75%) of the twelve ship rats interacted with live mice and seven showed aggression (58.3%) (e.g. Figure 3. 13) whilst ten ship rats (83.3%) interacted with a conspecific and just three showed any aggression (25%). Behaviour characteristics also differed with seven (4 food restricted, 3 food ad lib, male and female) of the twelve rats exhibiting raised hackles in

response to a conspecific intruder (e.g. Figure 3. 14.a) and performing lateral display and hip throwing behaviour (e.g. Figure 3. 14.b). One female rat held her mouth open during interactions with a conspecific. None of these characteristics were exhibited towards live or dead mice.

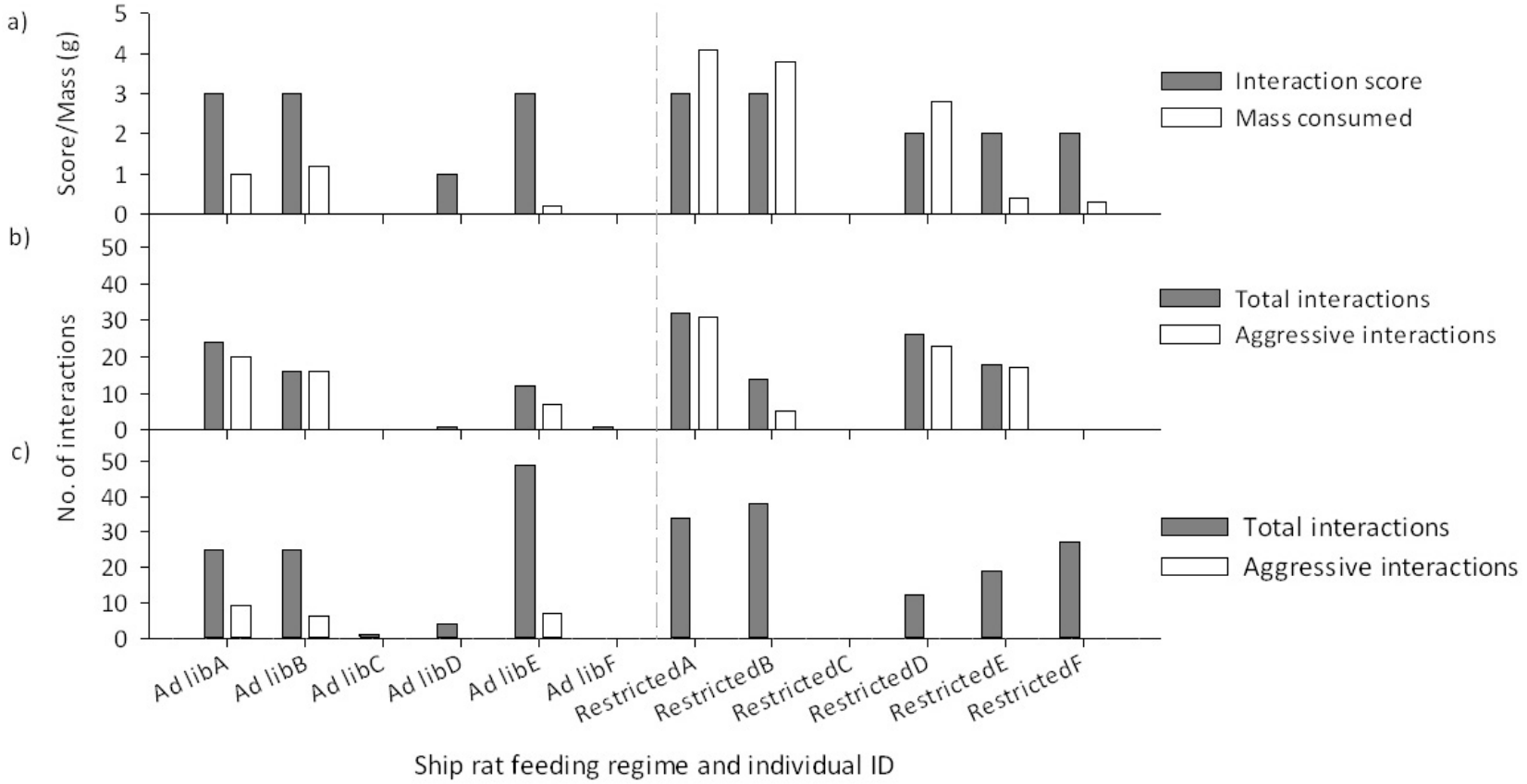


Figure 3. 11. Results for 12 ship rats, on either an ad lib or restricted diet, that were presented with an animated euthanased mouse (a), a live mouse behind a wire mesh screen (b) and a live conspecific behind a wire mesh screen (c). Data for a) are an interaction score where 1 = mouse was eaten, but restraining and attacking behaviours were not observed, 2 = mouse was restrained and eaten, but the moving mouse was not attacked, 3 = mouse was attacked, restrained and eaten. The mass of mouse consumed is also presented. Data for b) and c) are the number of interactions (defined as close proximity either side of the wire mesh screen) and of those how many interactions were aggressive (defined as biting and clawing at the screen).

Figure 3. 12. Paired images of ship rats interacting with an animated euthanased mouse. In a) and b) rats 'attack' the mouse as it moves. In c) a rat eats some of the mouse and then picks it up and carries it away.

Table 3. 5. Consumption of animated euthanased mice by twelve ship rats kept on either an ad lib or restricted feeding regime. Latency to begin eating is measured from the point of first contact with the mouse. NA refers to rats that did not interact and eat

Feeding regime/ID	Latency to begin eating (seconds)	Mass eaten (g)	Pattern of eating
Ad lib/A	00:00:18	1	Ears eaten
Ad lib/B	00:00:12	1.2	Gut opened and part of neck consumed
Ad lib/C	NA	0	NA
Ad lib/D	00:04:28	0	Weight of mouse unchanged as measured, but one eyeball eaten
Ad lib/E	00:01:02	0.2	Left eyeball eaten and tail almost chewed off at base
Ad lib/F	NA	0	NA
Restricted/A	00:00:00	4.1	Some of head eaten (starting with left eyeball) and also gut (intestines removed)
Restricted/B	00:00:06	3.8	Eating focused on neck which was eaten almost straight through
Restricted/C	NA	0	NA
Restricted/D	00:00:00	2.8	Head almost entirely eaten
Restricted/E	00:00:00	0.4	Eating focused on right eyeball and progressed through face
Restricted/F	00:00:01	0.3	Nose eaten

Figure 3. 13. Paired images of ship rats interacting aggressively with house mice, which are in a separate compartment behind a wire screen which prevents them from being harmed. In a) the rat lunges at the mouse and bites at the screen. In b) the rat jumps at the mouse.

Figure 3. 14. Paired images of subject ship rats interacting with same-sex conspecific opponents which are presented to them in a compartment separated by a wire screen. In a) the subject rat in the main enclosure approaches the opponent cautiously with raised hackles. In b) the subject rat exhibits hip throwing behaviour towards its opponent and aggressive clawing.

3.5 Discussion

The idea that ship rats are dominant to and perhaps even predators of house mice has been proposed previously (Lidicker 1976; Granjon & Cheylan 1988; Innes *et al.* 1995; Brown *et al.* 1996; King *et al.* 1996b; Harris & Macdonald 2007). However, there have been few direct observations of encounters between these animals, so the prevalence of such aggressive behaviour could not be assessed or predatory behaviour distinguished from other forms of aggressive fighting. Ethical constraints prevented me from observing the outcome of direct encounters between individuals, so I used a wire mesh screen and animated dead mice instead. I was able to compare interspecific and intraspecific behaviour, and to determine the relationship between aggression and feeding without placing animals at potential risk of suffering painful injuries.

3.5.1 Dominance hierarchy

As expected, house mice were undoubtedly subordinate to ship rats. In experiment 1, mice initiated fewer interactions than rats, and retreated from almost all interactions. The majority of ship rats were highly aggressive towards mice, which was reciprocated only on one rare occasion. House mice are not particularly passive animals; King (1957) found that house mice were highly aggressive towards another rodent species, similar in size to them, *Peromyscus maniculatus*. As ship rats are so much larger than house mice, and were often aggressive, house mice appeared to perceive that interacting with a rat presented a high risk, so they chose to retreat. The erratic jumping behaviour displayed by mice may be a general fear response because it was also described by Blaustein (1980) when studying interactions between house mice and a dominant, non-predatory species, *Microtus californicus*.

The proportion of ship rats that were aggressive to live mice during the three experiments (67, 75 and 58%) was similar to the proportion of wild-caught Norway rats that Karli (1956) reported were killers of mice (70%). Paul (1972) found that the muricidal response of laboratory Norway rats was strongly influenced by individual previous experience. I captured adult ship rats from the wild, so I did not know what their prior experience with mice had been, and it is possible that this affected whether they were aggressive or non-aggressive in trials. I suspect this is unlikely however, because in experiment 3 it was notable that ship rats that did not interact with live mice or dead mice also tended to interact little with conspecifics. This indicates a more general inherent characteristic of some rats to be more timid and less aggressive than others.

I found that mice were less active when exposed to ship rats than when the solid partition blocked their view of the rat or when they encountered a conspecific, which is in accordance with Bramley (1999). Remaining motionless seems to be a good strategy for avoiding detection, or, avoiding stimulating a predatory response in ship rats, which I observed were attracted to the movement of house mice. Juvenile mice spent least time motionless during trials. Lower propensity for remaining motionless during high-risk situations could make

juvenile mice more vulnerable to detection and attack by rats under natural conditions. This may help explain their low abundance compared to adults in field surveys of habitats where rats are prevalent though predation of nestling mice is another possibility (King *et al.* 1996b).

The proportion of interspecific interactions classed as aggressive was higher in experiment 2 than experiment 1 and there were also differences in the number of time intervals when mice were moving compared to engaged in 'other' activities. The most likely explanation for this is that the changes made to the aquarium lid altered the dynamics of the encounters slightly. This was because mice could no longer climb upside down on the lid, which was classed as 'moving' so instead they did 'other' activities and as mice were unable to climb away from rats by hanging on to the lid, rats appeared to have more opportunity to be aggressive towards them. These differences draw attention to the limitations of using the wire mesh divider system to observe aggression because the opportunity for rats to be aggressive was dependent on house mice coming close to the divider. However, this system had the advantage of allowing me to observe potential behaviours whilst preventing animals from injuring each other.

3.5.2 Is aggression of ship rats towards house mice predatory?

3.5.2.1 Interspecific vs. intraspecific behaviour

A feature of predatory aggression is that it differs from other forms of aggressive behaviours such as intraspecific fighting, which tend to involve display and threat characteristics (O'Boyle 1974; Blanchard *et al.* 2003). I found that for ship rats and house mice, behaviour during intraspecific encounters differed quantitatively and qualitatively from interspecific encounters. Ship rats interacted more frequently but far less aggressively with conspecifics than with house mice. Ship rats exhibited threat behaviours, such as raised hackles, lateral display and hip throwing during intraspecifc encounters but not during interspecific encounters. Their reactions were strongly similar to those of Norway rats, which are considered to be predators of mice (O'Boyle 1974; Blanchard *et al.* 2003).

House mice did not interact more often with conspecifics than with ship rats, however, they spent less time motionless when encountering a conspecific, indicating a lower perception of risk compared to when encountering a ship rat. They also showed occasional aggression which included one instance of tail rattling behaviour, a classic threat display used by mice (John 1973), which they did not exhibit during interspecific trials.

3.5.2.2 Association with feeding

Predation is the act of killing to acquire food, so for predatory aggression to be distinguished from other forms of aggression there must be an association with feeding. All rats that interacted in any way with a dead mouse in experiments 2B and 3 ate at least some of it; and eating generally began very soon after contact was made, indicating that the motive for contact was feeding, although rats in 2B appeared distracted by their surroundings. The majority of rats that interacted with dead mice in experiment 3 showed attacking and restraining behaviour, which indicates that they were not merely scavenging. Rats bit at the dead mouse and turned it in their forepaws which is similar to behaviour described for rodents preying on invertebrates (Timberlake & Washburne 1989) and indicates that ship rats viewed mice as prey.

Ship rats that were food restricted tended to eat more and with shorter latency than rats provided with continuous food. However, rats from both groups attacked dead mice, and were also aggressive towards live mice. This indicates that hunger is not a prerequisite for aggression. On the contrary, hunger, aggression and predatory behaviour are only loosely linked, as in classic predator-prey systems where carnivores will sometimes kill even when the prey are surplus to their feeding requirements (e.g. Macdonald 1977; Short *et al.* 2002; Gazzola *et al.* 2008). Similarly, Norway rats will kill mice on repeated occasions even when they are consistently prevented from eating them (Myer 1969).

The ethical advantages of using animated dead mice were balanced by some obvious drawbacks: dead mice did not move exactly as a live mouse would, they

did not emit sound and could not retaliate against an attacking rat by biting or clawing. Nevertheless, I consider that the dead mouse experiment provided credible information about the link between aggression and feeding because the trials identified four reasons for assuming that rats viewed dead mice as similar to live mice: 1) some rats showed characteristically similar, fiercely aggressive behaviour. 2) They exhibited none of the threat behaviour seen in intraspecific trials. 3) Latency to interact was not significantly different. 4) Individual rats that did not interact with dead mice also interacted little with live mice and showed no aggression to them.

3.5.3 Significance of results for wild populations

There is a risk that behaviour observed in captivity may be unrelated to the dynamics that occur in the wild (Pinter-Wollman *et al.* 2006). However, my findings that ship rats are dominant to house mice are consistent with field studies that have demonstrated a negative influence of ship rats on house mouse behaviour and abundance (Innes *et al.* 1995; Brown *et al.* 1996; Harris & Macdonald 2007; Harper & Cabrera 2010). The majority of ship rats behaved very aggressively towards house mice during trials, and the size difference between these species predicts that house mice would sustain lethal injuries, in accordance with previous reports of killing of mice by ship rats (Lidicker 1976; Granjon & Cheylan 1988).

Such aggressive behaviour towards house mice appeared to be predatory rather than a form of territorial or resource defence aggression. Several ship rats ate in such a way that they should have ingested parts of the mouse that would be identifiable, e.g. fur and bone of the skull. Although I did not perform any gut content analysis to confirm that implication, if predation of mice by ship rats is common in feral populations, mouse remains should be found during gut content studies, however, this is not usually the case (e.g. Daniel 1973; Innes 1979; Clout 1980; Copson 1986).

One study that did find remains of mice in rat stomachs was done during a mouse plague in beech forest of the South Island, New Zealand (McQueen &

Lawrence 2008). It is possible that when mice are at very high population density, ship rats encounter and kill them frequently, but at normal population density, rats would have fewer opportunities. Nevertheless, because even occasional predation can have a strong impact on small mammal community dynamics (Moura *et al.* 2009), predation could still be part of the mechanism by which ship rats negatively influence mouse populations. The mere risk of predation could be enough because, if house mice avoid ship rats because of the high risk associated with encounters, this in itself can indirectly negatively impact populations (Arthur *et al.* 2004) and, depending on the scale of avoidance, may prevent mice from inhabiting areas dominated by ship rats.

3.5.4 Conclusions

I have used novel methods to humanely investigate the aggressive response of ship rats towards house mice. I have demonstrated that aggression is predatory in nature because it lacks classic threat display features and is associated with feeding. Such information is important for understanding the dynamics of the relationship between these widespread and damaging pest species, although the ultimate cause of low house mouse abundance in ship rat dominated areas may be due to risk effects rather than direct mortality from predation.

4 Non-commensal house mice show strong avoidance of ship rats

4.1 Abstract

Interspecific interactions involving aggression are common in nature and subordinate or prey species may mitigate the negative effects by exhibiting avoidance behaviours. However, by avoiding an aggressor animals can suffer limited foraging opportunities, with consequences for their abundance, distribution and potentially also how reliably we detect them in field surveys. Direct encounters between two common coexisting rodents, ship rats (*Rattus rattus*) and house mice (*Mus musculus*) favour the larger rats. I investigated whether mice perceive ship rats as a significant threat and exhibit avoidance behaviour. In captive trials I gave mice the choice of foraging for seeds in artificial resource patches near to or away from a caged ship rat, and measured giving up density (GUD) of seeds remaining. Although caged ship rats could not physically prevent mice from foraging, quitting harvest rates were significantly higher in trays close to rats, indicating reduced willingness to forage. In the field I investigated whether mice foraged more intensively or extensively after rat removal in a rat-favoured habitat (forest) bordered by habitat offering refuge favouring mice (grassland/scrub). Mice responded by non-randomly expanding their foraging area away from refuge habitat into rat-free areas, allowing them to forage more widely. My findings support the hypothesis that house mice perceive a high level of threat from ship rats, stimulating anti-predator responses when rats are close. In habitat where ship rats are abundant and there are few refuges, the indirect effects of avoiding interactions may limit mice even if direct encounters are rare.

4.2 Introduction

Intraguild (IG) interactions involving aggression are widespread in nature (Schoener 1983; Arim & Marquet 2004) and are important for structuring ecological communities, including sympatric mammals (e.g. reviews in Grant 1972; Palomares & Caro 1999; Eccard & Ylönen 2003; Ritchie & Johnson 2009). Levels of aggression exhibited by dominant species vary. At the extreme end of the aggression scale, dominant species kill and consume subordinates, making them both competitor and predator, a case known as IG predation (Polis *et al.* 1989). There is evidence that subordinate (including IG prey) species mediate the negative effects of interference or predation by exhibiting avoidance behaviours (Sergio *et al.* 2007; Choh *et al.* 2010). They may restrict their use of habitats favoured by dominants (including IG predators) (e.g. Doncaster 1992; Palomares *et al.* 1996; Maitz & Dickman 2001; St-Pierre *et al.* 2006), or occupy the same habitats, but alter their activity and foraging behaviour (e.g. Ziv & Kotler 2003; Mukherjee *et al.* 2009).

Avoidance behaviours can be necessary for survival, but also incur costs which negatively influence fitness (Creel & Christianson 2008). The extent of avoidance must be balanced against the degree of risk posed by the dominant species as well as resource availability (Wilson *et al.* 2010). Strong avoidance is expected if predation occurs (Dickman 1991). The behavioural response of subordinate species to the threat posed by dominants can have a powerful influence on their abundance and distribution even when direct contact events are rare (Dickman 1991; Sergio *et al.* 2007; Moura *et al.* 2009).

For conservation and wildlife management it is important to recognise and understand how direct IG interactions involving aggression influence species for two main reasons: (1) loss or removal of dominant species can lead to increased abundance of subordinates, which may have negative consequences for the shared resource (Courchamp *et al.* 1999; Caut *et al.* 2007; Ritchie & Johnson 2009), (2) altered behaviour in the presence of dominant species may make subordinates difficult to detect or monitor (Harper & Veitch 2006).

Ship rats (*Rattus rattus*) and house mice (*Mus musculus*) are species that have been widely accidentally distributed beyond their natural range, and often coexist as pests, with damaging effects on native biodiversity. They are generalist omnivores, depending mainly on diets of seeds and invertebrates and may compete for food. Though they coexist, ship rats and mice are more abundant in different habitat types (King *et al.* 1996c). Mice appear to be suppressed by ship rats because control or eradication of rats for conservation often leads to increased mouse detections (Innes *et al.* 1995; Miller & Miller 1995; Brown *et al.* 1996; Gillies *et al.* 2003b; Harris & Macdonald 2007; Witmer *et al.* 2007; Harper & Cabrera 2010). This originally rather surprising effect, now routinely expected, is an unwanted outcome that undermines the benefits of rat control for native biodiversity (Caut *et al.* 2007). However, the extent to which increased detections are due to a change in mouse abundance or behaviour has been debated (Innes *et al.* 1995; Brown *et al.* 1996; Harper & Cabrera 2010).

A direct (interference competition or IG predation), rather than indirect (exploitation competition) mechanism is likely to underpin ship rat-house mouse interactions because mice have been observed to respond rapidly to pulse ship rat removal (Brown *et al.* 1996; Harper & Cabrera 2010). Response to resource availability alone is expected to be slower as resources build up (Dickman 1991). Specifically, Harris and MacDonald (2007) propose a mechanism of resource defence interference because they found that mouse abundance increased in the presence of rats when they supplemented food in a scattered regime, but not when the regime was patchy. Ship rats could monopolise patchy food resources, but not scattered ones. However, it is not clear whether ship rats defend these patches, or if house mice avoid them when they are associated with concentrated rat activity.

Ship rats are approximately eight times larger than mice, and known to kill other vertebrates (Brown *et al.* 1998). Predatory behaviour towards mice has been observed in captive trials (Chapter 3) and gut content analysis of ship rats kill-trapped in New Zealand beech forest at the time of a mouse plague found mouse DNA (McQueen & Lawrence 2008). Therefore removal of ship rats may minimise

a source of direct mortality for house mice, especially the juveniles (King *et al.* 1996b). However, no evidence of mouse consumption has been found in ship rat gut content analysis when animals are at normal population levels (Ruscoe *et al.* 2011), indicating that predation events, if they occur, may usually be rare. This observation is still compatible with a hypothesis of IG predation if mice exhibit avoidance, which itself influences foraging activity and habitat use.

To test the hypothesis that mice alter foraging activity to avoid encounters with ship rats I used giving up density (GUD) of seeds in artificial resource patches to measure willingness to forage (Brown 1988) and manipulated the presence/absence of rat stimuli. Previous studies have demonstrated that animals quit foraging at a higher resource density in response to threats such as predation risk (Kotler *et al.* 1993; Arthur *et al.* 2004) or interference (Ziv & Kotler 2003).

I paired a microcosm study with an unreplicated field manipulation (Oksanen 2001). In captive experiment 1, I investigated the foraging response of adult and juvenile wild-caught house mice to a caged ship rat (potential direct foraging risk) or provision of a sheltered vs. open foraging environment (varying indirect foraging risk). I predicted that mice would quit foraging earlier in patches associated with higher risk and that juvenile mice might avoid high risk situations less than adult mice do, which may explain their apparent vulnerability in habitat favoured by ship rats (King *et al.* 1996b). In captive experiment 2 I determined whether the response exhibited by mice to ship rats was general to live, moving animals, or specific to a potential threat, by comparing it with their response to a conspecific. I also investigated whether the foraging behaviour of mice was influenced by ship rat scent, a less direct cue of rat presence.

In the field, previous work has suggested that thick cover offered mice a partial protection from predation by rats (King *et al.* 1996c). Therefore I predicted that mice would forage more actively and/or extensively under cover in a grassland/scrub area than on a relatively open forest floor. Hence I measured foraging activity either side of a boundary between these two habitats. To

determine whether rat activity limited the willingness of mice to forage extensively and/or intensively in the forest, I carried out a pulsed removal of rats and measured the response of the resident mouse population.

4.3 Methods

4.3.1 Giving up densities (GUDs)

The theory behind GUDs is based on optimal foraging (Brown 1988). A foraging animal should leave a resource patch when the harvest rate (H) is less than or equal to the metabolic cost (C), predation cost (P) and missed opportunity cost (MOC) of foraging there (Brown 1988):

$H \leq C + P + MOC$

The density of the resource remaining once the animal has given up foraging reflects the point at which foraging at this patch results in no perceived net gain (Ziv & Kotler 2003). The usual method of applying the concept of GUD to small mammal studies is to mix a known quantity of small food items into a substrate so that harvest rate declines as the food resource is depleted and animals must work harder to find remaining food at lower density (Brown 1988). By presenting the same quantity of food and substrate and manipulating the presence or absence of a potential threat stimulus, the perceived threat level of the stimulus can be inferred by measuring the giving up density of food remaining (Kotler *et al.* 1993). Higher GUD is associated with higher foraging costs.

4.3.2 Captive experiments

4.3.2.1 Trapping and husbandry

I live-trapped wild house mice and ship rats at sites within the Water Treatment Reserve, Te Miro (30 minutes outside of Hamilton in the province of Waikato, North Island) and also on other privately owned land in the Waikato area. Trapping sites for mice were separated by >300 m (longer than a mouse home range, Ruscoe & Murphy 2005) so that I could select from groups of animals that were unfamiliar with each other to use in trials where an unknown conspecific was required as a stimulus.

For the capture of house mice I set groups of 10-40 Longworth live-capture small mammal traps containing polyester fibre for insulation in areas of scrub, or rank grassland at each site. Traps were spaced approximately 10 m apart. For the capture of ship rats I set wire cage traps (generic make, 200x200x300 mm) within native forest and pine forest at approximately 20 m spacing. Tin cans were wired inside cage traps to provide shelter, but bedding was not added because rats can become tangled in it. All traps were baited with carrot and peanut butter and checked daily. I weighed and examined captured animals which were then transported to the University of Waikato animal house facility within secure containers.

Mice and rats were housed in separate rooms. Each mouse was housed individually in a laboratory style mouse cage (300x200x200 mm) with plastic base and wire lid. Pine shavings and shredded newspaper were provided for bedding. Ship rats were housed separately in wire cages (600x400x1000 mm) and provided with nest tubes containing shredded newspaper. All animals were fed on a mixture of rodent lab pellets, oats, crisped rice, wild bird seed, pumpkin seeds, sunflower seeds, raisins, peanuts, cat biscuits and fresh carrot. Fresh water was available at all times. Animals spent a two week habituation period in captivity prior to beginning trials. I weighed and examined them after this time to ensure they were healthy. None lost weight, except females who were caught whilst pregnant and gave birth. These females were either not used in trials, or were used once their offspring had been humanely euthanized and they had had a further period of two weeks to recover and maintain steady weight.

4.3.2.2 Experiment set up

I used three outdoor, mouse-proof aviaries (approximately 5.2x3.3x2 m, with 6 mm square wire mesh) at the University of Waikato for experiments (see Figure 4. 1 for aviary layout). In each, two circular trays (200 mm diameter) filled with sand were placed 800 mm apart. An aluminium cage (200x300x200 mm) (‘stimulus cage’) containing shredded newspaper, a small amount of dry food and a water bowl were situated directly adjacent to each tray. The stimulus cages were solid on all sides except the one nearest to the tray which was 6 mm

mesh. An insulated nest tube was placed equidistant from the two trays. Water was available at all times. Apparatus were sheltered from rain. I introduced single mice to each aviary and gave them a habituation period of three nights. During this time they were fed ad lib sunflower seeds mixed with the sand in the two trays to get them accustomed to foraging there.

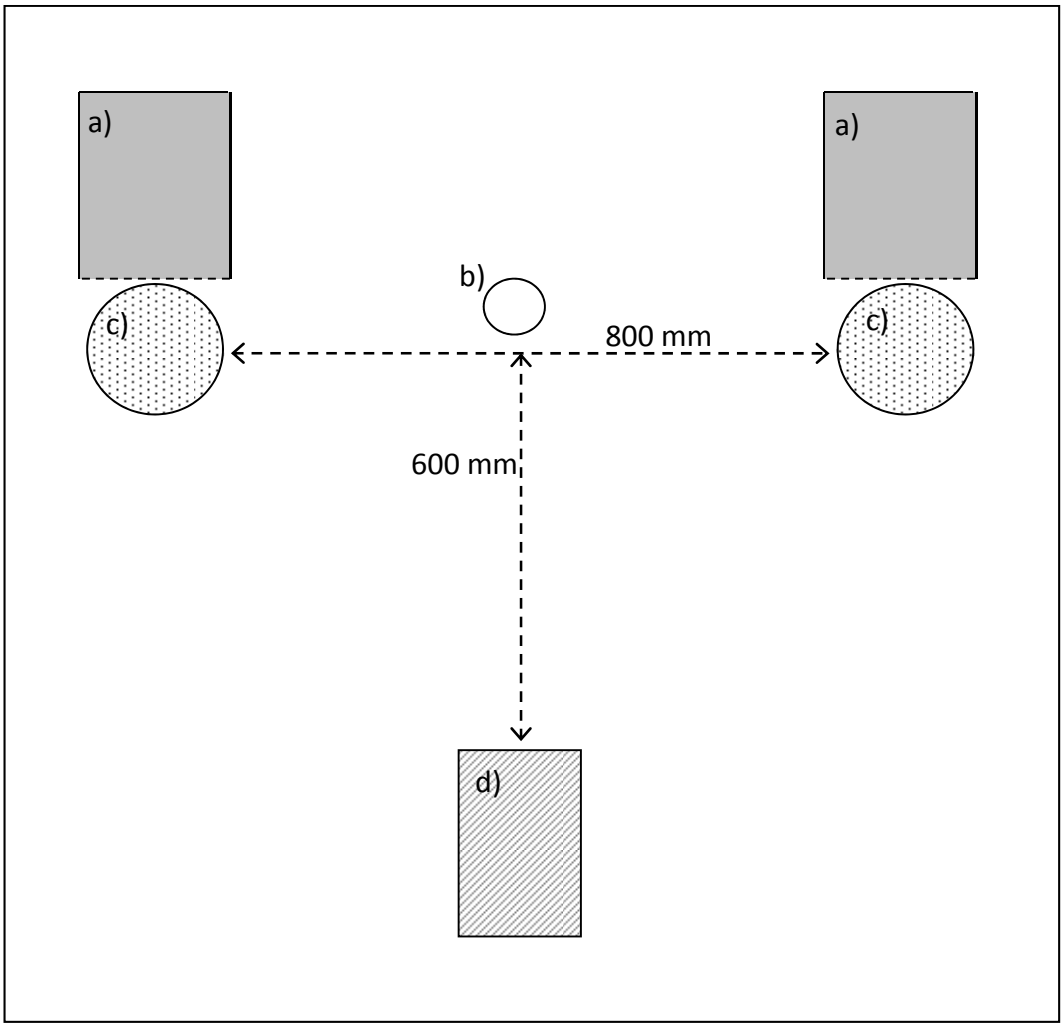


Figure 4. 1. Layout of apparatus for captive experiments. Items are as follows: a) 'stimulus cages', b) water bowl, c) trays containing sand and seeds, d) nest tube for mouse.

4.3.2.3 Experiment 1

In the evening of the fourth night, 50 sunflower seeds were mixed with the sand in each tray. This was the only source of food for mice at night. During the day rodent lab pellets were provided, but these were rarely eaten and were removed each evening prior to trials. The following (fifth) morning, remaining seeds were

sifted out and counted. This constituted a control night. On the fifth and sixth nights two treatments were presented in a random order. Either a ship rat was placed in the cage beside one of the trays, or a cardboard shelter was placed over one of the trays to provide cover (see Figure 4. 2). On the sixth and seventh mornings, remaining seeds were again sifted out and counted (See Table 4. 1 for a summary of treatments).

In total, 18 mice were used; six adult female, six adult male, and six juveniles of both genders. Mice were classed as juveniles if they were <13.5 g at the time of trials (King *et al.* 1996b). I used 12 rats in treatments, some more than once if necessary. Mice were randomly paired with same-sex rats for treatments, and rat or shelter treatments were randomly allocated to left or right cages/trays. All trials took place between November 2008 and February 2009.

Figure 4. 2. A stimulus cage with adjacent foraging tray with cardboard 'tent' creating a comparatively sheltered foraging location.

4.3.2.4 Experiment 2

In experiment 2 I repeated trials, but compared the response of mice towards rats with their response towards a same-sex conspecific (Table 4. 1). I also compared the response of mice towards the scent of a ship rat or scent of a same-sex mouse (Table 4. 1). Scent was collected by removing bedding (shredded newspaper) from the home cages of rats or mice immediately prior to trials. To test whether mice initially avoided foraging in trays associated with rat scent, but later became habituated, I videoed these trials and recorded the time of first forage in each tray.

All mice and rats used in treatments were selected randomly from the pool of available same-sex animals that were unknown to the subject mouse (trapped at different sites). Subject mice were always presented with different mice or rats for each treatment. Fifty seeds were mixed with sand in trays and counted each morning following treatment nights. In total 10 mice completed these trials (five female, five male) between February and April 2011.

Table 4. 1. Summary of captive experiments

Experiment	Treatment	Treatment abbreviation	Order	Subjects
1	Empty cage vs. empty cage	Control	1st	18 house mice - six adult females, six adult males, six juveniles of either sex (juveniles <13.5 g)
	Rat vs. empty cage	Rat	Random	
	Shelter vs. no shelter	shelter		
2	Rat vs. empty cage	R vs. e	Random (counterbalanced)	10 adult house mice (>13.5 g) – five females, five males
	Mouse vs. empty cage (intraspecific control)	M vs. e		
	Rat vs. mouse	R vs. m		
	Rat bedding vs. mouse bedding	Scent		

4.3.2.5 Data analyses

The main analyses of Experiment 1 and Experiment 2 data were performed in the same way. I used paired t-tests to determine whether differences in seed take between trays presented in each treatment were significant. To determine whether mouse sex or age influenced response to treatments, I calculated the absolute difference in seed take between trays within treatments and used generalised linear mixed effects models (GLMM) with Poisson distribution. Treatment, mouse type (male, female or juvenile) and the interaction terms were included as fixed effects in the model, and mouse ID as random intercept. I also included treatment as a random slope to account for variation in the strength of response to treatments for individual mice. I carried out backward removal of non-significant terms from the fully saturated model until the most parsimonious version was reached.

To investigate whether treatment and mouse type influenced the total number of seeds eaten by mice, I summed the number of seeds remaining in both trays and applied linear mixed effects models with mouse ID as random intercept. Models were fitted by maximum likelihood estimation and I carried out backward removal of non-significant terms. To determine whether the difference between first forage times in trays associated with rat or mouse scent differed from a null hypothesis of zero I used paired t-tests. Data for one mouse was not collected because of a video failure. I performed all statistical analyses in R (R Development Core Team. 2011) and for mixed effects models I used the lme4 package.

4.3.3 Field experiment

4.3.3.1 Study Area

Habitat at the Water Treatment Reserve, Te Miro, consists of a mixture of grassland dominated by tall (approximately 2 m) pampas (*Cortaderia* spp.) and exotic scrub, regenerating and mature pine forest (*Pinus radiata*) and native broadleaf forest. Introduced mammals observed in the area aside from rats and mice were rabbits, hares, ferrets and cats. At the time of the study brush-tail

possums *Trichosurus vulpecula* – widespread, introduced mammal pests - were being controlled by Matamata Piako district council using cyanide pellets (Ferratox®) and were at very low abundance. This was fortunate for my study because possums often interfere with monitoring devices used for rodents. Ferratox® cyanide pellets are coated in a repellent shown to effectively reduce consumption for rodents (Morgan & Rhodes 2000). I therefore assumed that this treatment would not affect rodent populations in my study area and this was supported by high rodent activity measured there.

4.3.3.2 Experiment design

Three square grids (90x90 m) were laid out in the reserve (Figure 4. 3). 'Scrub grid' was situated within the scrub/grassland habitat. 'Forest1' was situated within native forest habitat, c. 20 m from scrub grid, and 'forest2' was c. 300 m from forest1 at their closest points. Both forest grids were c.10 m from the scrub/forest boundary on one side. Each grid consisted of 16 stations spaced 30 m apart on a 4x4 square. Therefore forest grids comprised a row of stations 10 m from the border with scrub habitat, and three further rows 40 m, 70 m and 100 m from the scrub edge.

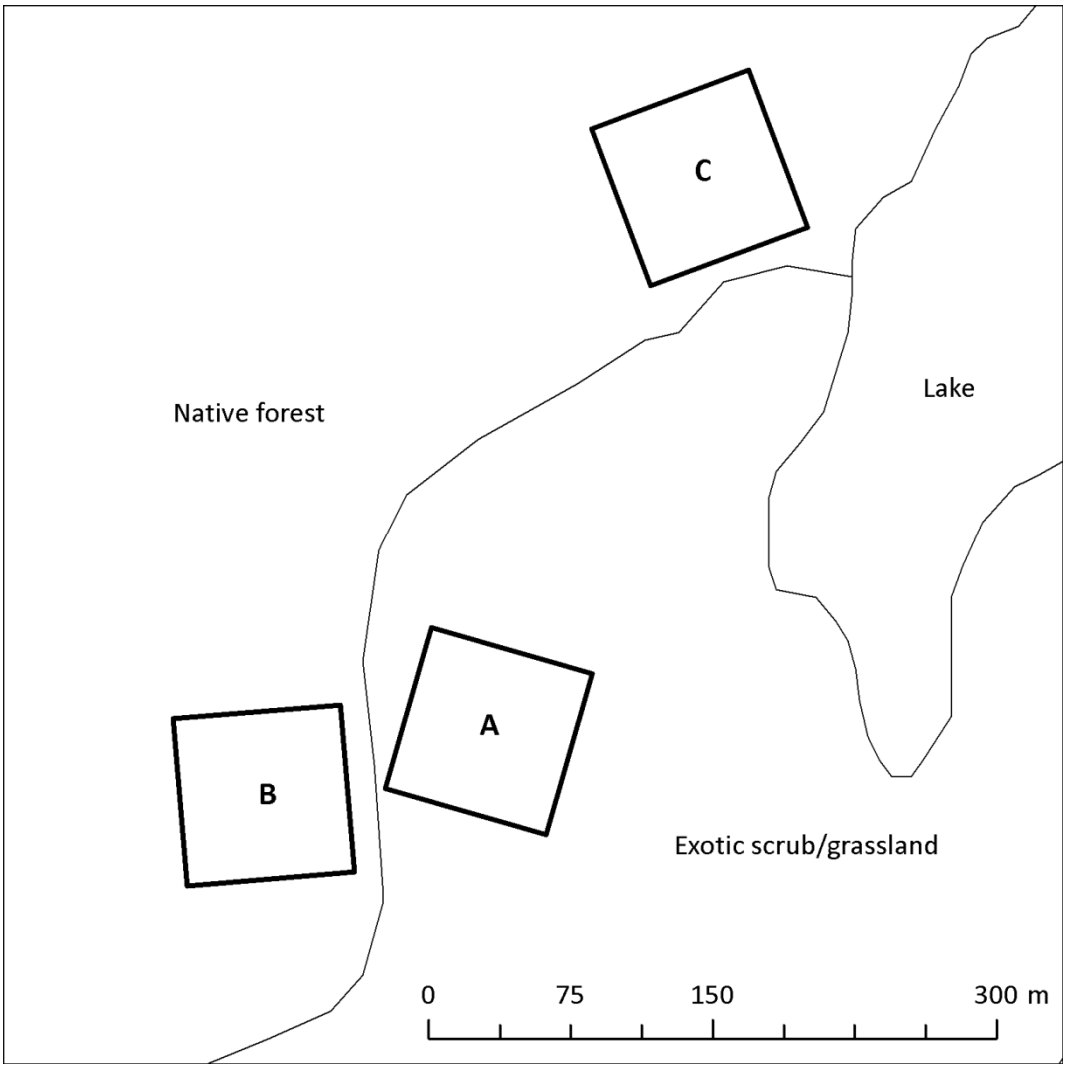


Figure 4. 3. The layout of grids within Native forest and Exotic scrub/grassland at the Water Treatment Reserve. Grids are: A – Scrub grid, B – Forest1, C – Forest2.

At each station a 200x200x50 mm square seed tray was placed, filled with sifted sand mixed with 80 sorghum seeds. Sorghum seeds were used because pilot trials revealed that sunflower seeds were removed too easily by rodents. The seed tray sat centrally upon a square sheet of brown parcel paper (300x300 mm) which was fixed to the centre of a square corflute board (500x500 mm). The edge of the board was coated with BlackTrakka™ ink so that animals visiting the seed tray left tracks on the paper and species identity could be recorded. The entire tray and board was covered with a wire mesh cage (500x500x100 mm). A pilot trial revealed that mesh with a 25 mm hole-size prevented access by ship rats, but was fully permeable to mice. A plastic cover over the top of the cage

kept off rain. The entire apparatus will be referred to as a 'tray' hereafter (Figure 4. 4) and its purpose was to detect visits by mice and measure their foraging activity. Similar equipment has been used in other studies (e.g. Strauß *et al.* 2008).

A Connovation™ tracking tunnel (450x100x100 mm) was placed beside the tray at each station. Each tunnel had an ink pad placed centrally with paper either side. Tunnels were baited with two pea-sized amounts of peanut butter smeared on both inside walls. Footprints of visiting animals were detected and identified to species. Tunnels could be accessed by both mice and rats and their purpose was to detect the presence of both species.

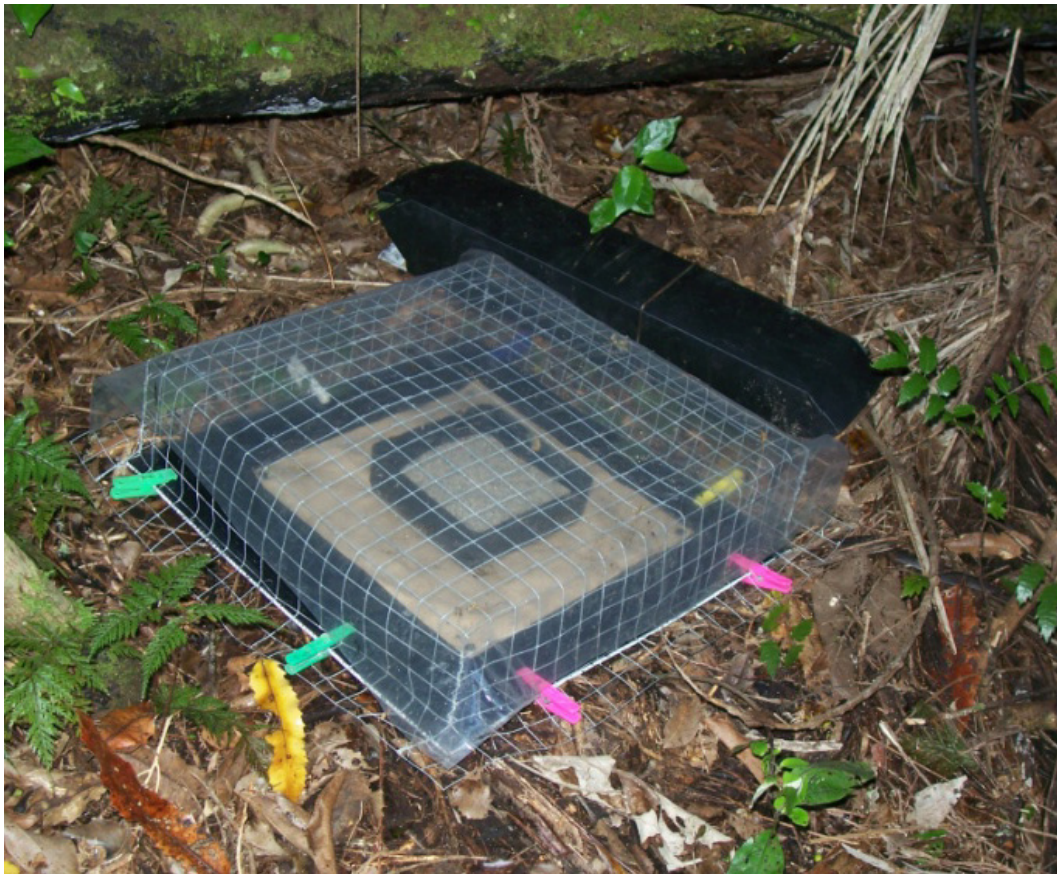


Figure 4. 4. Tray and tunnel apparatus used for investigating foraging behaviour in the field. The small square tray contains sand and 80 sorghum seeds. It sits in the centre of a square of brown paper surrounded by a strip of ink. Mice visiting the tray leave ink footprints on the brown paper. The BlackTrakka tunnel situated next to the tray detects both mice and rats using a similar ink and paper system.

Trays and tunnels were set for a habituation period of three nights before the first surveys at each location, then reset for seven nights and visited daily. On each visit, the presence or absence of footprints on paper was recorded, and the number of seeds remaining in trays was counted. Paper and seeds were then replaced. A survey was run on scrub grid, after which all devices were moved to forest1 for a habituation period and survey.

In the hope of making direct observations of interactions of mice and rats at stations, I set video cameras with infrared (NIR) lighting at eight stations, four on scrub grid and four on forest1 and recorded for one or two nights at each depending on the length of battery life. To detect crepuscular and nocturnal activity recording began at 15:00 and continued to 7:00 the following morning. I reviewed video footage and recorded the number of visits made by each species any instances when more than one animal was present at a station.

After monitoring on forest1, rat removal began. A mixture of trap types was set to maximise rat kill in minimal time and reduce chances of trap shyness. Victor Professional Rat Snap Traps and Fenn traps baited with peanut butter were set approximately 5 m from trays and tunnels at each forest1 station and in a buffer zone of 12 locations 50 m out from the grid. My objective was to reduce rat numbers, but have minimal impact on house mice or any other species. Fenn traps were placed on the ground and covered with a wire mesh tunnel to prevent by-catch of birds. Mice are usually too small to trigger Fenn traps so I considered them to be rat specific. Snap traps are sensitive enough to be triggered by mice so to avoid this I wired these traps vertically to tree trunks at human head height. Ship rats are highly arboreal so were likely to interact with the traps, but mice are considered more terrestrial (Ruscoe & Murphy 2005).

Traps were checked every one to two days. Tunnels were baited for one night every 5 days to monitor residual ship rat activity, and then for three consecutive nights once activity was low (≤2 tunnels tracked). This took 23 days, after which trays and tunnels were set for a second survey. To check that changes in mouse activity were not related to time and increasing familiarity with trays and tunnels

rather than rat suppression, the same procedure was carried out on forest2, but without rat trapping.

4.3.3.3 Data analyses

Foraging data consisted firstly of counts of visits by mice and rats to tunnels (presence/absence of each species per station, per night) and visits by mice to trays (presence/absence per station, per night). These data reflect the number of trays or tunnels where the initial benefit of visiting exceeded any foraging cost (Kotler *et al.* 1993). I based the analysis on individual stations as sample units and for each species/device combination I calculated the total number of nights (out of seven) in which animals were detected. Secondly, data consisted of the GUD (seeds remaining/80 supplied per station, per night) for house mice, which reflects patch use. I calculated average GUD per station per night.

Differences between forest and scrub habitat were large, so I graphed averages and standard errors for comparison. To compare foraging data before and after rat removal on forest 1, I performed paired t-tests on the averages per station. I also compared use of tunnels vs. trays by mice before and after rat removal by performing a paired t-test on the difference in detection rates. All the same comparisons were made between surveys 1 and 2 for forest2 as a control.

4.4 Results

4.4.1 Captive experiments

4.4.1.1 Experiment 1

Mice quit foraging at significantly higher giving up densities in trays adjacent to caged rats ($t = -8.676$, d.f. = 17, $P < 0.001$) (Figure 4. 5.a). Ten of 18 mice avoided foraging entirely in trays close to rats. There were no differences in GUDs between trays in control ($t = -0.334$, d.f. = 17, $P = 0.743$) and shelter treatments ($t = -1.134$, d.f. = 17, $P = 0.272$). Mouse type (sex/age) and the interaction term were not significant and so were removed from the GLMM leaving treatment. Absolute difference between trays was greater for rat treatments than for control or shelter treatments ($z = 4.810$, $P < 0.001$), confirming the t-test results.

Total seed take did not differ significantly according to either treatment (Figure 4. 6.a) or mouse type, or the interaction term. Mice compensated for foraging less in trays beside rats by foraging more intensively (to low GUDs) in the alternative tray.

4.4.1.2 Experiment 2

Where live rats were present, mice again quit foraging at higher GUDs, both where the alternative was to forage beside an empty cage (r vs. e: t = -8.155, d.f. = 9, P < 0.001) and beside a same-sex mouse (r vs. m: t = -7.958, d.f. = 9, P < 0.001) (Figure 4. 5.b). Five of 10 mice avoided foraging in trays near to rats, and took no seeds from these trays in either r vs. e or r vs. m treatments. There was no significant difference in GUDs for m vs. e treatment (t = 0.334, d.f. = 9, P = 0.746) or scent treatment (t = -0.626, d.f. = 9, P = 0.547). There was no evidence that mice initially avoided trays associated with rat scent, but later became habituated as first forage times were not significantly different, even where a one-tailed test was used (t = 1.859, d.f. = 8, P = 0.297).

Treatment was the only factor found to significantly influence the absolute difference between trays in the GLMM. Absolute difference between trays in treatments with live rats was greater than for other treatments (r vs. m: z = 2.345, P = 0.019. r vs. e: z = 2.814, P = 0.005). Treatment also significantly influenced total seed take ($F_{[2,49}$ = 8.7516, P < 0.001) ; when presented with live rats, mice left more seeds than when they were presented with a conspecific (r vs. m: t = 3.718 and r vs. e: t = 3.979) (Figure 4. 6.b). This indicates that in the absence of an obvious threat, mice foraged more when a conspecific was present. Other treatment comparisons were not significant.

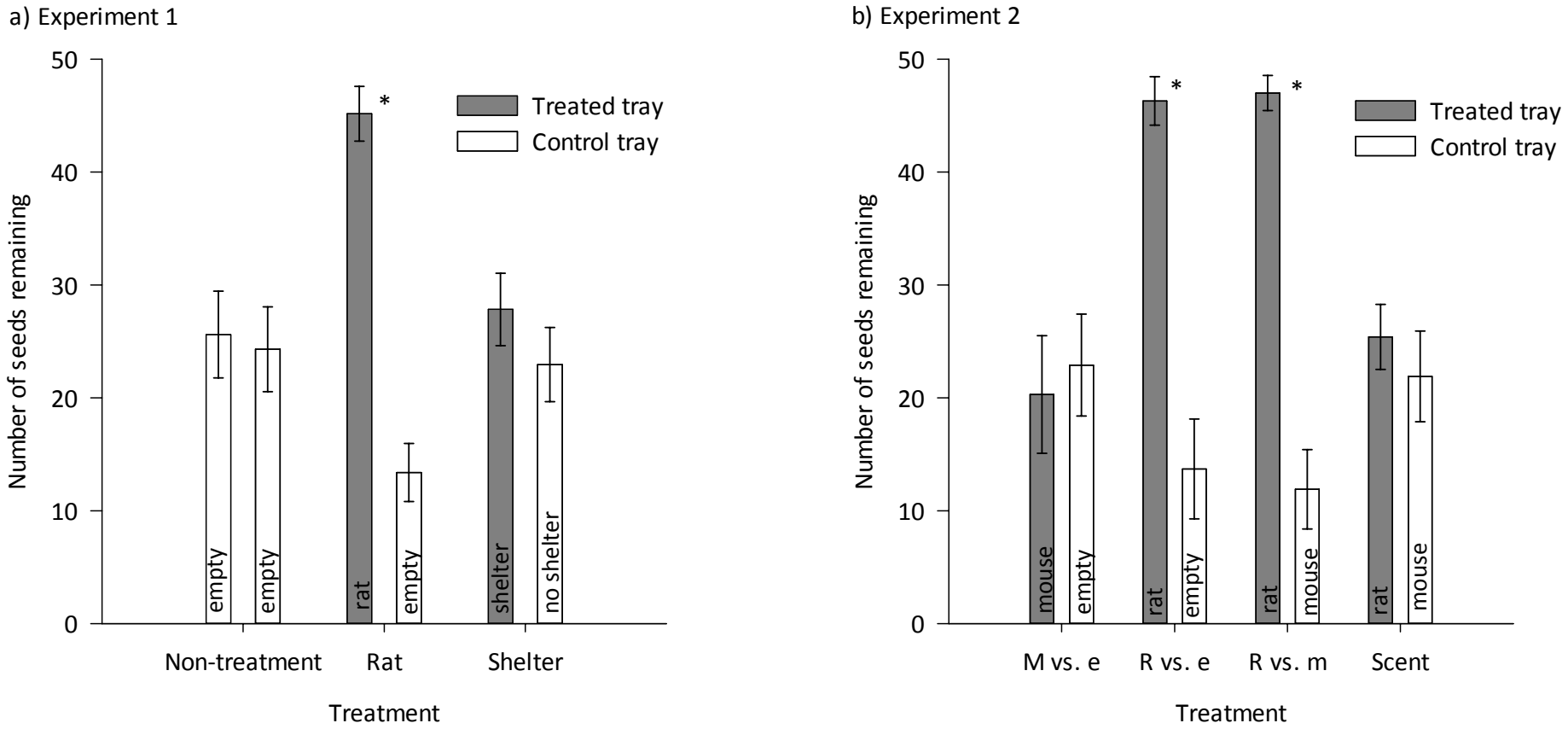


Figure 4. 5. Average number of seeds remaining (giving up density, GUD) in trays foraged by house mice. Mice could choose to forage in either of two trays in each treatment. Trays were placed beside a small wire cage. In experiment 1 (a), stimuli were inclusion of a live ship rat in one cage ('rat') or provision of a cardboard shelter over a foraging tray ('shelter') and were compared with non-treatment where cages were empty and no shelter was provided. In experiment 2 (b), foraging response to rats was compared with response to a same-sex conspecific. Response to scent was also tested. A significant difference between paired trays is indicated by *. Error bars show ±1 standard error.

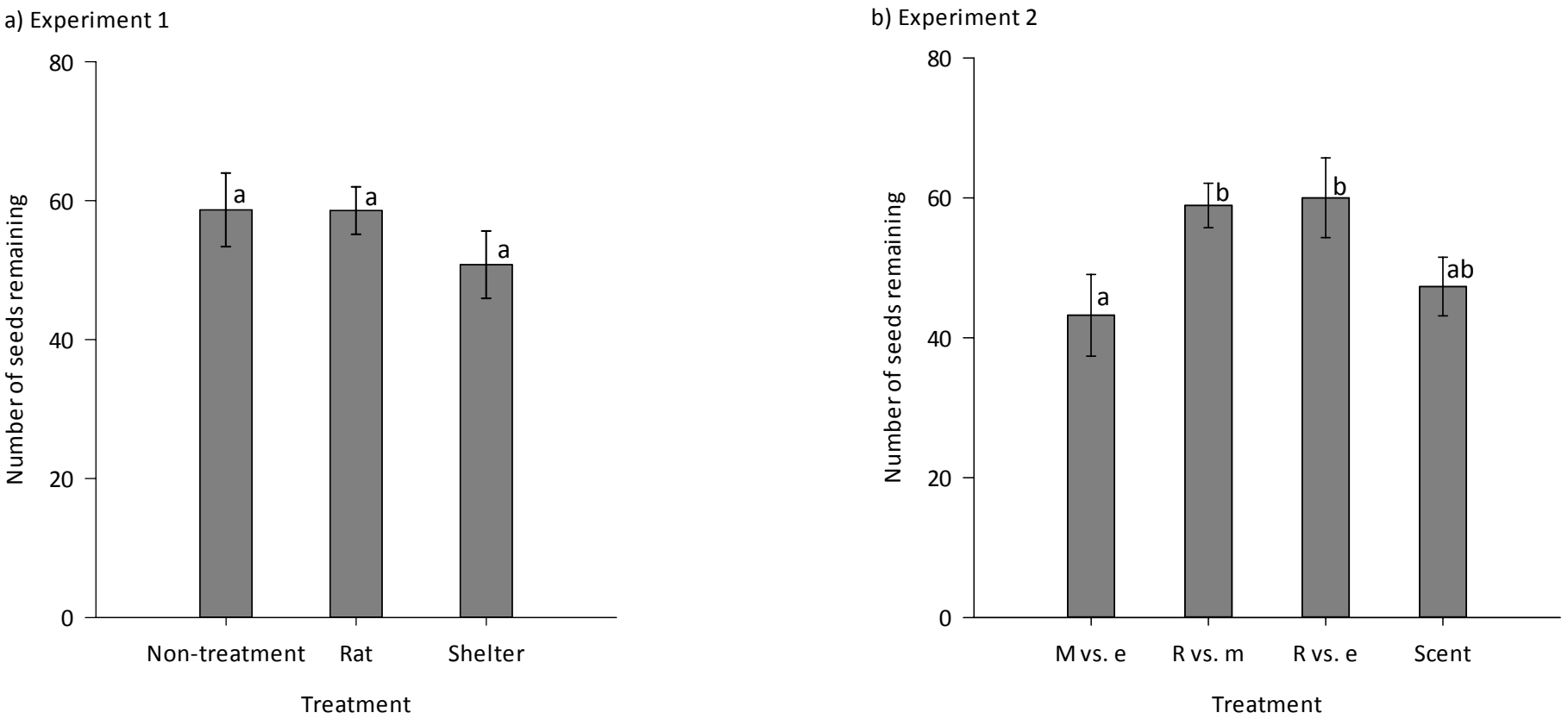


Figure 4. 6. Combined total number of seeds remaining (giving up density, GUD) from two trays foraged by house mice. Trays were placed beside a small wire cage. In experiment 1 (a), stimuli were inclusion of a live ship rat in one cage ('rat') or provision of a cardboard shelter over a foraging tray ('shelter') and were compared with non-treatment where cages were empty and no shelter was provided. In experiment 2 (b), foraging response to rats ('r') was compared with response to a same-sex conspecific ('m') or an empty cage ('e'). Response to scent was also tested. Bars with different letters indicate significant difference. Letters are only relevant within experiments, not between. Error bars show ±1 standard error.

4.4.2 Field experiment

4.4.2.1 Habitat differences

Mouse and rat activity differed considerably between habitat types (Table 4. 2, Figure 4. 7). As predicted, mouse activity was higher in the scrub than in forest. All trays and tunnels were visited each night in the scrub, and GUDs were low. In the forest fewer trays and tunnels were visited, and GUDs were notably higher. Trays and tunnels visited on forest grids were generally those on the edge closest to the grassland/scrub habitat. Rats were active in the scrub, but less so than in forest habitat where they visited almost all tunnels each night.

4.4.2.2 The effect of rat removal

Altogether 59 rats were removed from forest1 during rat suppression work, which significantly reduced rat activity in tunnels (Table 4. 2, Figure 4. 7.a). Two mice were also captured in snap traps. Despite this loss, mice began to be detected at stations they had not visited before as rats were removed. They appeared gradually as new detections recorded in tunnels on lines progressively further into the forest interior, until mice had visited all trays and tunnels (Figure 4. 8). This equated to a significant increase in mouse visit rate per tunnel between surveys 1 and 2 on forest1 (Table 4. 2, Figure 4. 7.b). Similarly, mouse tray visit rate increased significantly (Table 4. 2, Figure 4. 7.c).

Because mice were visiting more trays, there was a slight decrease in average GUD per tray between surveys 1 and 2, when compared with a one-tailed test (Table 4. 2, Figure 4. 7.d). Total seed take was considerably higher (1310 vs. 587). This was not due to greater foraging intensity, as those trays visited in survey 1 were not depleted to lower GUD in survey 2 ($t = 0.68$, d.f. = 15, $P = 0.528$). However, there was evidence that, on average, GUD was decreasing over time during survey 2 (Figure 4. 9.a). Prior to rat suppression, mice were more often detected using trays than tunnels. Following rat suppression on forest1, mice showed a preference for tunnels over trays ($t = 4.47$, d.f. = 15, $P < 0.001$).

No significant change in rat activity was detected between surveys on forest2 (Table 4. 2, Figure 4. 7.a). No change was detected in mouse visits to tunnels or

trays or in average GUD (Table 4. 2, Figure 4. 7.b, c and d). Total seed take did increase (Table 4. 2) due to greater intensity of foraging in just two trays. On average, seed take remained stable during surveys (Figure 4. 9.b). Mice were more often detected in trays than tunnels on forest2 and there was no change in preference between surveys 1 and 2 ($t = 0$, d.f. = 15, $P = 1$).

Table 4. 2. Summary of results for mouse and rat foraging activity on the three grids in two habitat types (scrub, forest1 and forest2) and comparisons between surveys 1 and 2 for forest grids. Each survey consisted of seven nights with devices checked each day. Rats were kill-trapped following survey1 on forest1. No kill-trapping occurred on forest2

Grid/survey		Scrub	Forest1/survey 1	Forest 1/survey 2	Forest2/survey 1	Forest2/survey 2
Rat tunnel visits	Total number of tunnels visited at least once	16	16	5	15	16
	Average number of nights visited per station (± SE)	5.2500 (±0.4610)	6.9375 (±0.0625)	0.3750 (±0.1548)	6.4375 (±0.4469)	7
	t value	NA	32.25		-1.26	
	P value	NA	< 0.001		0.227	
Mouse tunnel visits	Total number of tunnels visited at least once	16	5	16	5	4
	Average number of nights visited per station (± SE)	7	1.1875 (±0.5018)	5.6875 (±0.3381)	1.3750 (±0.6115)	0.8125 (±0.4674)
	t value	NA	-9.67		1.7811	
	P value	NA	< 0.001		0.095	

Mouse tray visits	Total number of trays visited at least once	16	6	16	6	6
	Average number of nights visited per station (± SE)	7	1.8750 (±0.7238)	5.0000 (±0.4378)	1.8125 (±0.6783)	1.2500 (±0.5737)
	t value	NA	-5.17		1.45	
	P value	NA	< 0.001		0.528	
Seed take	Total seeds removed from all trays and nights combined	8139	587	1310	452	859
	Giving up density (seeds remaining) per station per night	7.3304 (±1.6660)	74.7589 (±2.2455)	68.3036 (±4.0922)	75.9643 (±1.9703)	71.6161 (±5.3812)
	t value	NA	1.88		0.96	
	P value	NA	0.040 (one-tailed)		0.350	

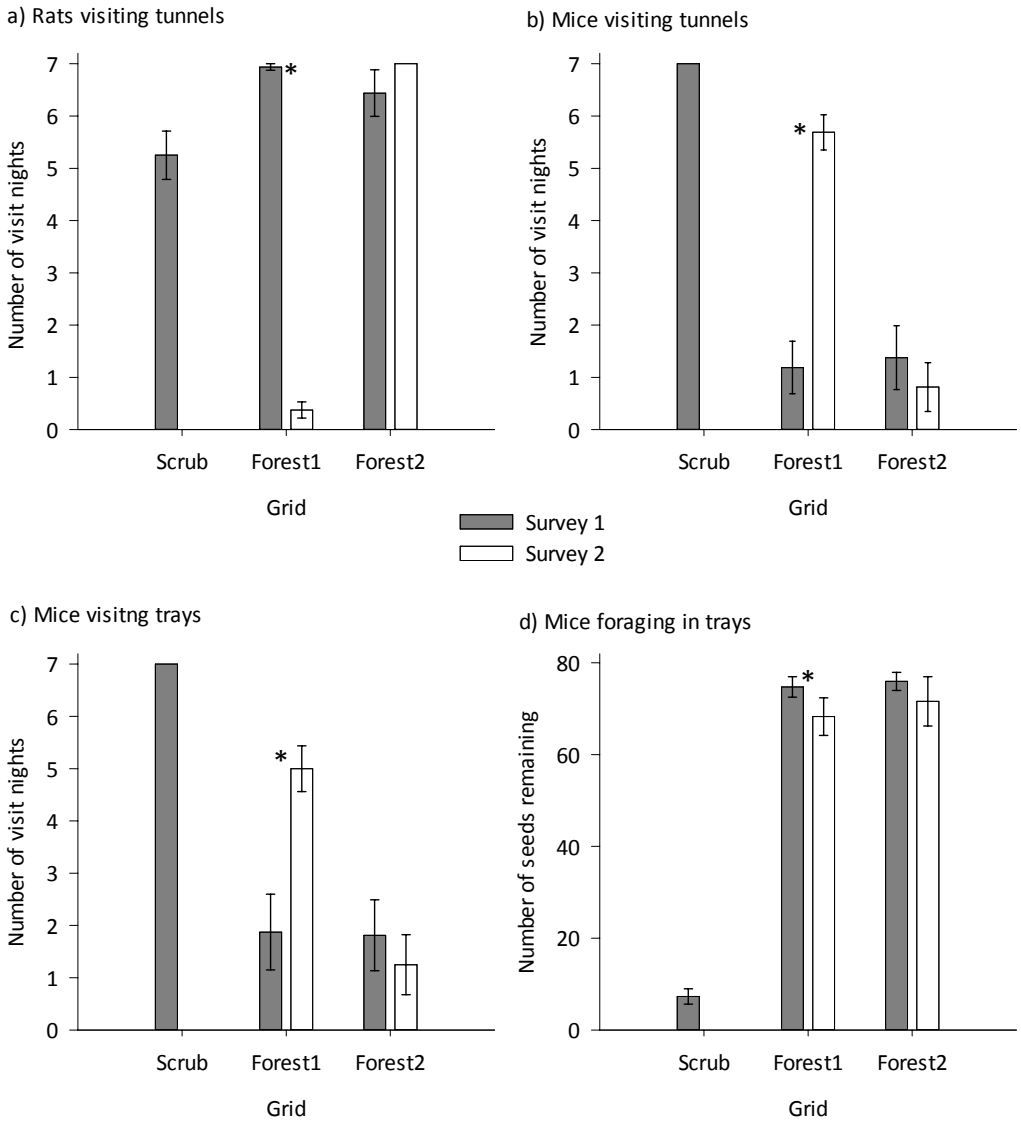


Figure 4. 7. Foraging activity of mice in artificial resource patches (trays) and mice and rats in tracking tunnels. Data are from three grids of 16 stations, one in scrub habitat and two in forest habitat close to the boundary with scrub. Forest grids received two surveys between which rats were kill-trapped on forest1, but not forest2 (non-treatment). Data are average number of visit nights (out of seven) in: tunnels by rats (a), tunnels by mice (b), trays by mice (c), and average number of sorghum seeds remaining (Giving Up Density, GUD, from an initial 80) per tray per night (d). A significant difference between surveys 1 and 2 is indicated by *. Error bars show ±1 standard error.

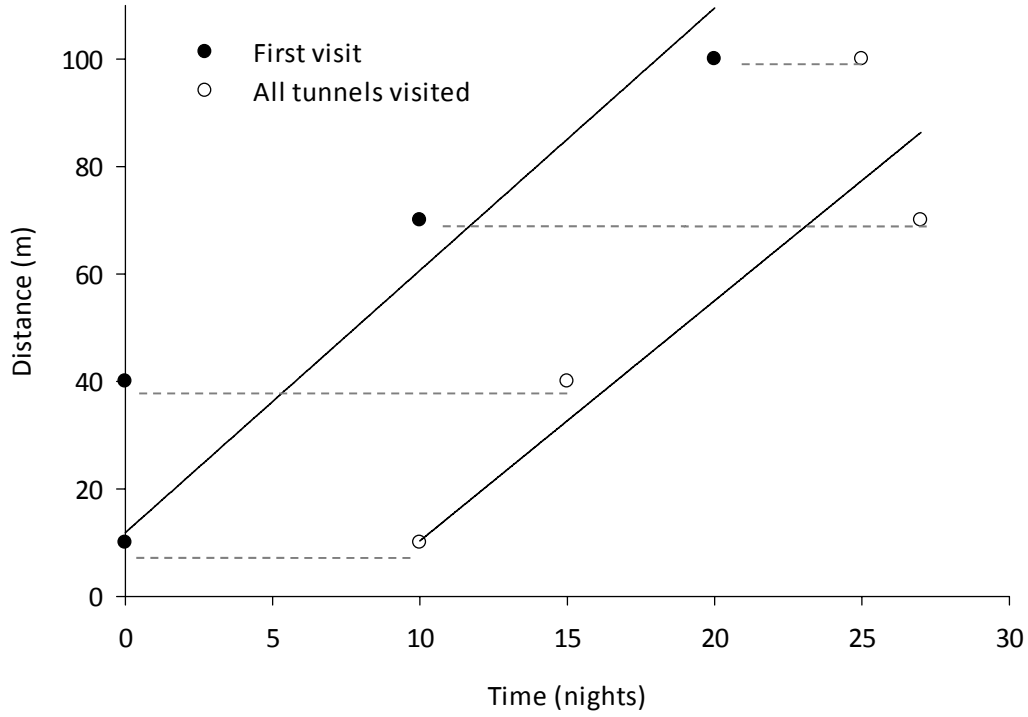


Figure 4. 8. Relationship between time since rat removal began and distance from scrub edge reached by mice. Data are from 16 tunnels distributed in four lines of four at 10, 40, 70 and 100m from refuge habitat. Data presented are time until first mouse detection at each distance and time until all tunnels are visited at each distance (broken lines illustrate the relationship between these points). A solid linear regression line is plotted for each dataset for illustrative purposes.

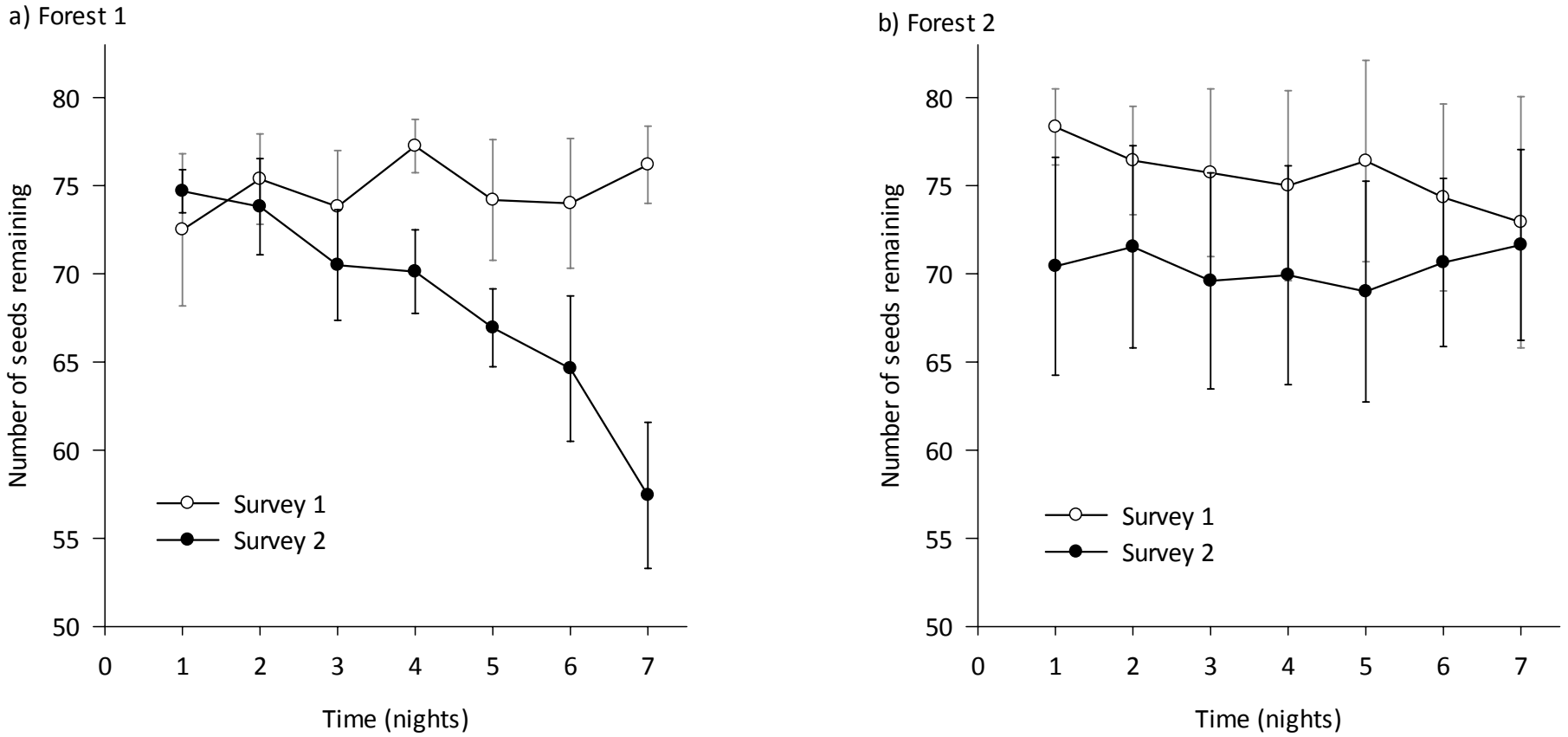


Figure 4. 9. Average number of seeds remaining (giving up density, out of 80) in artificial resource patches foraged by house mice over a period of seven nights. Data are from a grid where ship rats were removed from the area in between surveys 1 and 2 (a) and a grid where no ship rat removal took place (b). Error bars show ± 1 standard error.

4.4.2.3 Video results

A total of 223 hours of crepuscular and nocturnal video footage was recorded at the eight stations combined. Within this time 585 animal visits were observed. Mice made 9 visits to stations on forest1 and 502 visits to stations on scrub grid. Rats made 56 visits and 18 visits respectively. Most visits were made by single animals, but there were a few observations of simultaneous visits by two animals. There was one observation of a second rat arriving at a station when a first rat was present. Both animals appeared aware of each other, but did not interact and moved away slowly. On eight occasions two mice were observed at a station together. In all instances mice appeared to detect each other and one or both left the station, but no aggression was observed. A mouse and rat were present at the same station on three occasions (different stations) within scrub grid. Mice either retreated immediately, or hid initially and then retreated when the opportunity allowed. In this way they appeared to avoid being detected by rats so no direct interaction took place.

4.5 Discussion

My results show that house mice perceive ship rats to be a threat and avoid encounters with them by altering their foraging activity. I have demonstrated this effect for individual animals making foraging choices in captivity and for a mouse population utilizing different habitat types in the field.

4.5.1 Captive experiments

In captive experiments, mice quit foraging at higher resource density in trays beside rats even though rats were caged and therefore unable to physically exclude them. A large proportion of mice were deterred from foraging in these trays entirely. Video footage from the field experiment supported these results as mice were observed to avoid detection by ship rats by hiding or retreating when rats approached. In captive experiment 2, response to a rat was significantly different to the response to a conspecific, indicating that mice did not exhibit a general fear reaction to the presence of a moving animal. Instead, they distinguished between a potential threat and a comparably benign stimulus.

Such strong avoidance of rats by mice indicates an anti-predator response (Dickman 1991), which is compatible with a hypothesis of IG predation as an underlying mechanism of interaction between house mice and ship rats.

In contrast to avoidance of the direct risk posed by a live ship rat, mice did not avoid the indirect risk posed by foraging in the open compared to under a shelter, which was predicted in accordance with studies of house mouse habitat use (Dickman 1992; King *et al.* 1996c; Powell & Banks 2004). Despite no effect on seed take, there was evidence (seed remains and shells) that mice consumed seeds under the shelter, including those taken from the open tray. This suggests that mice valued the refuge, but, in the absence of a direct threat, they were willing to risk foraging in the open at higher resource density, rather than at an increasingly unprofitable rate under the shelter.

Contrary to predictions, juvenile mice showed similar levels of ship rat avoidance as adults of both sexes in experiment 1. Therefore it appears unlikely that reduced ability to perceive and avoid the risk posed by ship rats makes juvenile mice more susceptible to predation than adults (King *et al.* 1996b). However, it is possible that the vulnerability of juvenile mice is due to predation by rats whilst they are still in the nest, or when they first venture outside, after which they rapidly develop the ability to avoid such dangers. The wild-caught juvenile mice I used may have already passed this stage of their development.

Mice have fast metabolic rates and must feed regularly, therefore when avoiding rats, it was necessary for them to make up their food requirements by foraging at lower resource density in the alternate tray. Consequently there was no significant difference in total seed take between the rat treatment and control in experiment 1. In experiment 2, mice took significantly more seeds in total in the conspecific compared to live rat treatments. A possible explanation for this is that foraging risk was perceived to be lower when a conspecific was present, perhaps because another mouse provides additional vigilance. Alternatively, the presence of a conspecific stimulated foraging due to intraspecific competitive

pressure. Comparable social influences on foraging have been identified in Norway rats (Phelps & Roberts 1989; Whishaw & Whishaw 1996).

Despite strong avoidance of ship rats, mice did not show a foraging response to rat scent. I presented mice with bedding extracted from the sleeping quarters of rats. This provided odours associated with the skin and fur of rats as well as urine. The scent was strongly detectable, even to the human nose, so it is unlikely that mice were unable to distinguish it. Naïve laboratory mice exhibit an innate fear response to predator (cat and Norway rat) odour (Papes *et al.* 2010), however equivalent results have not always been observed in feral mice (Powell & Banks 2004). Ship rat scent may have been so common in the environment I captured mice from, that they were habituated to it and responded only to the auditory or visual cues of the live rat that gave more reliable information about its presence (Powell & Banks 2004). Although foraging decisions did not appear to be influenced by the rat scent I presented, it is possible that mice respond to subtle odour cues that I could not replicate (Masini *et al.* 2005), or at a scale that was not detectable in my study (Hughes & Banks 2010).

4.5.2 Field experiment

In the field, the prediction of greater mouse activity in scrub/grassland habitat compared with forest was confirmed, identifying scrub/grassland as a refuge for mice. In a previous study, mouse abundance measured by kill-trapping was also found to be greater in dense habitat compared with forest (King *et al.* 1996c) and later analyses revealed that this was not simply because mice were more detectable in denser habitat (Watkins *et al.* 2010b). At the Water Treatment Reserve it was apparent that house mice limited their use of forest habitat due to ship rat presence because kill-trapping rats was rapidly followed by increased detections of house mice, in accordance with other removal studies (Brown *et al.* 1996; Harper & Cabrera 2010).

I am able to distinguish between two possible explanations for this outcome which are: (1) mice initially showed avoidance of rat-favoured, forest habitat, but following rat suppression they were able to use this habitat more extensively, (2)

mice were already present across the forest, but following rat suppression they became more active and willing to forage and thus more detectable. My results support explanation (1) because I observed a gradual expansion of the number of stations visited by mice, away from the scrub edge, into the forest interior allowing more extensive foraging. Initially mice maintained low patch use (high GUD) indicating high perceived risk of foraging in the forest habitat despite rat suppression. However, patch use did show signs of increase over the survey period, secondary to the greater number of patches visited. Expansion out from refuges has been suggested previously (Harper & Cabrera 2010), but has not been clearly identified probably due to the scattering of refuge habitat throughout the area studied, rather than the clear demarcation between an identified refuge habitat and more open, rat-favoured habitat that I observed.

As well as a change in extent that house mice used forest habitat, I observed a change in the relative detection rate of mice in tunnels compared to trays. Trays were more likely to detect mice prior to rat suppression, but tunnels more likely post. Trays were accessible only to mice, but tunnels were accessible to both rats and mice. As rats were more prevalent than mice in the forest, a rat visit to a station was likely to occur prior to a mouse visit (also indicated by video footage). Early visitors to a tunnel remove bait and leave scent. The results of my captive trials indicate that scent is unlikely to deter foraging mice, however, removal of bait may reduce their motivation to enter tunnels. This competition between rats and mice for monitoring devices used to detect them both means that mice may be underestimated when rats are present. However, it should be noted that the pairing of tunnels and trays in close proximity in my experiment may have accentuated this result by providing mice with a convenient foraging alternative, which drew them away from tunnels they may otherwise have entered.

4.5.3 Conclusions

I have demonstrated strong avoidance of ship rats by house mice, which could be considered an anti-predator response. Avoidance behaviour leads to a scenario of low encounter rates between the two species, in opposition to the idea that

rats actively defend resources from mice. The implications for this are that even if direct encounters resulting in a predation event are rare, avoidance of rats may limit access to resources for mice with negative consequences for their survival and fitness. My results show that mice are likely to be sparse in open, rat-favoured habitat, as opposed to numerous, but undetected. I have demonstrated that mice constrained to limited use of forest, are rapidly able to detect the absence of ship rats and move in to take their place.

5 Investigating the effects of ship rat control and food supplementation on the abundance and activity of house mice in Pureora Forest Park

5.1 Abstract

Interactions between invasive ship rats and house mice can lead to unexpected consequences when abundance of ship rats is reduced and mice are released from constraints of food shortage, intimidation or predation. As a result, mice may become more abundant, but they may also become more active and detectable. To distinguish between these effects and investigate the role of food availability in determining mouse population dynamics I monitored mice at eight sites within Pureora Forest Park during periods of rat control and non-treatment, and I supplemented food in mouse-specific feeders to half of the sites. I used live-trapping to estimate mouse abundance, and tracking tunnels to detect activity. The rat control did not achieve the low rat abundance levels that have previously been associated with increased mouse detection rates, but despite this, both the abundance and activity of mice were positively influenced, and the two measures were correlated, indicating that activity reflected abundance. However, capture probability varied across seasons and according to rat abundance in unexpected ways, which indicates that mouse behaviour was also affected by rats at a more subtle level. Fluctuations in mouse abundance were driven by immigration, and there was evidence that mice were food limited in the presence of abundant ship rats. However, this effect could not be offset by supplementing food, so it is unlikely that it was due only to exploitation competition. Instead, the greater danger to mice when ship rats were abundant probably limited foraging opportunities for mice. Further evidence of direct predation of mice by ship rats was observed, but it is unclear what role direct predation plays in determining mouse abundance relative to risk effects.

5.2 Introduction

Invasion by alien species is one of the primary causes of native biodiversity loss worldwide (Clavero & Garcia-Berthou 2005; Blackburn *et al.* 2010). Mechanisms by which native species are negatively affected by invaders include predation (Salo *et al.* 2007), herbivory (Spear & Chown 2009), competition (Harris & Macdonald 2007; Dolman & Waber 2008; Stokes *et al.* 2009a), disease transmission (Gurnell *et al.* 2006), hybridisation (Rhymer & Simberloff 1996) and habitat modification (Crooks 2002). Advances in the science and technology of invasive species management have led to successful control or eradication operations over increasingly larger areas for species posing major threats (Towns & Broome 2003; Howald *et al.* 2007). However, where ecosystems are invaded by multiple alien species, management of just one can influence the abundance of others, for example, through mesopredator or mesocompetitor release (Courchamp *et al.* 1999; Caut *et al.* 2007). Such interspecific interactions can undermine the net benefit of the management operation (Tompkins & Veltman 2006) and in some cases lead to even worse outcomes for native species (Courchamp *et al.* 1999).

A further complication that arises from coexisting invasive species is when interactions between them are suspected of hindering accurate estimation of abundance and distribution. For example, within invasive rodent communities aggressive interference competition from dominant species may suppress activity of subordinates, which in turn reduces probability of detecting the subordinate species during field surveys (Harper & Veitch 2006). This has implications for invasive species management because detecting and reliably estimating populations of both dominant and subordinate species is important to help select appropriate control methods, monitor fluctuations in abundance and assess whether desired outcomes have been achieved (Caut *et al.* 2007; Mehta *et al.* 2007; Harper & Cabrera 2010).

House mice (*Mus musculus*) and ship rats (*Rattus rattus*) have been accidentally introduced in numerous locations beyond their native ranges worldwide and

frequently coexist. Where they are introduced, rodents often have negative effects on native biodiversity (Towns *et al.* 2006; Howald *et al.* 2007). Ship rats have proven to be especially damaging in otherwise mammal-depauperate ecosystems such as those of New Zealand where they have been implicated in the decline of native bird (Brown *et al.* 1998; Innes *et al.* 1999; Innes *et al.* 2010a), bat and invertebrate species (Atkinson 1989; St Clair 2011). For this reason eradication or control operations are implemented for ship rats where possible (Parkes & Murphy 2003; Towns & Broome 2003; Towns *et al.* 2006).

Following ship rat removal, house mice are often detected more frequently (Clout *et al.* 1995; Innes *et al.* 1995; Miller & Miller 1995; Brown *et al.* 1996; Gillies *et al.* 2003b; Harris & Macdonald 2007; Witmer *et al.* 2007; Harper & Cabrera 2010). These species exhibit some diet overlap (Chapter 2), so they are potential competitors for food resources. However, ship rats also kill and eat house mice (Granjon & Cheylan 1988; McQueen & Lawrence 2008, Chapter 3 of this thesis) making them intraguild (IG) predators (Polis *et al.* 1989). House mice actively avoid encounters with ship rats, and this behaviour in turn limits the foraging opportunities for mice in ship rat-dominated habitat, such as mature native podocarp-broadleaf forest (Chapter 4).

Ship rats could limit the activities and numbers of mice in New Zealand podocarp-broadleaf forest, via direct lethal encounters, avoidance behaviours (risk effects, (risk effects, Creel & Christianson 2008), or the indirect effects of exploitation competition due to food shortage, but the relative extent of these different mechanisms is unknown. In arid forest of the Galápagos, Harris and Macdonald (2007) demonstrated that house mice and ship rats were food limited because populations increased where supplementary food was provided, but only under certain conditions. Mice benefitted only from scattered food, indicating that rats monopolised patchy food, interfering with access to it for mice (Harris & Macdonald 2007).

In New Zealand, house mice increase in abundance when ship rats are suppressed (Ruscoe *et al.* 2011) possibly due to improved juvenile recruitment of

mice born in rat-free areas (King *et al.* 1996b). However, house mice may also change their behaviour when they no longer have to avoid ship rats. During a press removal of ship rats, Brown *et al*. (1996) and Harper and Carbrera (2010) observed increased mouse detections over too short a period to be explained by recruitment of juveniles, and perhaps even immigration. It therefore appeared that the mice were present all along, but their activity and therefore detection rates were suppressed in some way.

To address uncertainty about the relative influence of ship rats on the abundance and activity of house mice, I monitored house mouse populations under conditions of high and low ship rat abundance. I used two methods with different features and assumptions: (1) A relatively mouse-specific live-capture method that allowed individual animals to be identified to measure abundance. (2) A footprint-tracking method that measured activity of the population by an unknown number of individuals and was not mouse-specific. If it is the abundance of mice that is mainly influenced by rat suppression, I expected the number of mice captured to be positively associated with rat control and for mouse activity to correlate with the number of mice captured. Alternatively, if activity is influenced disproportionately to abundance, I expected rat control to have a stronger effect on mouse activity compared to abundance and for the two measures to be poorly correlated.

If shortage of food limits house mice in the presence of ship rats I expected mice to have lower body mass when ship rats were at high abundance compared to when suppressed (Eccard & Ylönen 2002; Harris & Macdonald 2007; Stokes *et al.* 2009a). To determine whether mice are affected by actual scarcity of food in the environment because of exploitation competition from ship rats, or disruption of mouse foraging due to risk of meeting rats, I supplemented food in mouse-specific feeders on half of the study areas. My expectation was that this would offset any effect of exploitation competition, but would not benefit mice limited by risk effects.

5.3 Methods

5.3.1 Study Area and Background Information

To study mice under conditions of high and low rat abundance, I took advantage of the ship rat control operations administered by the Department of Conservation (DOC) in Waipapa Ecological Area (Waipapa EA). This site is part of Pureora Forest Park and comprises 5,112 ha of tawa-podocarp dominated hardwood forest with emergent conifers, of which 3,533 ha are under management. In addition, there is an unmanaged area of native scrub/grassland through which the main access road runs. Pureora Forest Park is located in central North Island, New Zealand (Figure 5. 1.a.), 500-600 m above sea level. Waipapa EA has a history of research on introduced mammals (King *et al.* 1996a; 1996b; 1996c; Innes *et al.* 2001) and a number of other features that were advantageous for my study and allowed potentially confounding variables to be controlled.

Comparable, adjacent treatment and non-treatment areas were available for the study due to division of the managed section of Waipapa EA into north (1,924 ha) and south (1,609 ha) blocks. One of the two blocks receives ship rat control each year to protect nesting native birds during the breeding seasons (spring and summer). Control is ground-based, using toxin in bait stations, and begins in late winter, supplemented with some replenishment of bait in spring and summer if necessary. In operations of this kind, ship rat populations can remain suppressed into autumn, but recover quickly from then on due to immigration and recruitment (Innes *et al.* 1995). Management in Waipapa EA is switched to the alternate block every two years. This switch coincided with the second year of my study (Table 5. 1) allowing the effects of a reversal of treatments to be monitored.

Mouse populations may benefit from rat removal even when the method used to kill rats should also be lethal to mice (Innes *et al.* 1995; Caut *et al.* 2007). However, I considered that ship rat control within Waipapa EA would have low impact on house mouse populations for three reasons: (1) ground-based

operations consisted of applying first generation anticoagulant toxins or sodium fluoroacetate (1080) (Table 5. 1) both of which have limited effect on mice (Fisher 2005; Fisher & Airey 2009). (2) Toxins were distributed within bait stations on a 150x50 m grid which is broad compared to the usual spacing for mice (MacKay *et al.* 2007). (3) Bait stations are nailed to trees with base height 20-30 cm from the ground, making many stations inaccessible to mice (Taylor *et al.* 1998).

Brushtail possums (ship rat competitors: Sweetapple & Nugent 2007) and mammal carnivores such as stoats and feral cats (predators of rats and mice) are also susceptible to poisoning (Gillies & Pierce 1999; Murphy *et al.* 1999; Parkes & Murphy 2003). Their removal from the system when blocks were treated could present a confounding effect in my study which wished to address only the ship rat-house mouse relationship. However these effects were mediated by: (1) the occurrence of an aerial 1080 drop the year prior to the beginning of my study (winter 2008), which covered the entire management area and effectively removed possums for the duration of the study because their populations recover slowly, (2) the close proximity of Waipapa North (WN) and Waipapa South (WS) blocks where my monitoring sites were located meant that the large home ranges of surviving or repopulating carnivores were likely to overlap both. This assumption was supported by stoat and ferret detections in both treatment and non-treatment sites at intervals throughout the study.

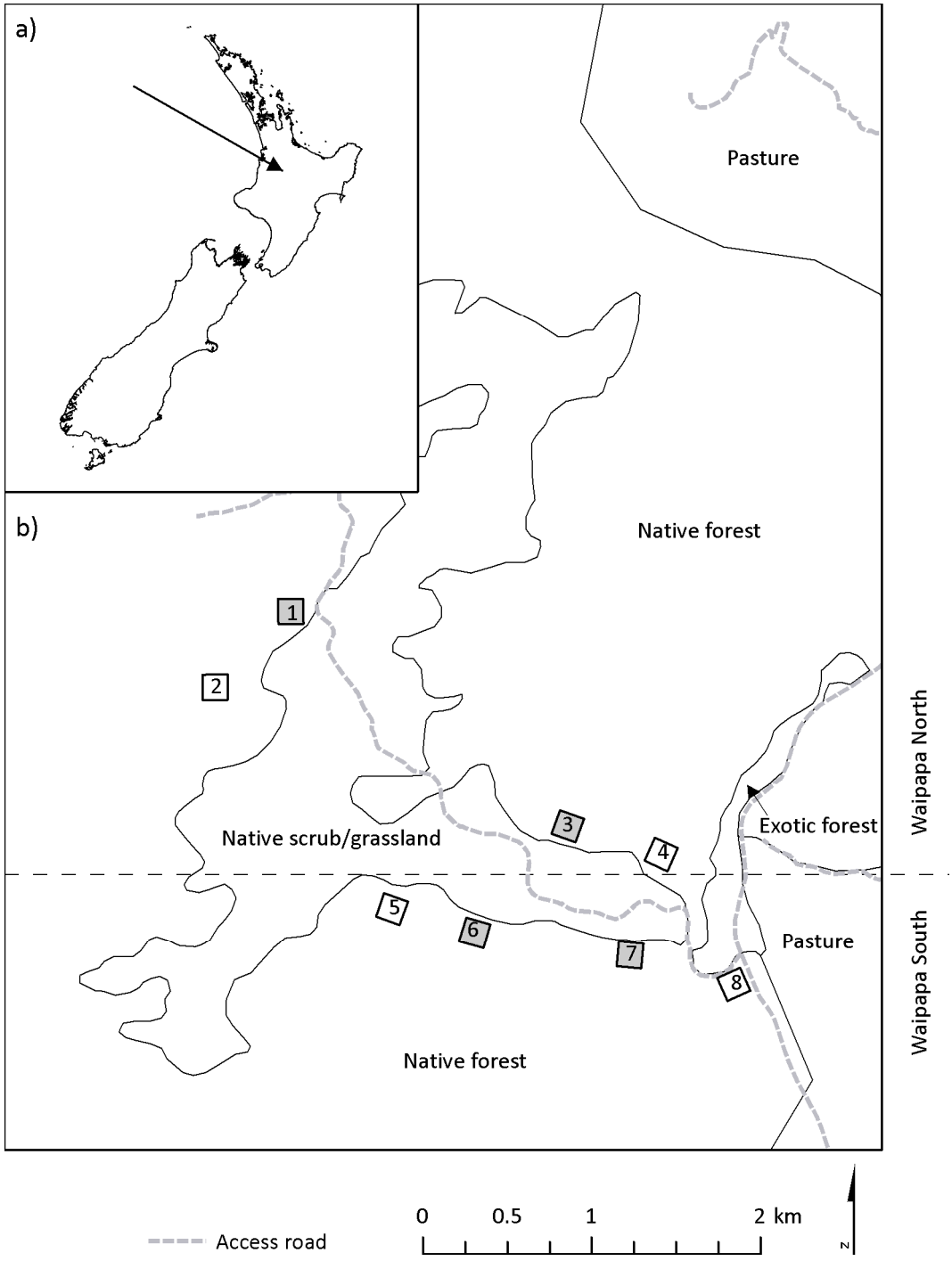


Figure 5. 1. The location of Waipapa Ecological Area, Pureora Forest Park within New Zealand (a). The layout of monitoring sites within Waipapa Ecological Area (b). Sites 1-4 are located within Waipapa North and 5-8 are within Waipapa South. Sites shaded grey received supplementary food. Ship rat management is implemented in the native forest.

Table 5. 1. Details of pest control activities undertaken in Waipapa Ecological Area, Pureora, New Zealand. Information in plain text describes the main operations undertaken by the Department of Conservation (DOC). Information in italics describes additional measures taken to bolster the main operations after they failed to reduce rat activity to low levels

Start	Undertaken by	Method	Area	Distribution	End
Year 1					
September 2009	DOC	Racumin® (Coumatetralyl)	Waipapa South	Ground based, bait stations, 150 x 50 m spacing	Replaced in November 2009 then removed in February 2010
5th November 2009	*My study*	*Victor Professional Rat Snap traps wired to trees at human head height. Baited with peanut butter. Checked every 3 – 4 weeks.*	*Waipapa South, monitoring sites only*	*16 per site, 4 x 4, 50 m spacing*	*I replaced these traps with DoC 250 traps (greater trigger weight) on 3rd March 2010 after several mice were killed by them*
3rd March 2010	*My study*	*DOC 250 kill traps baited with carrot and peanut butter. Checked every week for 3 weeks then every 2 weeks for the remainder*	*Waipapa South monitoring sites only*	*6 per site, 2 x 3, 50 m spacing*	*Traps closed 30th April 2010*

5th March 2010	*DOC*	*RatAbate® paste (diphacinone)*	*Waipapa South, monitoring sites and 500m buffer zone within forest*	*Ground based, bait stations, 150 x 50 m spacing*	*Bait removed May 2010*
Year 2					
September 2010	DOC	1080 cereal pellets (sodium fluoroacetate) prefeed used	Waipapa North	Ground based, bait stations, 150 x 50 m spacing	
7th November 2010	*My study*	*DOC 250 kill traps baited with carrot and peanut butter. Checked every 3-4 weeks*	*Waipapa North monitoring sites only*	*6 per site, 2 x 3, 50 m spacing*	*Traps closed 18th April 2011*
11th January 2011	*My study*	*Pestoff® cereal pellets (diphacinone*)	*Waipapa North, monitoring sites and 500 m buffer zone within forest*	*Ground based, bait stations, 150 x 50 m spacing*	*Replaced on 7th February 2011 and 12th March 2011 then removed 28th April 2011*

5.3.2 Monitoring

I selected eight sites for monitoring rodents within Waipapa EA, four in each of WS and WN (Figure 5. 1.b). Sites were not selected to be representative of Waipapa EA as a whole. For logistical reasons they were chosen from the ecologically similar and accessible regions of WS and WN and were all relatively close to the central scrub/grassland area which is habitat that favours mice (King *et al.* 1996c). There was potential for this habitat to act as a source of invading house mice when ship rat abundance was low (Chapter 4 of this thesis). Sites were spaced at least 400 m apart. This distance exceeds home range lengths recorded for house mice in forest (Fitzgerald *et al.* 1981; Ruscoe & Murphy 2005) so the sites were effectively biologically independent even though they fell within the same initial management operation. To bolster the pest control implemented by the DOC, I applied additional rat kill-trapping independently at each site (Table 5. 1). This study design was preferable to monitoring mouse populations in more distant areas receiving completely independent management because that would have introduced additional variables associated with differing climate, ecology and management techniques.

At each monitoring site I created a grid of 16 tracking tunnel stations (4x4) spaced 50 m apart. I chose this spacing because it is the same as that used in other studies where grids of tracking tunnels were created (e.g. (Innes *et al.* 1995; Brown *et al.* 1996; Blackwell *et al.* 1998; Innes *et al.* 2010b) and 50 m spacing is also used for tracking tunnel lines commonly used to monitor rodent abundance (Gillies and Williams, 2007). Connovation™ plastic tracking tunnels (without ink cards) were put in place on all grids during the setting up phase and were present for the study duration. Nested within the tracking tunnel grid was a second grid of 42 live trap stations (6x7) spaced 16.5 m apart. This spacing was selected based on other studies (e.g. Ruscoe *et al.* 2001), advice from researchers and for practical reasons of visiting all tunnel and trap stations as efficiently as possible. A single Longworth live-capture small mammal trap was placed at each trap station during surveys, but removed at other times.

Surveys at each site were carried out approximately every three months. A single survey consisted of five nights of live-trapping and, on a separate night, a one-night measure of activity in tracking tunnels. Live traps contained polyester fibre as bedding and were baited with peanut butter and carrot. I checked traps daily and newly captured mice were weighed, sexed, marked with a unique ear-hole punch combination (e.g. Figure 5. 2) and examined for signs of visible pregnancy or lactation before release. I classed juveniles as those animals weighing ≤13.5 g (King *et al.* 1996b). Recaptured mice were recorded and released. Traps were limited, so after trapping on four sites in survey week one, I moved the traps to the second four for week two (except in spring 2009 and summer 2010 when trap shortage meant that three survey weeks were required). Allocation of sites to survey week was random.

Figure 5. 2. A house mouse being restrained by the scruff of the neck for processing. The hole visible in its outer ear has been punched as an identification mark.

Tracking tunnels were run in the opposite week to trapping for each site, so they were independent. A Black Trakka™ inked card was placed into each tunnel along with two smears of peanut butter on the inside vertical wall as bait. Cards have an ink pad in the centre flanked by paper to record footprints as animals walk across. I collected cards after one night and identified prints as mouse or rat. For ship rats I used activity in tunnels as a proxy for abundance because the two measures have been shown to correlate for this species (Brown *et al.* 1996; Johnston 2003; Innes *et al.* 2010b). I therefore refer to ship rat abundance throughout the rest of the chapter. However, this relationship has not been demonstrated for house mice.

Surveys took place approximately every three months from spring (October/November) 2009 to autumn (late April) 2011 (Table 5. 2). This constituted three seasons (spring 2009–autumn 2010, year one) within which rats were controlled in WS, but not WN; a winter (July) 2010 survey when neither block received treatment; and then three seasons (spring 2010-autumn 2011, year two) within which rats were controlled in WN, but not WS. This made a total of seven surveys.

Table 5. 2. Details of rodent surveys on sites in Waipapa South (WS) and Waipapa North (WN)

Survey	Season	Period in which surveys took place	Block receiving rat control	Management year
1	Spring	26/10/2009 – 21/11/2009	WS	1
2	Summer	18/01/2010 – 12/02/2010	WS	1
3	Autumn	16/04/2010 – 29/04/2010	WS	1
4	Winter	10/7/2010 – 24/07/2010	Neither block	NA
5	Spring	7/11/2010 – 22/11/2010	WN	2
6	Summer	23/01/2011 – 8/02/2011	WN	2
7	Autumn	18/04/2011 – 28/04/2011	WN	2

5.3.3 Food supplementation

I began food supplementation immediately after spring surveys each year and ceased following autumn surveys. By discontinuing food supplementation over winter I allowed populations to return to normal levels before reversal of rat control treatments. Food was supplied in plastic containers (200x200x300 mm) with wire mesh hoppers inside (Figure 5. 3). Mice gained access via entrance tubes that were too small to allow rats to pass (25 mm diameter). Plastic containers were reinforced with wire mesh to prevent rats from chewing into them.

Two sites were randomly selected for food supplementation in each of WN and WS (sites 1, 3, 6 and 7, Figure 5. 1.b) and these same sites received supplemented food in both management years. Feeders were distributed at eighteen stations on each site, which were independent from tracking tunnel or live trap stations. Supplemented food consisted of standard rodent laboratory pellets (Speciality Feeds, Glen Forrest, Western Australia, see Appendix 4 for nutritional content). I tested that mice were willing and able to enter feed stations and eat laboratory pellets by presenting feeders to wild-caught mice in large enclosures in captivity. Approximately 200 g of pellets were placed into hoppers in each feed station. Feed stations were checked every three-four weeks. Evidence of visits by mice (faeces) was recorded and pellets were replaced if they showed any sign of deterioration.

a)

b)

Figure 5. 3. A feed station designed to provide supplementary food specifically to mice by excluding entry to ship rats (a). A wire hopper hanging inside contains the food (b).

5.3.4 Data analyses

5.3.4.1 Abundance and activity data

Data for each site and each survey consisted of: 1) an index of rat abundance (number of tunnels tracked by rats out of 16), 2) an index of mouse activity (number of tunnels tracked by mice out of 16) and 3) a measure of mouse abundance calculated from live-trapping results. For mouse abundance I calculated an index, the minimum number known alive (MNKA, Krebs 1966), rather than using closed capture models to estimate N. This was because sample sizes were small at the site level. For house mice in New Zealand forests, MNKA has been shown to correlate strongly with abundance estimated from closed capture models (Ruscoe *et al.* 2001).

I modelled each dataset in R (R Development Core Team. 2011) using the lme4 package. As I had only one winter survey, when no rat control was implemented, I excluded winter data from analyses so that rodent measures were compared between treatment and non-treatment periods over equivalent seasons. Time, treatment and block were the fixed effects along with all interactions. Where there was no effect of time, or there were seasonal fluctuations that were not well explained by changes over time, I explored these in separate analyses using the entire data set. Some correlation of season and time prevented including both as factors within models.

Rat data were analysed using linear mixed effects models after log(1+x) transformation to correct for non-normal distribution. There was little variance in rat abundance between sites within blocks in some surveys so block was included as the random effect, to account for the repeated measurements taken within WN or WS. Models were initially fitted by maximum likelihood estimation to allow them to be compared by AIC and overall significance of factors to be determined using ANOVA. Most parsimonious models were then fitted by restricted maximum likelihood estimation (REML) which produces unbiased estimates of variance and covariance parameters (Patterson & Thompson 1971).

Generalised linear mixed effects models (GLMM) with Poisson distribution were used for the mouse activity and MNKA data sets. Site was the random effect. The most parsimonious models were selected by backwards removal of non-significant factors. I used Spearman's Rank correlation to determine whether activity was related to MNKA. To determine whether there was any difference in capture of individual mice in traps and detection in tunnels I divided MNKA and number of tunnels tracked per site counts by the area covered by traps (82.5x99 m) or tunnels (150x150 m) and the number of nights the devices were available for (traps = 5 nights, tunnels = 1 night) and compared these values using a t-test.

5.3.4.2 Testing the assumption of equal capture probability

MNKA assumes equal capture probability for animals across all surveys. To test this assumption for house mice captured in different seasons and treatment periods, which were the main variables of interest relating to population size in my study, I pooled data and modelled variation in capture (p) and recapture (c) probability using the Huggins closed population models (Huggins 1989) in program MARK (White & Burnham 1999). I excluded capture histories of mice that died within traps part way through a survey. I constructed three models of capture histories based on constant capture probability (M_0, p(.) = c(.)), time varying capture probability (M_t, p(t) ≡ c(t)) and a behavioural response (M_b, p(.), c(.)) and selected the naïve model that best fit the data according to AIC_c. Based on the naïve model, I created further models that included rat abundance as a covariate and season as a grouping factor and ranked them according to AIC_c. As sample sizes for mice recorded within non-treatment periods were small and levels of rat activity were sometimes variable it was more appropriate to treat rat abundance as a covariate than use treatment as a grouping factor.

5.3.4.3 Investigating population characteristics

I performed separate GLMMs in R (R Development Core Team. 2011) to determine whether number of mice varied by sex, age (adult or juvenile) or signs of breeding (signs of pregnancy or lactating in females) in association with treatment, season or block (WN or WS). Site was the random effect and I

included all interactions in the saturated models prior to backwards removal of non-significant terms. To investigate any interaction between season and treatment it was necessary to exclude winter data from the analysis because no treatment took place at that time. However, where I observed no significant interaction between these factors I remodelled using the entire dataset.

I used linear models to investigate whether the weights of mice varied according to treatment, season, block or sex. Although I determined age class (adult or juvenile) based on weight, I also experimented with including this variable as a factor within models to assess whether any significant differences observed for other factors were in fact due to bias from disparity in the number of juvenile mice present.

I was unable to calculate survival rates of mice and determine whether these differed according to the rat control treatment because there were too few recaptures of mice in more than one survey.

5.4 Results

5.4.1 Abundance and activity data

5.4.1.1 Ship rat abundance

Time was not a significant factor in the linear mixed effects model of rat abundance (as inferred from tracking activity) so only the results of the model including season are provided. As anticipated, lower rat abundance was observed on sites receiving the rat control treatment compared to the same sites when they did not ($F_{[1, 49]}$ = 36.345, P < 0.001) (Figure 5. 4). There was a significant interaction between treatment and block indicating that the treatment was more effective in reducing rat abundance at sites in WN than WS ($F_{[1,49]}$ = 7.859, P = 0.007). There was also seasonal variation in rat abundance ($F_{[3, 49]}$ = 4.013, P = 0.012): in autumn rats were significantly more abundant than in summer, but not different to spring. Although rat activity was significantly lowered by the control treatment, the minimal achievable levels observed in other pest control operations (Innes *et al.* 1995) were not attained, despite the

additional methods used (Table 5. 1). At times the rat activity index was saturated (all devices visited) and this was reflected in the model output where predicted values greater than 16 were produced (Figure 5. 4).

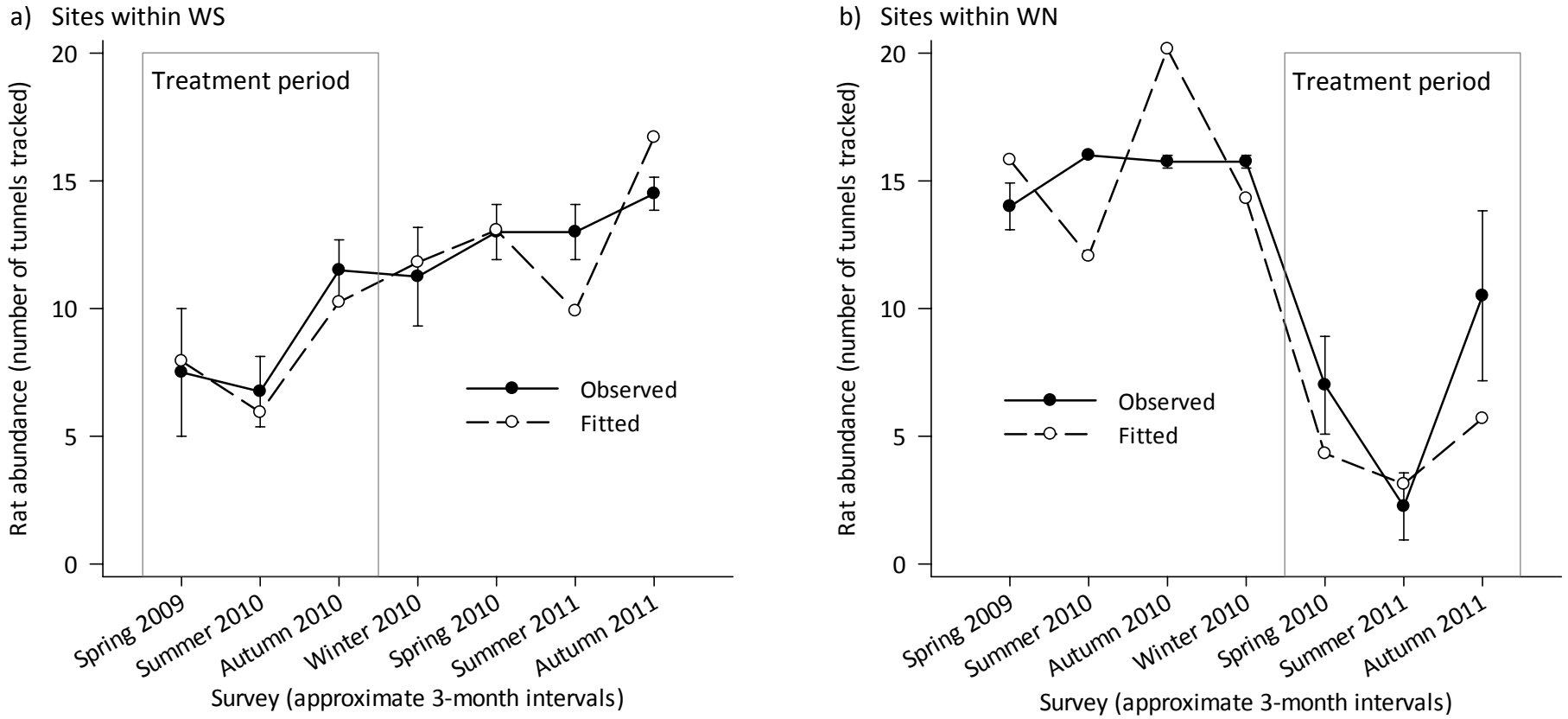


Figure 5. 4. Observed and fitted values for rat abundance at sites in Waipapa South (WS) (a) and Waipapa North (WN) (b). Abundance is inferred by the average number of tunnels tracked out of 16 per site (n = 4 sites in each of WN and WS). A rat control treatment was in place in WS during the first year of the study and in WN during the second. Fitted values were estimated by applying a linear mixed effects model following log(1+x) transformation of the data. Season + treatment*block (WS or WN) were the significant fixed effects. Block was also the random effect. Data were back-transformed for the purpose of graphing. Error bars are ± 1 standard error. Fitted values above 16 indicate that the index was saturated.

5.4.1.2 Food supplementation

When no rat control treatment was implemented, there was no sign that mice visited and ate food at any of the four sites where feeders were supplied. Response to feeders at sites when rat control was implemented was mixed. In year 1, there was no evidence that mice used feeders during late spring and summer, however, at the beginning of autumn (March) 2010 mice began using feeders on site 7 in WS. By April all 18 feeders at this site showed signs of frequent use (faeces present, pellets gnawed and removed). This site had the highest mouse abundance during the autumn (April) 2010 survey (MNKA = 16). Mice did not use feeders provided at site 6 in WS, even though mice were present, albeit in smaller numbers (MNKA = 6 in autumn).

In year 2 at the beginning of autumn (March) 2011, minimal use of feeders (two of 18) was observed at site 3 in WN. By April the same three feeders continued to be used, but no more were visited. This site had the largest mouse population out of the WN sites in the autumn (April) 2011 survey, but differences were minimal (MNKA = 4 compared to 1, 2 and 3 at other sites). Mice were present, but did not use feeders provided at site 1 in WN. The limited and varied response to supplemented food indicated that it did not increase mouse abundance in my study. Instead use of feeders appeared to be an effect of greater mouse abundance rather than a cause. For this reason, I pooled data from all sites for further analysis.

5.4.1.3 House mouse activity

The rat control treatment significantly influenced mouse activity over time, but there were differences associated with blocks. At WN sites rat control was associated with a significant increase in activity over time (Z = 2.764, P = 0.0057) compared to a decrease when no treatment was taking place (Figure 5. 5, Figure 5. 6). For WS sites, there was greater overall mouse activity in treated compared to untreated periods in WS (Z = 2.770, P = 0.006) (Figure 5. 5, Figure 5. 6), but the effect over time was not as great as for WN sites (Z -2.564 = 0.010) (Figure 5. 5). Season significantly influenced mouse tracking rates, with highest activity in

autumn and significantly lower activity in summer (Z = -4.094, P < 0.001) (Figure 5. 7). Low summer activity explains areas of poor fit for the model that included time (Figure 5. 6). The season analysis also highlighted that the overall effect of treatment was significantly more mouse activity (Z = 4.618, P < 0.001) (Figure 5. 8).

```
Generalized linear mixed model fit by the Laplace approximation
Formula: Mouse.activity ~ Months * Treatment * Block + (1 | Site)
   Data: PDatanoW
   AIC   BIC logLik deviance
 110.6 127.5 -46.31    92.61
Random effects:
 Groups Name        Variance Std.Dev.
 Grid2  (Intercept) 0.15953  0.39941
Number of obs: 48, groups: Site, 8

Fixed effects:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                       0.2649     0.4589   0.577   0.5638
Months                           -0.2561     0.1731  -1.479   0.1391
Treatment[Yes]                  -10.7732     4.6063  -2.339   0.0193 *
Block[WS]                        -6.5147     4.6101  -1.413   0.1576
Months:Treatment[Yes]             0.9059     0.3277   2.764   0.0057 **
Months:Block[WS]                  0.5897     0.3371   1.750   0.0802 .
Treatment[Yes]:Block[WS]         18.0144     6.5027   2.770   0.0056 **
Months:Treatment[Yes]:Block[WS]  -1.1363     0.4431  -2.564   0.0103 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Figure 5. 5. Output for a generalized linear mixed effects model (GLMM) of mouse activity data from footprint tracking tunnels. Time is represented by 'months', 'treatment' refers to whether a ship rat control operation was taking place (Yes or No) and 'block' refers to the grouping of sites within the management areas Waipapa North (WN) or Waipapa South (WS) which received treatment in opposite years.

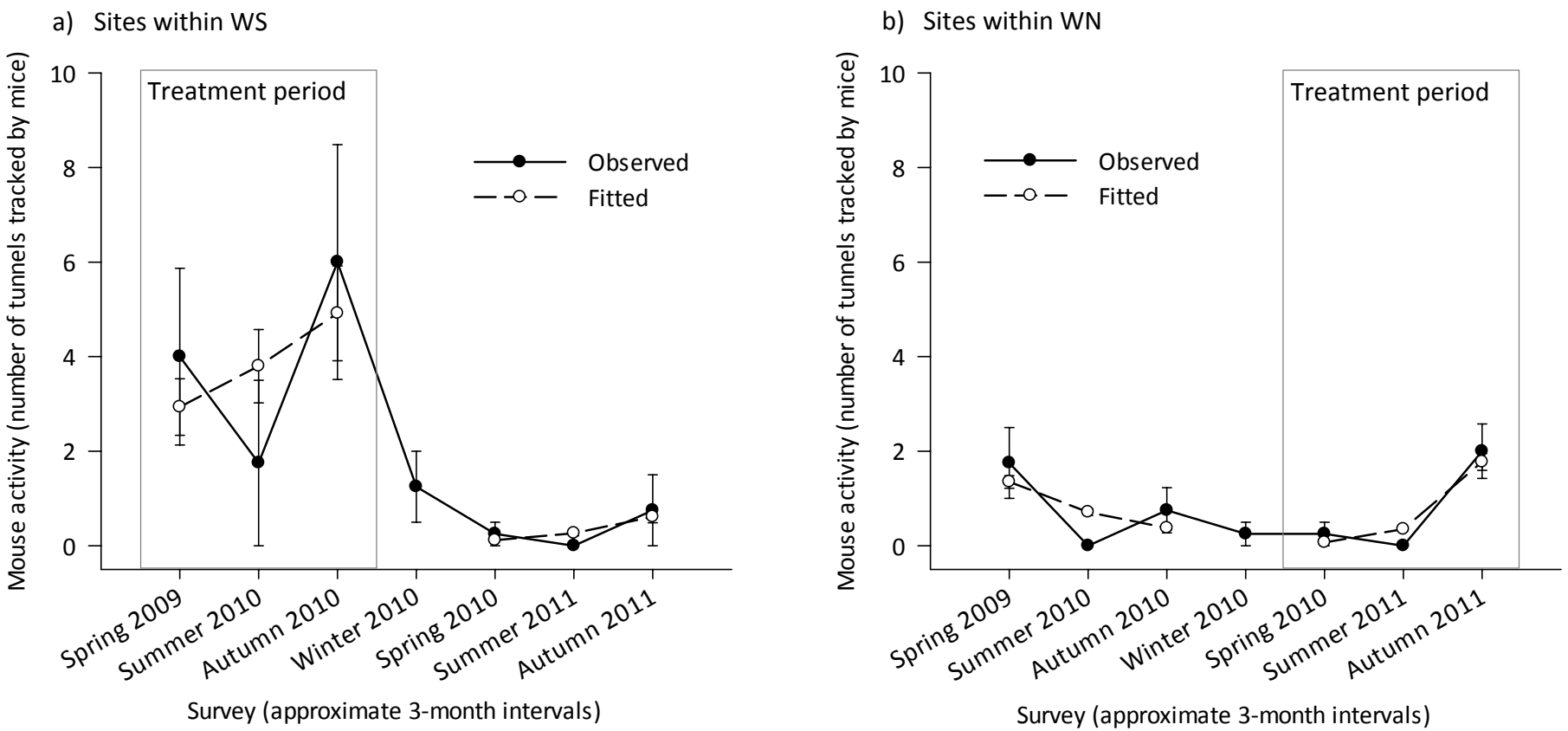


Figure 5. 6. Observed and fitted values for mouse activity on sites within Waipapa South (WS (a) and Waipapa North (WN) (b). Data are the number of tunnels tracked out of 16. A ship rat control treatment was in place in WS from spring 2009 to autumn 2010 and in WN from spring 2010 to autumn 2011. Fitted values were estimated by applying a generalized linear mixed effects model. Time (months), treatment and block were the significant fixed effects along with interactions. Site was the random effect. Winter data is presented, but was not included in the model due to imbalance in the design. Error bars are ± 1 standard error.

```
Generalized linear mixed model fit by the Laplace approximation
Formula: Mouse.activity ~ Season + Treatment + (1 | Site)
   Data: PData
 AIC   BIC logLik deviance
 123 135.2  -55.5      111
Random effects:
 Groups Name        Variance Std.Dev.
 Grid2  (Intercept) 0.45806  0.6768
Number of obs: 56, groups: Site, 8

Fixed effects:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)       -0.2837     0.3816  -0.743    0.457
Season[Spring]    -0.4187     0.2587  -1.619    0.106
Season[Summer]    -1.6917     0.4132  -4.094    4.23e-05 ***
Season[Winter]    -0.2364     0.5024  -0.471    0.638
Treatment[Yes]     1.3863     0.3002   4.618    3.87e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Figure 5. 7. Output for a generalized linear mixed effects model (GLMM) of mouse activity data from footprint tracking tunnels. Autumn is the reference category for the fixed effect 'Season'. 'Treatment' refers to whether a ship rat control operation was taking place (Yes or No). The interaction term was not significant.

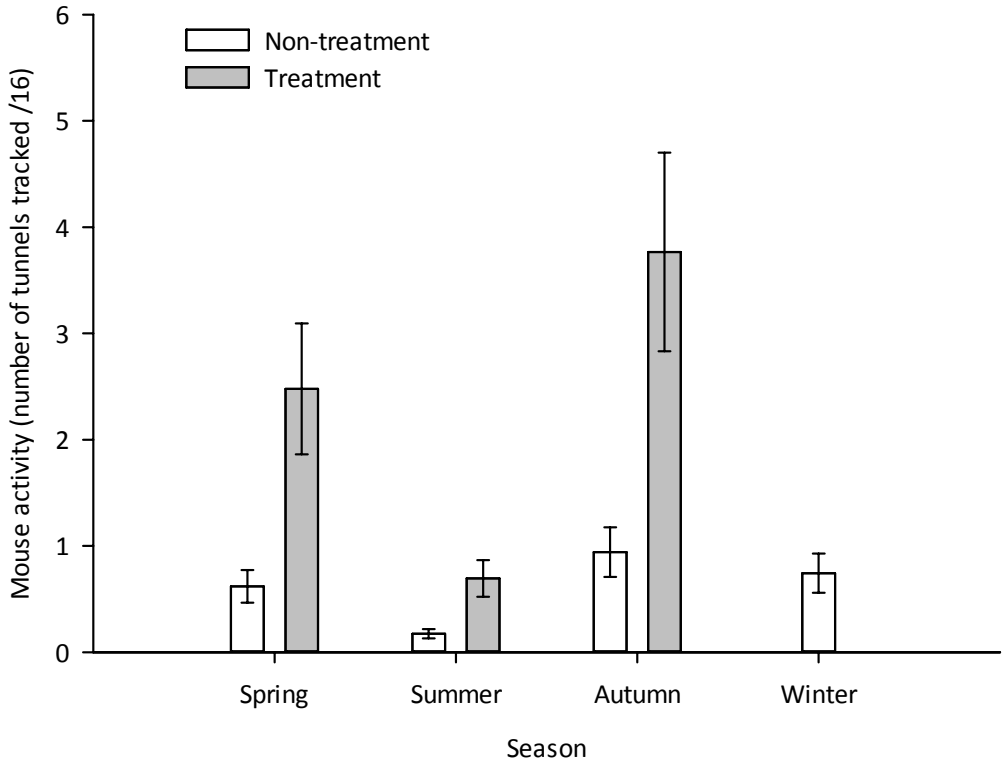


Figure 5. 8. Mouse activity by treatment (ship rat control) and season. Data are estimates of activity per site (Waipapa South and Waipapa North combined, n = 8) extracted from a generalized linear mixed effects model in which site was the random effect and treatment and season with no interaction were the significant fixed effects. All sites were surveyed in spring, summer and autumn during a year with treatment and a year without treatment. There was just one winter survey in which no treatment took place. Error bars are ± 1 standard error.

5.4.1.4 House mouse abundance

Trends for mouse abundance were very similar to mouse activity (Figure 5. 9). In WN mouse abundance increased over time during rat control periods compared to a decrease for non-treatment (Z = 2.415, P = 0.016) (Figure 5. 10). Mouse abundance increased significantly more over time on WS compared to WN sites (Z = 3.440, P < 0.001) during both treated and untreated years, though in the latter mice were captured only on two of four sites in autumn (sites 7 and 8). However, treatment was associated with overall greater mouse abundance on WS sites (Z = 3.911, P < 0.001). Seasonal effects were evident from the GLMM of season and treatment (Figure 5. 11). Mouse abundance was significantly lower in

spring (*Z* = -3.575, P < 0.001) compared to autumn, but lowest in summer (*Z* = -4.670, P < 0.001). The analysis with season confirmed that the overall effect of treatment was significantly higher mouse abundance (Z = 4.959, P < 0.001) (Figure 5. 11, Figure 5. 12).

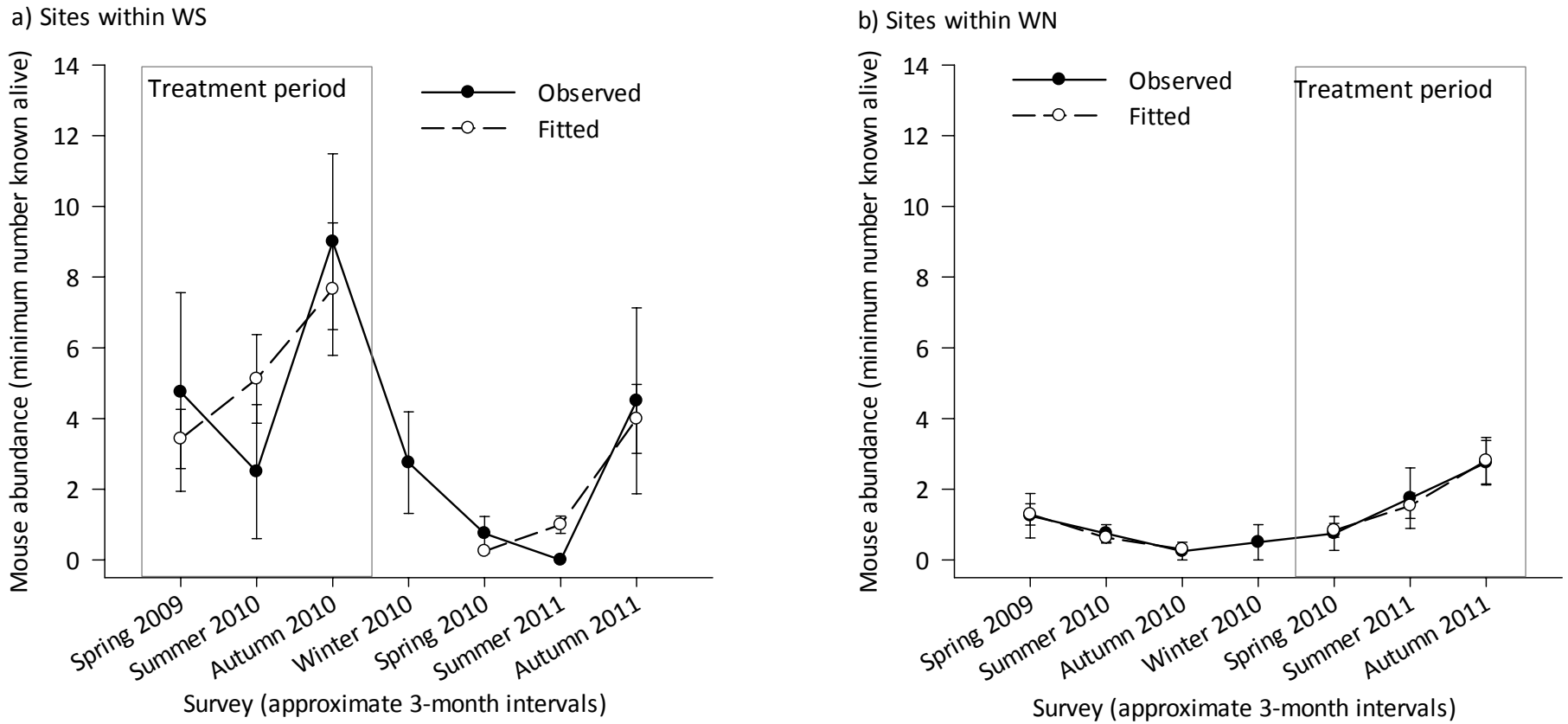


Figure 5. 9. Observed and fitted values for mouse abundance on sites within Waipapa South (WS (a) and Waipapa North (WN) (b). Data are the minimum number known alive (MNKA). A ship rat control treatment was in place in WS from spring 2009 to autumn 2010 and in WN from spring 2010 to autumn 2011. Fitted values were estimated by applying a generalized linear mixed effects model. Time (months), treatment and block were the significant fixed effects along with interactions. Site was the random effect. Winter data is presented, but was not included in the model due to imbalance in the design. Error bars are ± 1 standard error.

```
Generalized linear mixed model fit by the Laplace approximation
Formula: MNKA ~ Months * Treatment * Block + (1 | Site)
   Data: PDatanoW
   AIC   BIC logLik deviance
 126.7 143.6 -54.36    108.7
Random effects:
 Groups Name        Variance Std.Dev.
 Grid2  (Intercept) 0.31123  0.55788
Number of obs: 48, groups: Site, 8

Fixed effects:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                       0.1212     0.5120   0.237 0.812904
Months                           -0.2893     0.1861  -1.555 0.120052
Treatment[Yes]                   -3.3408     1.8787  -1.778 0.075354 .
Block[WS]                        -8.2930     2.6760  -3.099 0.001942 **
Months:Treatment[Yes]             0.5316     0.2202   2.415 0.015743 *
Months:Block[WS]                  0.8439     0.2453   3.440 0.000581 ***
Treatment[Yes]:Block[WS]         12.6146     3.2254   3.911  9.2e-05 ***
Months:Treatment[Yes]:Block[WS]  -0.9250     0.2793  -3.312 0.000926 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Figure 5. 10. Output for a generalized linear mixed effects model (GLMM) of mouse abundance data (minimum number known alive, MNKA) from live-trapping. Time is represented by 'months', 'treatment' refers to whether a ship rat control operation was taking place (Yes or No) and 'block' refers to the grouping of sites within the management areas Waipapa North (WN) or Waipapa South (WS), which received treatment in opposite years.

```
Generalized linear mixed model fit by the Laplace approximation
Formula: MNKA ~ Season + Treatment + (1 | Site)
   Data: PData
   AIC   BIC logLik deviance
 138.9 151.1 -63.47    126.9
Random effects:
 Groups Name        Variance Std.Dev.
 Grid2  (Intercept) 0.69774  0.8353
Number of obs: 56, groups: Site, 8

Fixed effects:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)        0.4530     0.3633   1.247  0.21246
Season[Spring]    -0.7884     0.2205  -3.575  0.00035 ***
Season[Summer]    -1.1939     0.2557  -4.670 3.01e-06 ***
Season[Winter]    -0.2723     0.3423  -0.796  0.42630
Treatment[Yes]     1.0531     0.2124   4.959 7.10e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Figure 5. 11. Output for a generalized linear mixed effects model (GLMM) of mouse abundance data from live-trapping. Autumn is the reference category for the fixed effect 'Season'. 'Treatment' refers to whether a ship rat control operation was taking place (Yes or No). The interaction term was not significant.

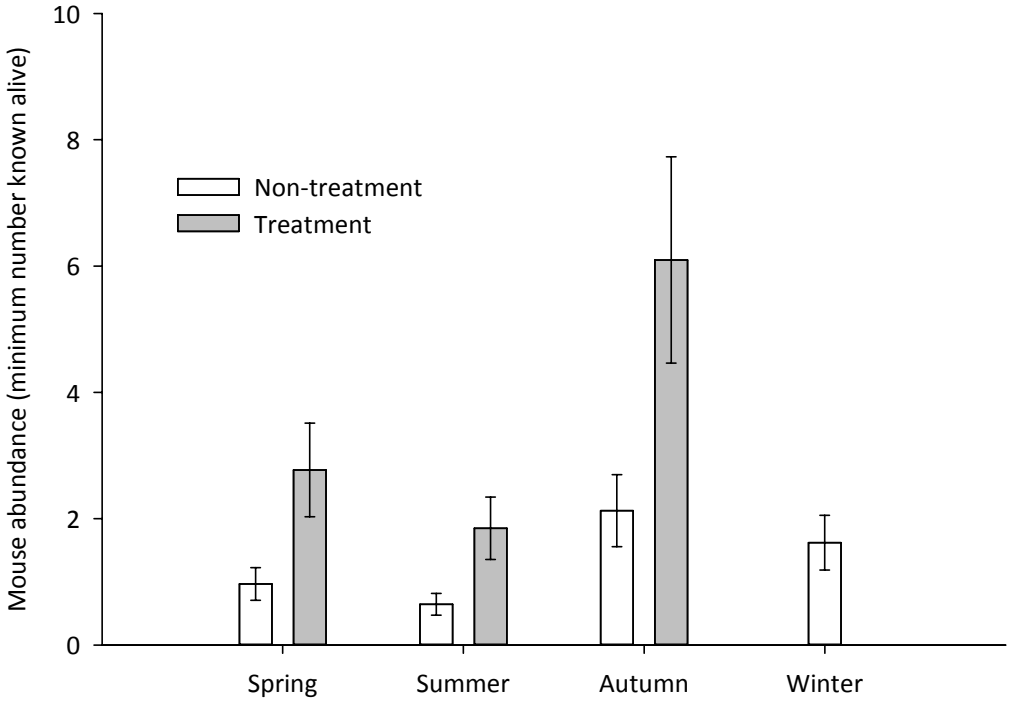


Figure 5. 12. Mouse abundance by treatment (ship rat control) and season. Data are estimates of abundance per site (Waipapa South and Waipapa North combined, n = 8) extracted from a generalized linear mixed effects model in which site was the random effect and treatment and season with no interaction were the significant fixed effects. All sites were surveyed in spring, summer and autumn during a year with treatment and a year without treatment. There was just one winter survey in which no treatment took place. Error bars are ± 1 standard error.

5.4.2 Relationship between abundance and activity for house mice

There were strong similarities in trends for mouse abundance measured via trapping and activity measured in tracking tunnels (Figure 5. 6, Figure 5. 9). The two measures were moderately correlated when compared directly (Spearman's rho = 0.54, $P < 0.001$) (Figure 5. 13). The results of the t-tests found that there was no significant difference in the number of mice captured in traps and the number of tunnels that detected mice when area and effort were standardised ($t = -0.035$, d.f = 55, $P = 0.973$). This result held when data collected during treatment and non-treatment periods were analysed separately (rat control: $t = -0.8774$, d.f = 23, $P = 0.389$, non-treatment: $t = 0.397$, d.f = 23, $P = 0.695$, winter data excluded).

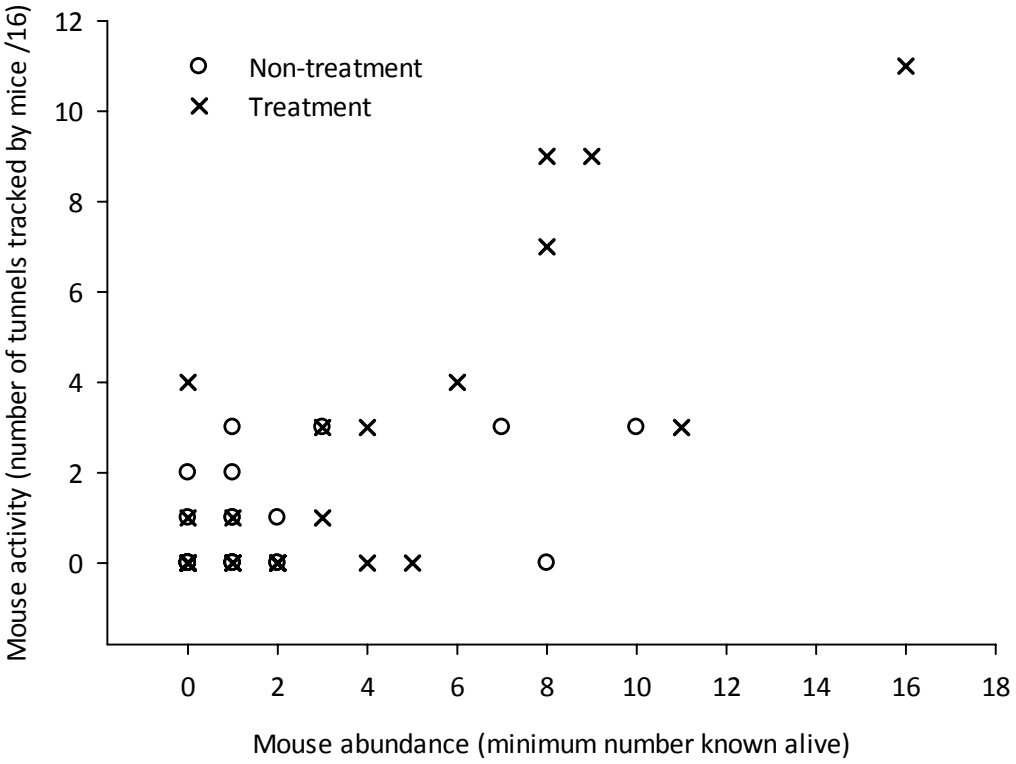


Figure 5. 13. Mouse abundance plotted against mouse activity. Data were collected by live-trapping on grids of 42 stations spaced 16.5 m (6x7 array) over five nights and by detecting mouse footprints in baited tunnels in a grid of 16 stations spaced 50 m apart (4x4 array) on one night. A ship rat control treatment was implemented during some survey periods. Trapping grids were nested within tunnel grids. There was moderate correlation between the two measures (Spearman's rho = 0.54, P < 0.001).

5.4.3 Capture probability

Constant probability of capture (M_0) was the most strongly supported naïve model in the analysis using program MARK (Table 5. 3, Model 5). The model with season included as a grouping factor performed better than the naïve model (Table 5. 3, Model 2), but including season and rat abundance with an interaction term produced the model with greatest AIC weight (Table 5. 3, Model 1).

Capture probability (p) therefore varied by season (Figure 5. 14), which meant that MNKA underestimated abundance more in some seasons than others (Table 5. 4). However, rat abundance also influenced p differently within seasons (Figure 5. 15). In spring there was a positive relationship between rat abundance

and p, but in autumn the relationship was negative. In summer there was no strong relationship and in winter there was a negative trend but high variability. Winter results should be treated with caution as data were only available for one year, sample size was small and whilst rat abundance varied, no rat control was in place.

Table 5. 3. Ranked models of probability of first capture (p) and probability of recapture (c) for house mice in Waipapa EA. Modelling was performed using the Huggins closed population models in program MARK. Constant p (No. 5), time (t) dependent p (No. 8) and a behavioural response (No. 6) were investigated as naïve models, after which season was included as a grouping factor and rat activity ('rat') as a covariate

No.	Model	AIC_c	Delta AIC_c	AIC_c weight	No. of parameters	Deviance
1	p(season*rat)=c(season*rat)	793.536	0.000	0.718	8	777.298
2	p(season)=c(season)	796.286	2.750	0.181	4	788.221
3	p(rat effect for each season)=c(rat effect for each season)	797.438	3.902	0.039	5	787.339
4	p(season+rat)=c(season+rat)	798.291	4.755	0.067	5	788.193
5	p(.)=c(.)	801.123	7.587	0.016	1	799.116
6	p(.), c(.)	801.977	8.441	0.011	2	797.957
7	p(rat)=c(rat)	803.136	9.600	0.006	2	799.116
8	p(t) ≡ c(t)	805.318	11.788	0.002	5	795.219

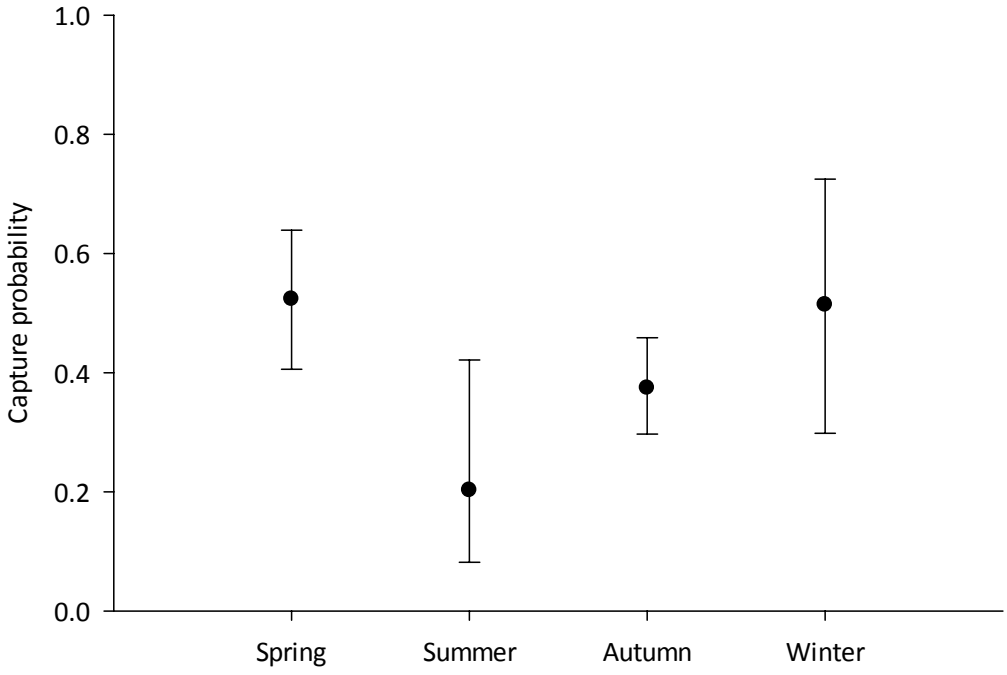


Figure 5. 14.Capture probabilities of house mice live-trapped in Waipapa EA, Pureora Forest Park. Estimates were generated by modeling mouse capture histories with constant p (M_0) using Huggins closed population models. Seasonal effects are presented from the preferred model selected based on AIC_c (Table 5. 3, Model 1). Data are from two years for spring summer and autumn, but just one year for winter. Sample sizes are: spring 29, summer 18, autumn 65, winter 11. Error bars are 95% confidence intervals.

Table 5. 4. Abundance of house mice as measured by the minimum number known alive (MNKA) and Huggins closed population models (N). Standard error (SE) and confidence intervals (CI) are provided for N and the effect of rat abundance on probability of capture is described

Season	MNKA	N	SE	Lower 95% CI	Upper 95% CI	Effect of rat abundance on probability of capture
Spring	28	31.4	1.9	29.6	38.6	positive
Summer	18	25.2	4.9	20.2	42.2	no effect detected
Autumn	65	78.2	5.5	71.0	93.9	negative
Winter	11	11.6	0.9	11.1	16.3	weak negative

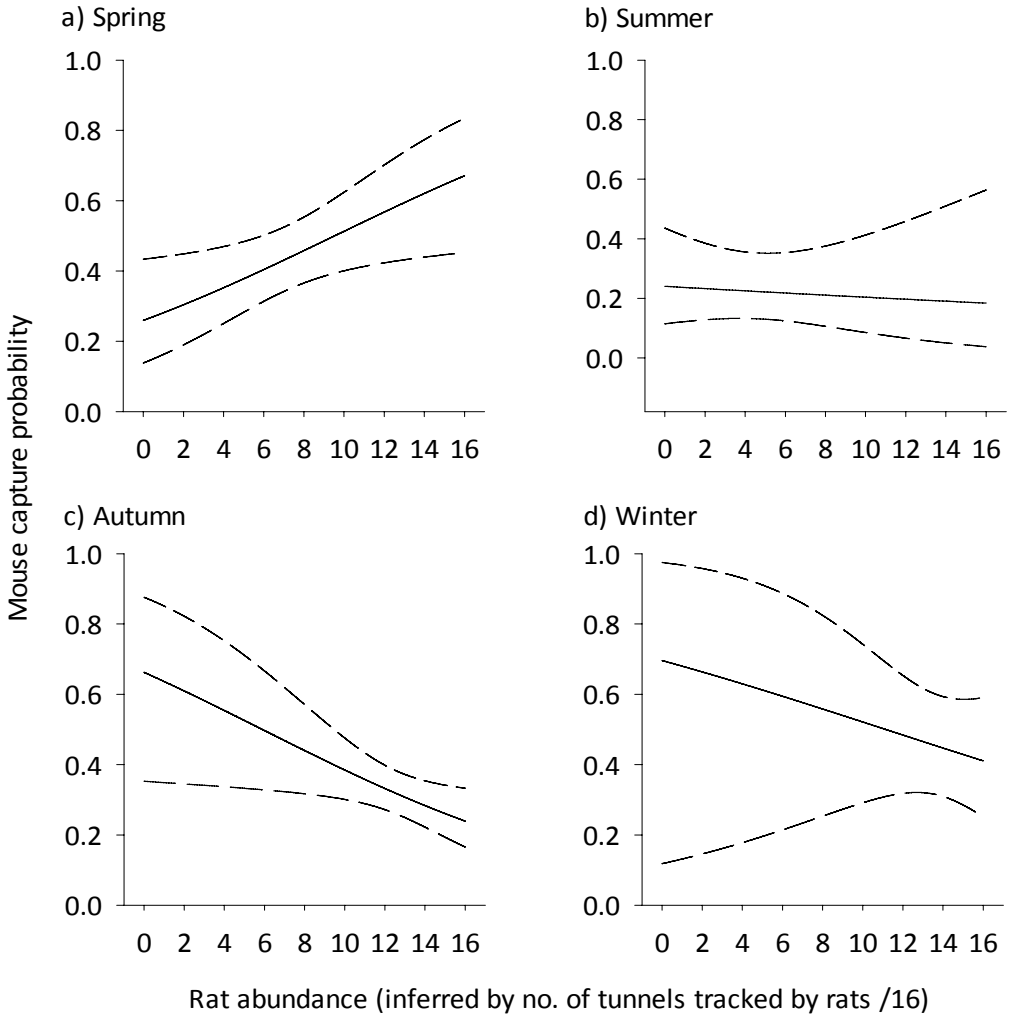


Figure 5. 15. Seasonal difference in the relationship between ship rat abundance and capture probability (p) of house mice in live traps. Estimates were generated by modeling mouse capture histories with constant p (M_0) using Huggins closed population models. Ship rat activity was included as a covariate and season as a grouping factor (Table 5. 3, model 1). Solid lines are estimates and broken lines are upper and lower 95% confidence intervals.

5.4.4 Investigating population characteristics

Mouse populations were very sparse on most sites throughout the study period. A total of 116 different individual mice were trapped. Although mice were frequently recaptured within surveys, just nine mice were recaptured in different surveys so data were too sparse to compare survival between treatment and non-treatment periods. Five of the nine mice were captured in consecutive surveys, whilst the other four were captured in one survey, then undetected in a

second and reappeared in a third. Mice were only ever recaptured at the same site.

The fates of six marked mice were known. Five died in live traps during the study. Two had blood around their mouths indicating poisoning from toxin in bait stations. The causes of death of the other three were unknown. A sixth mouse was present in traps each day for the first four days on a WN site in spring 2009, when he was the only mouse detected. On the final day, he was not found alive in any traps, but one trap had been pulled apart (separating entrance tunnel and nest box) and there were blood and remains of a mouse inside along with both mouse and rat faeces, indicating a predation event by a ship rat. Another five mice were found dead in snap traps in summer (January) 2010 (see Table 5. 1). They were too decomposed to determine if they were marked individuals from spring (November) 2009.

Of the 116 different individual mice captured during the study, 51 were female and 65 male (percentages per season and treatment summarised in Table 5. 5). There was no significant difference in the number of male or female mice captured during surveys and no significant interaction of sex with treatment, season or block in the GLMM. Signs of breeding were apparent for some female mice during summer and autumn and to a lesser extent winter (Table 5. 5). There was no significant difference observed according to season or treatment, but data were very sparse.

There were significantly fewer juvenile than adult mice in spring (Z = -3.30667, P = 0.002) and summer (Z = -1.32566, P = 0.031) compared to autumn (Table 5. 5, Figure 5. 16, Figure 5. 17). In autumn juvenile recruitment or immigration along with adult immigration, contributed to peaks in mouse abundance levels. However, there was no interaction between age and treatment in the model, which indicates that there was no significant effect of rat control on juvenile abundance disproportionate to the highly significant positive effect of treatment on total mouse abundance.

Weight of mice varied significantly according to season ($F_{[4, 120]}$ = 6.685, P < 0.001). However, when age was included in the model, season was no longer significant, which indicates that seasonal differences in weights of mice were explained by the presence of a greater number of mice weighing ≤ 13.5 g, which I classed as juveniles, in autumn. Mice captured when the rat control treatment was implemented were significantly heavier than mice captured during non-treatment periods ($F_{[2, 122]}$ = 15.954, P < 0.001) (Table 5. 5). This was true for both adult and juvenile mice as there was no interaction between treatment and age.

Table 5. 5. Break down of mouse population characteristics across surveys and seasons. Numbers are minimum number known alive within sessions. Differences in totals are due to inability to determine breeding state or weight for animals that were not captured, but assumed to be present (captured in surveys prior and post). (See Appendix 5 and Appendix 6 for additional summaries of mouse population characteristics)

Season/treatment	% Female		% Females breeding		Percent Juvenile		Average weight adults		Average weight juveniles	
	n	%	n	%	n	%	n	Weight (g) (±SD)	n	Weight (g) (±SD)
Spring/ treatment	22	45.5	10	0	22	4.5	20	17.4 (± 2.1)	1	13.0
Spring/non-treatment	8	25	1	0	8	0	8	16.8 (± 1.6)	0	NA
Spring/combined	30	40	11	0	30	3.3	28	17.3 (± 2.0)	1	13.0
Summer/treatment	17	52.9	8	37.5	17	23.5	12	17.8 (± 3.2)	4	9.9 (± 2.9)
Summer/non-treatment	3	33.3	1	100	3	0	3	16.0 (± 2.3)	0	NA
Summer/combined	20	50	9	40	20	20	15	17.4 (± 3.1)	4	9.9 (± 2.9)
Autumn/treatment	47	38.3	18	55.5	47	44.7	26	17.3 (± 2.0)	21	11.7 (± 1.4)
Autumn/non-treatment	19	47.4	9	50	19	57.8	8	15.4 (± 1.3)	11	9.7 (± 1.5)
Autumn/ combined	66	40.9	27	51.9	66	48.5	34	16.8 (± 2.0)	32	11.0 (± 1.7)
Treatment combined	**86**	**43**	**37**	**32.4**	**86**	**30.2**	**58**	**17.4 (± 2.3)**	**26**	**11.5 (± 1.8)**
Non-treatment combined	**30**	**40**	**11**	**54**	**30**	**36.6**	**19**	**16.2 (± 1.7)**	**14**	**10.1 (± 1.8)**
Winter (all non-treatment)	13	46.2	5	20	13	23.1	8	15.9 (± 1.7)	3	11.7 (± 2.4)
Total captures (mice known to be present, but not captured (n = 4) also included if appropriate)	**129**	**42.6**	**53**	**35.8**	**129**	**31.3**	**85**	**17.0 (± 2.2)**	**40**	**11.0 (± 1.9)**
Total individuals	**116**	**44**								

```
Generalized linear mixed model fit by the Laplace approximation
Formula: MNKA ~ Treatment + Season * Age + (1 | Site)
   Data: PDataAJ
   AIC   BIC logLik deviance
 173.6 200.7 -76.78    153.6
Random effects:
 Groups Name        Variance Std.Dev.
 Grid2  (Intercept) 0.69775  0.83531
Number of obs: 112, groups: Site, 8

Fixed effects:
                         Estimate Std. Error z value Pr(>|z|)
(Intercept)              -0.21033    0.38247  -0.550  0.58236
Treatment[Yes]            1.05315    0.21238   4.959  7.09e-07 ***
Season[Spring]           -0.15906    0.25318  -0.628  0.52983
Season[Summer]           -0.75377    0.30365  -2.482  0.01305 *
Season[Winter]            0.12862    0.39321   0.327  0.74359
Age[J]                   -0.06062    0.24669  -0.246  0.80588
Season[Spring]:Age[J]    -3.30667    1.04815  -3.155  0.00161 **
Season[Summer]:Age[J]    -1.32566    0.61184  -2.167  0.03026 *
Season[Winter]:Age[J]    -1.14343    0.70398  -1.624  0.10433
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Figure 5. 16. Output for a generalized linear mixed effects model (GLMM) of mouse abundance by age (Adult – A or juvenile – J). Autumn is the reference category for the fixed effect 'Season'. 'Treatment' refers to whether a ship rat control operation was taking place (Yes or No). Non-significant terms were removed from the model.

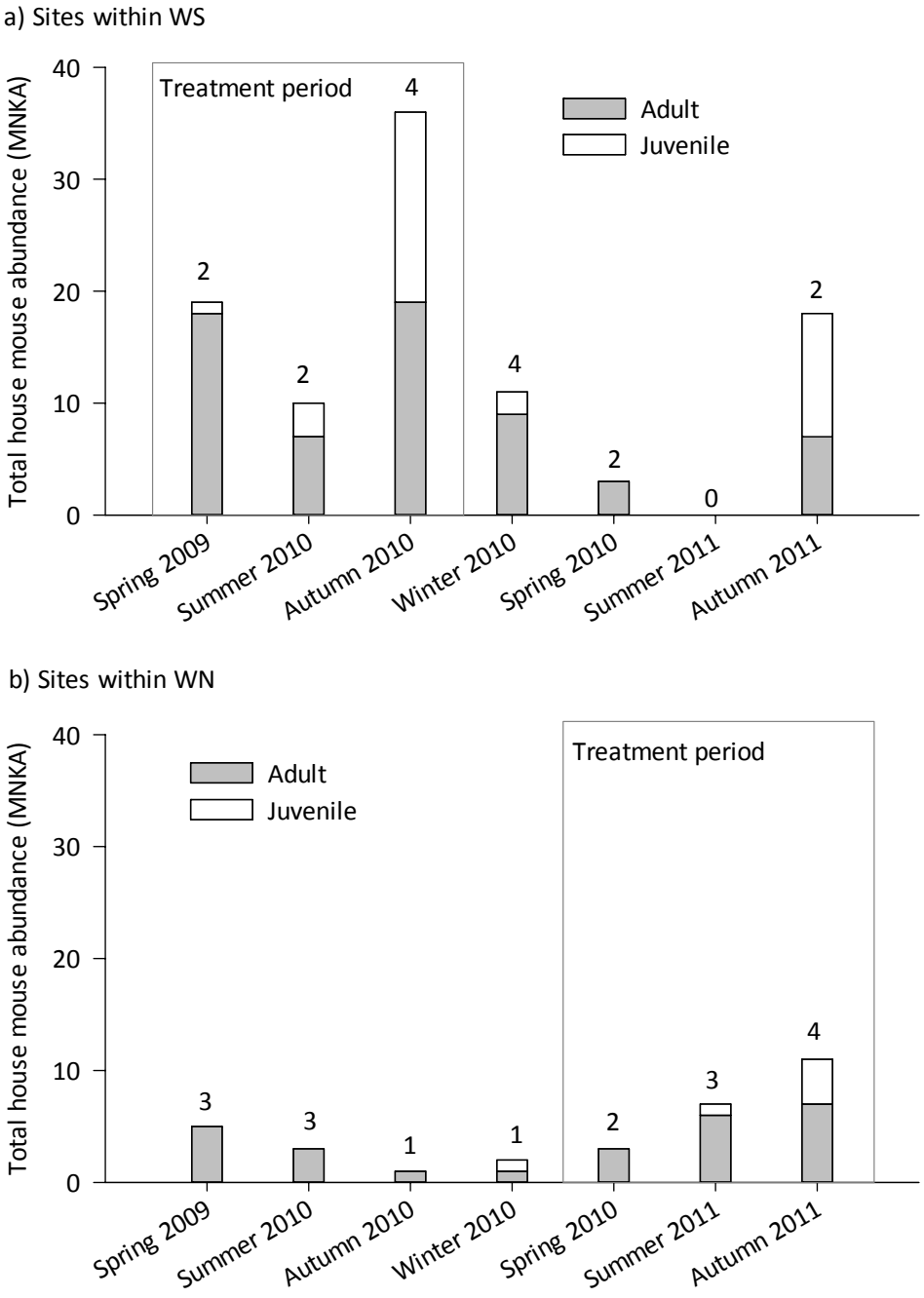


Figure 5. 17. Total adult and juvenile house mouse abundance (minimum number known alive, MNKA) from sites within Waipapa South (WS) (a) and Waipapa North (WN) (b) blocks. A ship rat control treatment was applied for a spring to autumn period in each block. The number of grids that mice were captured on (out of four) is stated above each bar.

5.4.5 Other small mammal pest species detected in the study area

A ferret, two stoats and a hedgehog were captured in DOC 250 traps (baited with peanut butter and carrot) during the study. There were also single instances of ferret, stoat and possum prints observed in tunnels. A juvenile Norway rat (*Rattus norvegicus*) was captured on two nights in a live trap at site 3 (WN) in spring 2009. The trap location was not near to a water course and was just over 1 km from the site where most Norway rats were captured during a previous study at Pureora (King *et al.* 1996c; Innes *et al.* 2001). All other rats captured in kill-traps or occasionally in Longworth traps were ship rats.

5.5 Discussion

5.5.1 Ship rat control

Waipapa Ecological Area (Waipapa EA) was selected as a study area because it offered advantages over other sites including a background of previous small mammal research (King *et al.* 1996a; 1996b; 1996c; Innes *et al.* 2001); ship rat control treatment and non-treatment areas with a conveniently scheduled reversal; operational use of toxins with low efficacy for mice; and very low possum abundance. Although rat control significantly lowered rat abundance (as inferred by tracking indices) on my monitoring sites in Waipapa North (WN) and Waipapa South (WS), it was unfortunate that in neither year was the low level (<10 % of tunnels tracked) reached which has previously been associated with significant changes in mouse detection rates in New Zealand (Innes *et al.* 1995). The Department of Conservation (DOC) monitored rat abundance in Waipapa EA independent of my study and also found that minimal achievable levels were not reached (H. Matthews pers. comm.) so this was widespread across the area, not just at the sites I selected.

Failure to reach target levels may have been correlated with abnormally high rat abundance following the removal of possums in 2008. Sweetapple and Nugent (2007) reported an increase in numbers of rats after successful possum control. The grid spacing of bait stations used by DOC may also have contributed as not

all rats may have access to stations spaced 150 x 50 m (which is variable in places) and 100 x 100 m is recommended (Innes *et al.* 1995). However, this system, originally designed for possum control, has been successful for suppressing rats in the past. Low bait take was noted as a potential factor (H. Matthews pers. comm.), for reasons unknown but possibly including high availability of alternative food in the environment, low palatability of bait and aversion to the bait station design (Clapperton 2006; Spurr *et al.* 2007). Attempts to bolster the main control operation with kill-trapping and additional toxin helped to reduce rats on WN sites to lower levels in summer 2011. However, this effect was not maintained, and rat populations were higher again by autumn despite constant supply of toxin in bait stations. Low bait take in autumn has been reported previously for ship rats (Gillies *et al.* 2003a).

5.5.2 House mouse abundance and activity

Mouse abundance (minimum number known alive, MNKA) measured by live-trapping and activity measured by footprint tracking were low throughout most of the study period, particularly for sites in WN. Similar findings have been recorded previously for mice in podocarp-hardwood forest in New Zealand (Innes *et al.* 1995; King *et al.* 1996b; 1996c). Despite the limitations of the rat control treatment, it was associated with higher abundance and activity of mice. Although there were small sample sizes and variability between sites, this correlation was robustly demonstrated by the reversal of treatments in the second year of the study.

The independent measures of abundance and activity showed very similar trends. They were also significantly correlated and when area and effort were controlled, the number of house mice captured was not dissimilar to the number of tunnels tracked by mice. This indicates that abundance of house mice was positively associated with ship rat control, and greater activity levels measured were the result of more mice being present, as opposed to a similar number of mice that were more active and therefore interacting with a greater number of tunnels or more willing to enter them. Other studies have demonstrated

increased abundance (Ruscoe *et al.* 2011) or activity (Innes *et al.* 1995) of house mice following ship rat control in New Zealand, however, to my knowledge, this is the first attempt to understand the relative influence of the two factors.

The MNKA is commonly used as an index of abundance where sample sizes are small. It inevitably underestimates the number of animals present because probability of capture is rarely equal to one (100 % probability of capturing all individuals present). However, MNKA has been shown to correlate well with abundance estimated using closed capture models which incorporate probability of capture to calculate N (Ruscoe *et al.* 2001) and MNKA may even be more robust under some conditions (McKelvey & Pearson 2001). An assumption of MNKA is that probability of capture is constant across surveys. This assumption proved incorrect in my study as there was variation in mouse capture probability which was associated with the main variables of interest: season and ship rat abundance.

The probability of an animal being captured in a trap is determined by many factors, one of which is the abundance of alternative food available in the environment. Food availability can affect the searching behaviour of animals and their willingness to interact with traps (King & White 2004). The seasonal fluctuations in mouse capture probability that I observed appear to be consistent with differences in the quantity of food expected to be available for them. Mice were most likely to be captured in spring and winter when food is sparse which may force them to search more actively and enter traps more willingly. The opposite is true for summer, the season when mice were least likely to be captured. Poor capture probability contributed to the low MNKA observed for mice in summer compared to other seasons. Fitzgerald *et al*. (2004) also suggested that mouse abundance measured using trapping indices may suffer from variable capture probability across seasons.

Probability of capturing an animal also has potential to be influenced by other species present in the environment (Harper & Cabrera 2010). I observed a negative correlation between house mouse capture probability and ship rat

abundance in autumn. This is consistent with avoidance of abundant predatory ship rats by house mice, which limits the likelihood of mice being captured and recaptured in traps, perhaps due to suppressed movement behaviour. However, the positive correlation of house mouse capture probability and ship rat abundance observed in spring is unexpected and difficult to explain. The differing seasonal relationships of rat abundance and mouse capture probability mean that the effect of the rat control treatment on mouse abundance was underestimated in spring, but overestimated in autumn. Due to the magnitude and direction of these differences the overall conclusion that removal of ship rats is associated with increased mouse abundance is not altered. However, variation in capture probability points toward more subtle and complex influences of ship rat abundance on the behaviour of house mice which may contribute to the population level effects observed.

5.5.3 Population characteristics

There was rapid turnover of house mice on all sites during the study regardless of rat abundance. Improved survival of individuals is unlikely therefore to have been a factor contributing to the higher abundance of house mice observed when rat control was implemented. I found no evidence of better recruitment (inferred from a higher proportion of small juvenile mice) as a consequence of ship rat control as expected from the data of King *et al*. (1996b). However, it remains a possibility because my sample sizes were small and immigration of juvenile mice at sites 7 and 8 in autumn 2011 may have masked some effects on recruitment. Population fluctuations appeared to be mainly driven by higher immigration rates or better establishment success of adult mice throughout the year, along with immigration or recruitment of juvenile mice in autumn. Immigration of house mice on to sites where ship rats were removed was also observed by Harris and MacDonald (2007) in the Galápagos Islands and they did not detect any significant difference in survival rates or juvenile recruitment either.

House mice captured during rat control treatment periods had significantly greater body weight compared to animals captured when rats were at normal high abundance. This indicates that the latter suffered from food shortage, which could be interpreted as a sign that they were negatively affected by exploitation competition from ship rats (Eccard & Ylönen 2002). However, there was no shortage of food for mice at sites that received supplementary food. At each of these sites, eighteen mouse-specific feeders provided a total of 3.6 kg of nutritionally balanced rodent food at any one time. It seems unlikely that some aspect of the feeder design prevented mice from using this resource, as feeders were used by mice both in captivity and at two sites when rat control was implemented. Instead, it seems more likely that the need to avoid abundant ship rats prevented mice from accessing resources including the feeders I supplied and caused them to have lower body weight.

Avoidance of abundant ship rats may have caused the poor immigration and establishment rates of house mice at sites during non-treatment years. Non-lethal risk effects associated with predators can have important consequences for prey populations (Lima 1998; Palomares & Caro 1999; Preisser *et al.* 2005; Creel & Christianson 2008; Ritchie & Johnson 2009). However, it is also possible that mice were directly killed by ship rats. The evidence of predation of a trapped house mouse by a ship rat supports other accounts that ship rats are predators of mice (Lidicker 1976, Chapter 3 of this thesis; Granjon & Cheylan 1988). However, most studies of ship rat diet have failed to find evidence of mouse consumption (e.g. Daniel 1973; Innes 1979; Miller & Miller 1995; Craddock 1997) indicating that this behaviour is rare. One exception was during a mouse plague in beech forest when house mouse DNA was detected in six of ten ship rat stomachs tested, and there was further unconfirmed sign of mouse consumption in other samples (McQueen & Lawrence 2008). Predation may be common when mice are very abundant, but it is unknown if or how predation levels vary with mouse density and whether ship rats could kill mice frequently enough to influence their abundance. Specialised predators of rodents, such as stoats have

limited influence on the abundance of their prey (King 1983; Jones *et al.* 2011; Ruscoe *et al.* 2011). However, these predators are sparse compared to ship rats.

5.5.4 Variation in mouse abundance across sites

The differences in mouse abundance (and also activity) trends over time between sites within WS compared to WN were mainly due to two sites (7 and 8) exhibiting relatively high mouse abundance in autumn of the non-treatment period despite no detections in summer. It is unclear why this occurred on these sites whilst no mice were captured on others (sites 5 and 6), as rat abundance was high at all WS sites. It is possible that because of some feature of their location, sites 7 and 8 experienced strong immigration pressure, despite rat presence, due to high density of mice in nearby refuge habitat. Sites 7 and 8 were not closer than other sites to scrub-grassland habitat, which offers refuge for mice (King *et al.* 1996c). However, distribution of house mice can be patchy in this habitat at Pureora for unknown reasons (Watkins *et al.* 2010a; C. Gillies pers. comm.).

It is also unclear why mouse abundance did not increase to higher levels in WN compared to WS when rat control was implemented, especially as additional measures taken to bolster rat control succeeded in bringing rats to lower abundance in WN compared to WS. Although manipulating rat abundance significantly influenced mouse populations, there were clearly also other influences on the demographics of the mouse populations I monitored that were not captured in this study.

5.5.5 Conclusions

My results support the hypothesis that house mice are more abundant when released from the negative effects of an IG predator, the ship rat, and that measures of activity in tracking tunnels at 50 m spacing reflect abundance, at least for relatively sparse house mouse populations. However, more subtle influences of rat abundance on the probability of capturing a mouse indicate that mouse behaviour is affected by ship rats, but the opposing relationships

between rat abundance and mouse capture probability in spring and autumn are difficult to explain. Fluctuations in mouse abundance were driven by immigration (implying more successful settlement when rats were few) and there was evidence that mice were food limited in the presence of abundant ship rats. However, it is unlikely that this was due to exploitation competition. Instead, avoidance of ship rats probably caused mice to suffer limited foraging opportunities. I observed further evidence of direct predation of house mice by ship rats, confirming captive observations, but it is unclear what role direct predation plays relative to risk effects on foraging behaviour in determining mouse abundance.

6 General discussion

Investigating how interspecific interactions influence the distribution and abundance of species has featured prominently in ecological research (Grant 1972; Schoener 1983; Polis *et al.* 1989; Eccard & Ylönen 2003; Ritchie & Johnson 2009; Salo *et al.* 2010). Far from being merely of theoretical interest, species interactions have great relevance for wildlife management and conservation, not least in the field of invasive species science (Zavaleta *et al.* 2001).

Interactions between alien species and the ecological communities they invade can result in loss of native species, which can usually only be reversed to any extent by removal of the invaders (Clavero & Garcia-Berthou 2005; Blackburn *et al.* 2010). However, where multiple species are introduced to an environment, the importance of interspecific interactions may be further demonstrated by processes that complicate management such as mesopredator or mesocompetitor release (Courchamp *et al.* 1999; Zavaleta *et al.* 2001; Tompkins & Veltman 2006; Caut *et al.* 2007). The only way to predict and prevent these effects is to have a thorough mechanistic understanding of the way species interact (Tilman 1987).

The broad aim of this project was to fill gaps in what is known about the relationship between two widespread introduced species, the ship rat and house mouse, and thereby reach a better understanding of how and why controlling or eradicating ship rats results in an increase in house mouse detections. These terrestrial, omnivorous small mammal species can be considered guild members because they use similar resources: they can occupy the same habitat types and they have broadly similar diets, consisting mainly of invertebrates, seeds and fruit (Innes 2005b; Ruscoe & Murphy 2005). However, release from resource shortage as a result of the indirect mechanism of exploitation competition may not be the main reason why house mice become more abundant when ship rats are controlled. Intraguild (IG) interactions can also feature direct interference or predation (Grant 1970; Schoener 1983; Polis *et al.* 1989).

IG interactions are complex and can best be understood by studying different ecological and behavioural attributes of the relationship between species, which broadly include niche overlap, direct interactions, effects on resource use, impacts on fitness parameters and life history characteristics, and population level effects (Table 6. 1). I used this holistic approach to distinguish between indirect (exploitation competition) and direct (interference competition or IG predation) mechanisms hypothesised to underpin the relationship between ship rats and house mice.

Table 6. 1. Ecological or behavioural attributes of intraguild interactions and how they have been interpreted in the literature as intraguild predation, interference competition or exploitation competition (compiled based on the reviews in: Grant 1972; Schoener 1983; Tilman 1987; Palomares & Caro 1999; Eccard & Ylönen 2003; Sergio & Hiraldo 2008; Ritchie & Johnson 2009). Repeated from the introduction

	Direct mechanisms		**Indirect mechanism**
	Intraguild predation	**Interference competition**	**Exploitation competition**
Niche overlap	Diet or other resource overlap is evident and may be limiting	Diet or other resource overlap is evident and may be limiting	Diet or other resource overlap is evident and is limiting
Direct interactions	Direct interactions involve killing and eating of individuals of one species by those of another IG prey may show strong avoidance of IG predators The IG predator is usually larger than the IG prey	Direct interactions involve antagonistic behaviour by the dominant species towards the subordinate species Antagonistic encounters may be lethal, but are not predatory Subordinate species may avoid dominant species The dominant species is usually larger than the subordinate species	Direct interactions do not occur or are neutral Subordinate species do not avoid dominant species The dominant species in the environment may be smaller than the subordinate species

Effects on resource use	IG predator may limit access to resources for the IG prey as a result of the latter avoiding predation	Dominant species interferes with access to resources for the subordinate species due to territorial aggression or antagonistic encounters	Dominant competitor uses resources causing shortage for the subordinate competitor Dominant competitor may use resources more efficiently or effectively Food shortage may cause subordinate species to take more risks when foraging
Impacts on fitness parameters and life history characteristics	Survival may be reduced by direct effects of the IG predator Vulnerable life stages may be disproportionately affected No effect on body condition or growth indicates that poor survival was due to direct effects of predation However, body condition, growth, reproduction and residency may be influenced due to risk effects and stress	Survival may be reduced by direct effects of the dominant competitor Vulnerable life stages may be disproportionately affected No effect on body condition or growth indicates that poor survival was due to direct effects of antagonistic encounters However, body condition, growth, reproduction and residency may be influenced due to risk effects and stress	Survival, reproduction and juvenile recruitment may be affected indirectly by resource shortage Poor body condition or decreased growth rates of the subordinate species may be evident indicating food shortage rather than direct effects due to interference or predation Vulnerable life stages may be disproportionately affected

Population level effects	Abundance or distribution may be spatially or temporally negatively correlated with that of the IG predator Pulse removal of the IG predator may lead to increased abundance usually through immigration Press removal of IG predators may lead to increased abundance through enhanced survival, reproduction or recruitment Food addition does not increase population size	Abundance or distribution may be spatially or temporally negatively correlated with that of the dominant competitor Pulse removal of the dominant competitor may lead to increased abundance usually through immigration Press removal of dominant competitors may lead to increased abundance through enhanced survival, reproduction or recruitment Food addition does not increase population size	Abundance or distribution may be spatially or temporally negatively correlated with that of the dominant competitor Pulse removal of dominant competitor does not influence abundance Press removal of dominant competitors leads to increased abundance through enhanced survival, reproduction or recruitment Food addition increases population size

6.1 Indirect vs. direct mechanisms

6.1.1 Niche overlap

My review of information from diet studies (Chapter 2) confirmed that the dietary niches of ship rats and house mice do overlap, hence the two species have potential to be resource competitors as suggested by several authors (e.g. Sweetapple & Nugent 2007; Ruscoe *et al.* 2011). There was moderate overlap for the invertebrate component of the diet, which is important because invertebrates are a rich source of the nitrogenous foods needed for growth and fecundity. In some locations, ship rats and house mice shared a common food type as the main item in their diet and would therefore be more likely to compete (Craddock 1997).

6.1.2 Direct interactions

Although ship rats and house mice exhibit overlap in resource use, my experiments investigating encounters between house mice and ship rats (Chapter 3) indicated that indirect exploitation competition alone may not determine the relationship between them. Instead, ship rats have the potential to directly suppress house mouse populations through aggressive behaviour. The majority of ship rats I observed chased, bit and clawed at house mice. House mice responded by retreating and, in accordance with Bramley's (1999) findings, they were less active when in close proximity to a rat, significantly more so than when in proximity to a conspecific.

These results support previous reports that ship rats may be aggressive towards house mice and even kill them (Lidicker 1976; Granjon & Cheylan 1988). Ship rats therefore have the potential to defend resources against house mice. However, it is more likely that house mice actively avoid encounters with, and would never challenge a rat over a common resource, considering that rats represent a very high risk of injury or death for mice.

6.1.3 Effects on resource use

The captive trials I carried out to investigate foraging behaviour (Chapter 4) demonstrated that house mice do avoid ship rats and they will forgo foraging opportunities to do this. I provided house mice with the option of foraging in a tray near to or away from a caged ship rat. Although rats could not physically prevent mice from accessing the resources in trays situated beside them, mice still chose to avoid this location and instead foraged in the alternative tray at lower resource density. Harris and MacDonald (Harris & Macdonald 2007) found that mice did not become more abundant where patchy, as opposed to broadly scattered, food was supplied to them and reasoned that ship rats defended food patches, but mice may also have avoided them. My results indicate that the latter is more likely.

Avoidance behaviour was also observed in video footage from field trials where, despite high rates of rodent activity at stations, heterospecifics were very rarely present at the same time and when they were, mice hid or retreated and evaded detection by rats. I provided mice with foraging trays that excluded ship rats and the resources therefore could not be competed for via exploitation competition. However, whilst mice foraged both intensively and extensively from trays in dense grassland/scrub habitat where ship rats were moderately active, foraging was much lower in neighbouring, relatively open forest habitat where ship rat activity was high. It was not until I removed ship rats within the forest habitat that mouse foraging increased there, which shows that whilst rats were present, mice were unable to use forest habitat extensively despite food being available for them there.

6.1.4 Impacts on fitness parameters and life history characteristics

In the Galápagos Islands, Harris and MacDonald found that body weight, a fitness parameter associated with food availability, was not higher for mice where ship rats were suppressed, the opposite result from what would be expected if mice protected from rats were released from food shortage caused by exploitation competition, so therefore this hypothesis was rejected. However, at Pureora

Forest Park I found that mice captured when the abundance of ship rats was being reduced by a rat control treatment were significantly heavier than those captured in the same habitat during the non-treatment period. This indicates that the mice in my study were food restricted in the presence of abundant rats. During non-treatment periods at sites where I provided supplementary food, which rats could not deplete, this additional resource should have mitigated any effects of exploitation competition, and yet mice did not use it. When ship rats were controlled, mice did use feeders (albeit variably) indicating that it was not some fault of the design that inhibited them. The most likely explanation is therefore that avoidance of ship rats limited the ability of house mice to reach or access resources, including the feeders I provided, when ship rats were abundant. Similarly, large, dominant adult rats can discourage smaller conspecifics from entering confined spaces such as bait stations or tracking tunnels for fear of intraspecific aggression (Quy 2003; King *et al.* 2011b).

The reason why mice were lighter when ship rats were unmanaged in my study but not in Harris and MacDonald's study may be due to the environmental context. House mice were generally much more abundant in the Galápagos, under conditions of both high and low ship rat abundance, compared with at Pureora. This indicates that the Galápagos environment offered more resources and refuges for house mice compared to New Zealand podocarp-broadleaf forest, where a combination of sparse resources and few refuges along with high density of ship rats may create a more hostile environment for mice with consequences for their foraging ability and numbers.

6.1.5 Population level effects

Short term pulse removal experiments readily detect the effects of direct influences on populations such as interference competition, but not the indirect influences associated with exploitation competition (Bender *et al.* 1984; Dickman 1991). Two previous studies have demonstrated rapid increases in mouse activity or abundance following pulse removals of ship rats, indicating that exploitation competition does not limit mice (Brown *et al.* 1996; Harper & Cabrera 2010). In

support of these studies, I found that mice rapidly became more active within forest habitat in response to pulse ship rat removal (Chapter 4).

It is more difficult to distinguish between direct and indirect effects from a competitor using longer term press experiments (Bender *et al.* 1984; Harris & Macdonald 2007). All else being equal, species suppressed by exploitation competition should respond to supplementary food (Schoener 1983). At Pureora Forest Park (Chapter 5) I found that the abundance and associated activity of house mice were higher when ship rats were controlled, mainly because of greater immigration or establishment success. Because supplemental food did not mitigate the effects of high ship rat abundance when ship rats were not controlled, I conclude that exploitation competition alone is very unlikely to explain the differences in mouse abundance.

6.2 Interference competition vs. intraguild predation

Having established that ship rats and house mice exhibit moderate niche overlap, but that indirect exploitation competition is unlikely to be the main mechanism underpinning the relationship between them (for reasons summarised in Table 6. 2), there remain two direct mechanisms to be distinguished: interference competition and IG predation. Determining the importance of either one or the other is difficult because IG predation may be regarded as an extreme form of interference competition, and hypotheses considering interference or predation risk may produce similar results (Polis *et al.* 1989; Stapp 1997) (Table 6. 1). However, a distinction can be made based on whether ship rats primarily kill mice to reduce resource competition, or more simply as an act of opportunistic predation of a profitable prey item (Polis *et al.* 1989; Stapp 1997).

The results of the captive experiments I carried out to investigate encounters between individual animals (Chapter 3) indicate that opportunistic IG predation best describes the interaction between ship rats and house mice (summarised in Table 6. 2). Most ship rats were attracted to the movements of live mice and chased them aggressively. Aggression was exhibited both on neutral territory and when mice were presented to a resident ship rat in its cage. In neither

situation did rats exhibit threat behaviours, such as the raised hackles and lateral display which often characterised their interactions with conspecifics and which I expected to observe if defence of a resource (in this case space) was driving the behaviour (O'Boyle 1974; Polis *et al.* 1989). This evidence indicates that ship rats viewed mice as prey items rather than competitors.

The response of many ship rats to the euthanased mice further supported the hypothesis that rats exhibited predatory aggression, as opposed to other forms of aggressive behaviour which would be associated with competition. All ship rats that interacted with the euthanased mouse ate at least a small part of it, indicating that their behaviour was linked to feeding (O'Boyle 1974). Ship rats grasped the mouse, bit it and turned it repeatedly in their paws, which are all behaviours observed when rodents handle prey items such as invertebrates (Timberlake & Washburne 1989).

Out of a total of 26 mice whose behaviour during encounters with ship rats was observed in the modified aquarium (experiments 1 and 2, Chapter 3), only one exhibited any aggressive behaviour, and this was limited to a single brief instance. Therefore there was little evidence that interacting with house mice presented any risk to ship rats, although given that I could not observe direct encounters between ship rats and live mice, I could not determine whether mice can defend themselves at all during an attack. However, considering the vast size difference between the two species and the levels of aggression exhibited by many ship rats, it is doubtful that opportunistic predation on house mice presents much risk to ship rats, and they stand to gain a substantial protein reward. The rat at Pureora that broke into a live trap to reach a mouse inside (Chapter 5) provided evidence that wild ship rats do take advantage of opportunities to kill house mice and consume them.

The behaviour of ship rats towards house mice differs from that reported for ship rats interacting with Polynesian rats (*Rattus exulans*), which involved no killing and Polynesian rats were the aggressors (McCartney & Marks 1973). Size may be a cue that determines whether an animal is treated as prey. Polynesian rats,

whilst considerably smaller than ship rats, are larger than house mice. Behaviour is also likely to be important as attacking an aggressive animal poses a greater risk than attacking a meek one. Between closely related species social cues may also be important as McCartney (1973) described how Polynesian rats and ship rats appeared to recognise each other as 'rats' and engaged in social behaviours that usually characterise intraspecific interactions, such as ritualistic grooming.

Not all ship rats interacted with house mice in captive trials, and some interacted but were not aggressive. These same individuals also exhibited minimal interaction with conspecifics so it is likely that they were by nature or juvenile experience more timid animals. However, it is impossible to know whether they were in fact less aggressive individuals or whether their behaviour was inhibited more than that of other individuals by being in captivity. Regardless of whether all ship rats are a threat, it is in the interests of mice to avoid ship rats, and they did so in captive foraging trials (Chapter 4). The high levels of avoidance observed were consistent with an anti-predator response (Dickman 1991).

Opportunistic predation of mice is consistent with the generalist feeding habits of the ship rat, a species that feeds at multiple trophic levels (Landry 1970; Daniel 1973; Brown *et al.* 1998; Innes 2005b; Cassaing *et al.* 2007; Sweetapple & Nugent 2007; Innes *et al.* 2010a; St Clair 2011). This characteristic has played a large part in the success of ship rats invading habitats around the world and in their negative impacts on native species (Towns *et al.* 2006; Cassaing *et al.* 2007; Howald *et al.* 2007; Harris 2009; St Clair 2011). By opportunistically consuming animals that pose low risk, ship rats supplement the plant component of their diet with protein and may also get the incidental benefit of removing potential competitors.

Table 6. 2. Studies providing information about ecological and behavioural attributes of the relationship between house mice and ship rats and whether, in aggregate for each category, this evidence supports, is consistent with or does not support a hypothesis of intraguild predation, interference competition or exploitation competition. This table is repeated from the introduction but also includes the results of the studies described in this thesis highlighted in bold

				Direct mechanisms		Indirect mechanism
Attribute	**Evidence**	**Location**	**Reference**	**Intraguild predation**	**Interference competition**	**Exploitation competition**
Niche overlap	Ship rats and house mice can occupy many of the same habitat types, although they are most abundant in different types when both species are present	New Zealand	(King *et al.* 1996c)	Consistent with	Consistent with	Consistent with
	However, ship rats are arboreal, whilst house mice are more terrestrial	New Zealand	(Ruscoe & Murphy 2005)			
	Some overlap in diet, but uncertain what extent	New Zealand	(Ruscoe & Murphy 2005)			

	Ship rats sometimes rely more on plant matter than mice do, but there is at least moderate overlap in the invertebrate component of the diet, which may be greater in some environments	**New Zealand**	**This study (Chapter 2)**	**Consistent with**	**Consistent with**	**Consistent with**
Direct interactions	Ship rats exhibit traits that characterise intraguild predators	New Zealand	(Innes 2005b)	Support, but evidence anecdotal or circumstantial	Not supported, but evidence anecdotal or circumstantial	Not supported
	Some evidence that ship rats will kill house mice and eat them	France Australia	(Granjon & Cheylan 1988) (Lidicker 1976)			
	House mouse remains in ship rat stomachs	New Zealand	(McQueen & Lawrence 2008)			
	House mice were less active when in close proximity to ship rats	New Zealand	(Bramley 1999)			
	Ship rats exhibited aggressive predatory behaviour towards house mice. Mice were less active in proximity to rats	**New Zealand**	**This study (Chapter 3)**	**Support**	**Not supported**	**Not supported**
	A trapped house mouse was killed and eaten by a ship rat	**New Zealand**	**This study (Chapter 5)**			

Effects on resource use	Ship rats dominated patchy food resources by defending them against house mice or house mice avoided them because ship rats were present	Galápagos Islands	(Harris & Macdonald 2007)	Consistent with	Consistent with	Not supported
	House mice showed strong avoidance of foraging in proximity to ship rats despite not being physically prevented from doing so indicating an anti-predator response **House mice foraged extensively and intensively in grassland-scrub habitat, but were limited in forest habitat until rats were removed**	**New Zealand**	**This study (Chapter 4)**	**Support**	**Less support**	**Not supported**
Impacts on fitness parameters and life history characteristics	Ship rats may have influenced the recruitment of juvenile mice in forest habitat	New Zealand	(King *et al.* 1996b)	Consistent with	Consistent with	Not supported
	House mice immigrated on to sites where ship rats were removed, but survival, recruitment and body weight were unaffected	Galápagos Islands	(Harris & Macdonald 2007)			

	Mice captured when ship rats were not controlled were lighter and yet did not consume supplementary food. No detectable effects on survival or recruitment so greater mouse abundance when rats were controlled was most likely due to immigration	**New Zealand**	**This study (Chapter 5)**	**Consistent with**	**Consistent with**	**Not supported**
Population level effects	Abundance of ship rats and house mice was spatially negatively correlated	New Zealand	(King *et al.* 1996c) (Miller & Miller 1995)	Consistent with	Consistent with	Not supported
	Pulse removal of ship rats resulted in increased abundance or activity	New Zealand	(Brown *et al.* 1996)			
		Galápagos Islands	(Harper & Cabrera 2010)			
	Press removal of ship rats resulted in increased abundance of house mice	New Zealand	(Ruscoe *et al.* 2011)			
		Galápagos Islands	(Harris & Macdonald 2007)			
	Press removal of ship rats resulted in increased activity or abundance of house mice	New Zealand	(Innes *et al.* 1995) (Miller & Miller 1995) (Gillies *et al.* 2003b)			
		USA Virgin Islands	(Witmer *et al.* 2007)			

Supplementing food increased mouse abundance where it was distributed in a scattered regime, but not where it was patchily distributed	Galápagos Islands	(Harris & Macdonald 2007)			
Pulse removal of ship rats led to relatively rapid expansion of mouse detections away from refuge habitat into forest allowing them to forage at patches that were available, but unused previously	**New Zealand**	**This study (Chapter 4)**	**Consistent with**	**Consistent with**	**Not supported**
Press removal of ship rats increased abundance of house mice which was reflected by activity in tracking tunnels though there were also more subtle, complex influences of varying ship rat abundance on the probability of capturing mice, which differed by season	**New Zealand**	**This study (Chapter 5)**			
Supplementary food was not used by house mice when ship rat abundance was high though it was used, albeit variably when ship rats were controlled	**New Zealand**	**This study (Chapter 5)**			

6.3 Direct mortality vs. risk effects

The numerous diet studies for ship rats occupying podocarp-broadleaf forest that have failed to find evidence of predation by rats on mice seem to be inconsistent with a mechanism of IG predation (Daniel 1973; Innes 1979; Craddock 1997; Blackwell 2000; Sweetapple & Nugent 2007). However, diet studies can be unreliable for determining the impact of predators on vertebrate prey populations because the material consumed may be difficult to identify (e.g. soft tissue) (Stapp 1997). Predation events may also be relatively infrequent, but still affect species at the population level as is the case for birds, which feature rarely in ship rat stomachs, but monitoring nests has revealed that ship rat predation has a major impact (Innes *et al.* 2010a). However, the main influence of an IG predator is often not direct mortality, instead IG prey species are limited via risk effects associated with avoiding IG predators (Palomares & Caro 1999; Sergio & Hiraldo 2008; Ritchie & Johnson 2009).

I found evidence that risk effects negatively influenced the foraging behaviour of house mice (Chapter 4), prevented them from accessing resources in ship rat dominated habitat lacking refuges (Chapter 4 and Chapter 5) and caused them to suffer lower body weight (Chapter 5). Risk effects associated with opportunistic IG predation from ship rats therefore influenced immigration rates into high rat areas, and, given that house mice can die within 24 hours without sufficient food, disruption of foraging could conceivably cause mouse mortality. Risk effects are therefore very likely to play a major part in the mechanism by which ship rats suppress house mice though I am unable to determine the extent to which direct mortality contributes.

McQueen and Lawrence (2008) found evidence of mouse consumption in a high proportion of ship rat stomachs they sampled during a mouse plague in beech forest. Ship rats are generally not as abundant in beech forest compared to podocarp-broadleaf forest, but masting events cause rodent population eruptions (primarily house mice, but also ship rats) due to dramatic changes in resource availability (King 1982; Murphy 1992; Fitzgerald *et al.* 1996; Fitzgerald

2004). It is conceivable that when mice are at high density ship rats have greater opportunity to prey on them, but in the more stable podocarp-broadleaf forest system relatively consistent, high ship rat density keeps mouse numbers low, mainly through risk effects and occasional opportunistic predation events. However, this scenario requires confirmation.

An aspect of the ship rat-house mouse relationship that I was unable to study directly was the possibility that ship rats prey on nestling mice. King *et al*. (1996b) suggested this as an explanation for why recruitment of juvenile house mice was low in mature native forest at Pureora compared to habitat with dense ground cover, even though reproductive rates were similar in all habitats. I was alerted to the fact that female mice captured for captive experiments had given birth by the frequent high pitch squeaking of their offspring, so it is reasonable to assume that rats would also be able to detect nestling mice this way, perhaps also using olfactory cues. However, confirming this idea in the wild presents many practical and ethical difficulties.

I failed to find any difference in the proportion of small, juvenile mice compared to adults when ship rats were controlled versus non-treatment at Pureora (Chapter 5). However, the effect of ship rats on recruitment may have been masked by immigration of independent juvenile mice at two study sites in autumn 2011. It is also possible that, had the ship rat control operation reduced rat abundance to lower levels, I may have observed effects on house mouse recruitment, whilst as it was, the major impact was only on the success of immigrant mice establishing when rats were controlled.

Captive trials indicated that newly independent juvenile house mice displayed behaviours that could make them more susceptible to ship rat predation after they leave the nest. Small juvenile mice were less likely to remain motionless during encounters with ship rats compared to adults (Chapter 3) and, as ship rats were stimulated by movement of house mice, this could make juvenile mice more vulnerable than adults to being attacked. However, during foraging trials

juvenile and adult mice showed equally strong avoidance of encounters with ship rats (Chapter 4), showing an early ability to avoid this threat.

6.4 Abundance vs. activity and detectability

A number of studies have questioned the extent to which increased mouse detections following removal of ship rats correspond to either increased mouse abundance or activity and detectability (Innes *et al.* 1995; Brown *et al.* 1996; Gillies *et al.* 2003b; Harper & Cabrera 2010). Pulse removals of ship rats which are rapidly followed by increased mouse detections give the impression that mice were present all along, but that their detection rates were suppressed due to disruption of activity and foraging behaviour, or unwillingness to interact with detection devices. However, removal of ship rats may also permit mice to immigrate into the removal area. In my study of foraging behaviour in the field (Chapter 4), immigration from refuge habitat appeared to primarily explain the increase in detections. Other studies have also found that subordinate species alter their habitat use or migrate into areas where dominant species have been removed (e.g. Chappell 1978; Maitz & Dickman 2001).

Immigration also appeared to explain the differences in mouse abundance associated with the ship rat control treatment at Pureora (Chapter 5). Mouse activity measured as the number of tracking tunnels with positive mouse detections, and mouse abundance estimated from live-trapping using the minimum number known alive (MNKA) index, showed very similar trends. This indicates that increased mouse detections in tunnels were predominantly the result of more mice moving into areas when rats were removed rather than more active mice tracking many more tunnels than before.

However, both methods of indexing mouse populations assumed that the probability of detecting mice (which is itself a function of activity) was constant across surveys. By pooling live-capture data I was able to test this assumption, and found that it was incorrect because there were fluctuations in detection (capture) probability for individual mice that were correlated with season and also with ship rat abundance. However, the opposite seasonal trends in mouse

capture probability correlated with rat abundance are difficult to explain and point towards more subtle, complex influences of rat abundance on the probability of detecting mice, which are secondary to the overall effect of ship rats on mouse abundance.

6.5 Implications for rodent research and management

Evidence that ship rats are opportunistic IG predators of mice and that mice actively avoid them provides a better understanding of the dynamic interactions between these two species, and of how ship rats suppress mouse populations. Previous studies have suggested that ship rats and house mice are competitors or predators, but the concept of IG predation is more useful because it recognises that aspects of both occur. As direct mortality from ship rats may be rare, it could be argued that the mechanism resembles interference competition. However, interference competition does not explicitly acknowledge the underlying reason for house mice to avoid ship rats, which is to escape predation, and for ship rats to attack house mice, which is to prey on them, though rats may also incidentally benefit from some reduced competition for shared resources if they are limited.

Both the foraging experiment (Chapter 4) and the study at Pureora (Chapter 5) emphasised how adaptable and mobile individual mice can be in moving into areas where ship rats have been removed. This has also been shown in previous studies and reinforces the need to be aware of this outcome when planning ship rat management operations (Caut *et al.* 2007; Harris & Macdonald 2007; Witmer *et al.* 2007; Harper & Cabrera 2010).

Rodent management is done on different scales and with different aims, which are broadly divided between eradication or sustained management (Parkes & Murphy 2003). During the planning stages of ship rat eradication operations, it is imperative to determine whether mice are present and therefore very likely to increase once ship rats are gone. Decisions such as the choice of toxins to be used and the manner in which they are distributed may depend on whether or

not mice are detected. Some assessment may also be made about whether an outbreak of house mice is acceptable when balanced against the benefit of removing ship rats and the criteria for this will be the predicted net outcome for biodiversity. Mice may be present even if not detected so decisions will need to be made about the risk of this, how undesirable a mouse outbreak would be, and what options might be available to use a method that would potentially eradicate both species, whilst still avoiding non-target losses.

Surveys aiming to detect the presence of house mice prior to ship rat eradication should focus on dense habitat offering refuge for house mice from ship rats. Given that during the foraging experiment (Chapter 4) I found that house mice preferred trays that excluded ship rats, rather than the tracking tunnels that were accessible to both species, it would be prudent to use monitoring devices that exclude ship rats. This is mainly to ensure that bait is not taken by ship rats, because I found no evidence that house mice were repelled by ship rat odour. My results from Pureora indicate that house mice are most detectable during winter and spring or, by inference whenever resources are scarce, so surveying for mice during these times would be optimal.

During sustained rodent control, populations are monitored in order to assess whether or not a control operation has reached target levels, and to compare with non-treatment areas to ensure that the management rather than natural population fluctuation achieved the result. In this situation, my results indicate that indices derived from activity in tracking tunnels provide reasonable agreement with those based on captured animals when mice are at low densities in podocarp-broadleaf forest, which gives confidence in the use of tracking tunnels to assess mouse populations. However, as the probability of capturing mice, and by inference detecting them in tunnels, was lowest in summer, population levels may be underestimated in this season compared to others. If this is indeed because they have a higher background level of food, mouse population size may be underestimated by indices any time when food is highly abundant.

Ship rats have been implicated in the loss or decline of native small mammals, particularly on islands (Harris 2009). Insights gained from exploring the ship rat-house mouse relationship may help to understand the potential mechanism underpinning those interactions where the species are similar in size and behaviour to house mice.

6.6 Further research directions

Fruitful research questions suggested by my work include the following.

(1) The need to better understand how direct mortality from ship rat predation (including killing nestlings) contributes to suppressing mouse populations and whether house mice are an important resource in sustaining ship rat populations following masting events, as suggested by McQueen and Lawrence (2008).

(2) The link between resource availability and the probability of mice and other rodents being detected or interacting with poison bait needs to be addressed.

(3) Aspects of the interactions between ship rats and house mice and the other two rodent species in New Zealand (Norway rats and Polynesian rats or kiore), require further investigation in order to understand their distribution and abundance (Atkinson & Towns 2005; Innes 2005a; King *et al.* 2011a).

(4) Research is required to understand the impacts of house mice at a range of densities on New Zealand native biodiversity, particularly on the mainland. My results show that suppressing ship rats is very likely to lead to more house mice with less restricted foraging behaviour, but it is necessary to understand what this means for native species and what levels of house mice numbers are acceptable whilst still achieving the varying conservation goals of different management projects.

6.7 Conclusions

Through studying behavioural and ecological attributes of the relationship between ship rats and house mice I conclude that ship rats primarily suppress house mice via IG predation. These two species have overlapping dietary niches,

making them potential competitors, but I observed that ship rats also exhibit predatory behaviour towards house mice. House mice appear to respond to the risk of predation from ship rats by exhibiting avoidance behaviours which influence their foraging decisions and limit their use of habitat that is dominated by ship rats and offers few refuges. House mice had lower body weight when ship rats were at high compared to lower abundance despite supplementary food being available, which is consistent with disrupted foraging due to avoiding abundant ship rats. Risk of ship rat predation therefore appears to have a strong influence on house mice, though it is unclear to what extent direct mortality from ship rats contributes.

At the population level, press removal of ship rats during a management operation was associated with greater mouse abundance, and activity in tracking tunnels was related to the number of mice trapped. However, I observed variation in probability of capturing or detecting mice according to season and rat abundance, which indicates more subtle and complex influences of ship rats on house mouse behaviour. To best detect house mice in order to determine their presence prior to ship rat eradication, my results indicate that surveys should concentrate on habitat offering refuges inaccessible to rats, use mouse-specific methods, and target times of food shortage. To monitor fluctuations in mouse populations, my results provide some support for the use of tracking tunnels to capture major trends, with the caveat that any index of abundance may be unreliable when comparing between seasons, and there may be subtle influences of rat abundance on probability of detection, not necessarily negative. Future research is required to better understand the role of direct mortality of mice from predation by ship rats, particularly in eruptive systems, and information is needed about the effects of house mice on native biodiversity.

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Appendices

Appendix 1. Studies and categories used to calculate Pianka's index of overlap for animal matter consumed by ship rats and house mice. Data presented are for ship rats. See appendix 2 for equivalent data for house mice

Author	Blackwell (2000)1.	Blackwell (2000)2.	Daniel (1973)	Clout (1980)	Rickard (1996)	Sturmer (1988)	Weighted average
n	49	121	173	17	28	415	803
Aranaea	16.3	9.9	1	29.4	32.1	22	15.8
Blattodea	0	0	0	0	53.6	12	8.1
Chilopoda	0	0	0	0	0	24	12.4
Collembola	0	0	0	0	0	0	0
Coleoptera	12.2	5.8	4	5.9	21.4	23	15.2
Coleoptera larvae	0	0	0	0	25	4	2.9
Diptera	0	0	2	41.2	3.6	8	5.6
Gastropoda	0	0	1	0	0	11	5.9
Hemiptera	0	0	5	0	0	0	1.1
Hymenoptera	0	0	1	0	17.9	0	0.8

Lepidoptera	0	0	1	0	0	0	0.2
Lepidopteran larvae	0	0	2	70.6	0	21	12.8
Lepidopteran pupae	0	0	0	0	0	0	0
Oligochaeta	0	0	0	0	0	0	0
Opiliones	0	0	0	0	35.7	27	15.2
Orthoptera (weta)	46.9	20.7	40	58.8	60.7	85	61.9
Orthoptera (grasshoppers)	0	0	0	0	0	0	0
Phasmatodea	34.7	47.9	3	0		16	18.3

Appendix 2. Studies and categories used to calculate Pianka's index of overlap for animal matter consumed by ship rats and house mice. Data presented are for house mice. See appendix 1 for equivalent data for ship rats.

Author	Badan (1986)	Badan (1986)	Badan (1986)	Fitzgerald *et al* (1996)	Jones & Toft (2006)	Watts 2001	Miller & Webb 2001	Wilson *et al* (2006)	Weighted Average
n	260	334	117	830	66	30	102	67	
Aranae	0	0	0	44.6	47	67	58.8	34	27.9
Blattodea	0	0	0	0	0	0	0	0	0
Chilopoda	0	0	0	0	0	0	0	0	0
Collembola (sprintail)	0	0	0	0	0	0	1.9	0	0.1
Coleoptera	0	0	0	12	27	67	9.8	0	8.2
Coleoptera larvae	0	0	0	14.5	8	16.7	54.9	0	10.3
Diptera	0	0	0	0	6	10	2.9	0	0.5
Gastropoda	0	0	0	0	23	6.7	0	0	1.0
Hemiptera	0	0	0	0	0	3.3	7.8	0	0.5
Hymenoptera	0	0	0	0	0	0	0	0	0
Lepidoptera general	0	0	0	0	0	0	0	0	0
Lepidopteran larvae	91	79	27	50.2	66	73	66.6	22	60.75

Lepidopteran pupae	24	15	0	0	0	0	0	0	6.25
Oligochaeta	4	3	0	0	0	6.7	3.9	0	1.5
Opiliones	0	0	0	0	0	0	0	0	0
Orthoptera (weta)	0	0	0	17.1	16	13.3	11.7	36	10.7
Orthoptera (grasshoppers)	0	0	0	0	0	0	0	13	0.5
Phasmatodea	0	0	0	0	0	0	0	0	0

Appendix 3. Description and classification of activity states of house mice and ship rats in a staged encounter in a modified aquarium set up.

Activity	Description	Category
Chasing	Following the movement of the other animal along the wire mesh divider.	Moving
Climbing	Travelling up the wire mesh divider or hanging from the lid	Moving
Digging	Using front limbs to move the substrate	Moving
Eating	Holding substrate in front feet and nibbling on it	Other
Falling	Dropping from wire divider or wire lid to the base of the aquarium	Moving
Freezing	Pausing either on the ground or whilst climbing in an alert, tense posture	Motionless
Gnawing	Biting at the wire divider	Other
Grooming	Cleaning the body	Other
Jumping	Propelling body into the air usually from the base of the aquarium to the wire divider or wire lid	Moving
Listening	Ears pricked and moving head from side to side	Other
Still	Sitting or lying without moving	Motionless
Sitting up	Sitting up on haunches. Usually accompanied by moving the head and sniffing the air	Other
Sniffing	Smelling the substrate and edges of the aquarium	Other
Stretching	Reaching up with the front quarters. Usually at the divider or sides of the aquarium. Often accompanied by sniffing	Other
Walking/running	Movement from one part of the aquarium base to another	Moving
Yawning	Stretching mouth wide	Other

Appendix 4. Standard rodent diet laboratory pellet manufacturers information

Specialty Feeds
3150 Great Eastern Hwy
Glen Forrest
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Email: info@specialtyfeeds.com

Diet

Meat Free Rat and Mouse Diet

A fixed formulation diet for Laboratory Rats and Mice fortified with vitamins and minerals to meet the requirements of breeding animals after the diet is autoclaved or irradiated.

- Minor modifications were made to this fixed formulation on 27 Jan 2009. Please contact us for details.
- All nutritional parameters of this diet meet or exceed the NRC guidelines for Rats and Mice.
- The diet has been designed as a general ration for breeding and early growth in all rat and mouse strains. The total fat content has been deliberately kept low at around 5%, to maximise the long term breeding performance of most strains.
- The formulation is designed to be fed ad-lib to rodents of all ages. There is some indication that growth performance in a minority of strains can be improved by increasing dietary energy (fat content). BalbC mice, DA rats and some of the modified strains appear to be most susceptible to this problem. Please contact us if you are concerned about this issue.
- Mammalian meals have been excluded from the diet, however the diet does contain fish meal. We have formulated totally vegetarian diets, and maintained colonies for some time on these diets. Please contact us if you require such a diet.
- The feed is manufactured in a cylindrical form with a diameter of around 12 mm, length is variable from 10 mm to 30 mm. We have found that this form is ideal for overhead hopper feeding, maximising the ease of handling whilst minimising fines formation and the risk of bridging in the feed hopper. Pellet strength has been kept lower than conventional pelletised diets. While this leads to a slight increase in transit and storage damage to the diet (fines generation), we have found that juvenile mice often have a lower feed intake on harder pellets.
- The diet is packed in permeable bags suitable for direct loading into an autoclave. It is recommended that the diet be autoclaved at 120° C for 20 minutes with a post autoclaving vacuum drying cycle. Some clumping of the diet can be expected, but the diet clumps can usually be easily broken. Modifying the drying time to leave some residual moisture in the diet can minimise the clumping. Do not autoclave at 135° C as this will result in significant clumping that will be difficult to break.

Calculated Nutritional Parameters	
Protein	20.00%
Total Fat	4.80%
Crude Fibre	4.80%
Acid Detergent Fibre	7.60%
Neutral Detergent Fibre	16.40%
Total Carbohydrate	59.40%
Digestible Energy	14.0 MJ / Kg
% Total Calculated Energy From Protein	23.00%
% Total Calculated Energy From Lipids	12.00%

Ingredients

A Fixed formula ration using the following ingredients:
Wheat, barley, Lupins, Soya meal, Fish meal, Mixed vegetable oils, Canola oil, Salt, Calcium carbonate, Dicalcium phosphate, Magnesium oxide, and a Vitamin and trace mineral premix.

Added Vitamins	
Vitamin A (Retinol)	10 000 IU/Kg
Vitamin D (Cholecalciferol)	2 000 IU/Kg
Vitamin E (a Tocopherol acetate)	100 mg/Kg
Vitamin K (Menadione)	20 mg/Kg
Vitamin B1 (Thiamine)	80 mg/Kg
Vitamin B2 (Riboflavin)	30 mg/Kg
Niacin (Nicotinic acid)	100 mg/Kg
Vitamin B6 (Pryridoxine)	25 mg/Kg
Calcium Pantothenate	50 mg/Kg
Biotin	300 ug/Kg
Folic Acid	5.0 mg/Kg
Vitamin B12 (Cyancobalamin)	150 ug/Kg

Diet Form and Features

- Cereal grain base diet. 12 mm diameter pellets.
- Pack size 10 and 20 Kg Bags.
- Diet suitable for irradiation, also suitable for autoclave.
- Lead time 2 weeks

Added Trace Minerals	
Magnesium	100 mg/Kg
Iron	70 mg/Kg
Copper	16 mg/Kg
Iodine	0.5 mg/Kg
Manganese	70 mg/Kg
Zinc	60 mg/Kg
Molybdenum	0.5 mg/Kg
Selenium	0.1 mg/Kg

Calculated Amino Acids	
Valine	0.87%
Leucine	1.40%
Isoleucine	0.80%
Threonine	0.70%
Methionine	0.30%
Cystine	0.30%
Lysine	0.90%
Phenylanine	0.90%
Tyrosine	0.50%
Tryptophan	0.20%

Calculated Total Minerals	
Calcium	0.80%
Phosphorous	0.71%
Magnesium	0.20%
Sodium	0.18%
Potassium	0.82%
Sulphur	0.20%
Iron	200 mg/Kg
Copper	23 mg/Kg
Iodine	0.5 mg/Kg
Manganese	104 mg/Kg
Cobalt	0.7 mg/Kg
Zinc	90 mg/Kg
Molybdenum	1.2 mg/Kg
Selenium	0.4 mg/Kg
Cadmium	0.05 mg/Kg

Calculated Total Vitamins	
Vitamin A (Retinol)	10 950 IU/Kg
Vitamin D (Cholecalciferol)	2 000 IU/Kg
Vitamin E (a Tocopherol acetate)	110 mg/Kg
Vitamin K (Menadione)	20 mg/Kg
Vitamin C (Ascorbic acid)	No data
Vitamin B1 (Thiamine)	80 mg/Kg
Vitamin B2 (Riboflavin)	30 mg/Kg
Niacin (Nicotinic acid)	145 mg/Kg
Vitamin B6 (Pryridoxine)	28 mg/Kg
Pantothenic Acid	60 mg/Kg
Biotin	410 ug/Kg
Folic Acid	5 mg/Kg
Inositol	No data
Vitamin B12 (Cyancobalamin)	150 ug/Kg
Choline	1 600 mg/Kg

Calculated Fatty Acid Composition	
Myristic Acid 14:0	0.03%
Palmitic Acid 16:0	0.50%
Stearic Acid 18:0	0.14%
Palmitoleic Acid 16:1	0.01%
Oleic Acid 18:1	1.90%
Gadoleic Acid 20:1	0.03%
Linoleic Acid 18:2 n6	1.30%
a Linolenic Acid 18:3 n3	0.30%
Arachadonic Acid 20:4 n6	0.01%
EPA 20:5 n3	0.02%
DHA 22:6 n3	0.05%
Total n3	0.37%
Total n6	1.31%
Total Mono Unsaturated Fats	2.00%
Total Polyunsaturated Fats	1.77%
Total Saturated Fats	0.74%

Calculated data uses information from typical raw material composition. It could be expected that individual batches of diet will vary from this figure. **Diet post treatment by irradiation or auto clave could change these parameters.**

We are happy to provide full calculated nutritional information for all of our products, however we would like to emphasise that these diets have been specifically designed for manufacture by Specialty Feeds.

Appendix 5. Break down of mouse population characteristics across treatments and seasons. Numbers are based on minimum number known alive within sessions. Differences in totals are due to inability to determine breeding state and weight for animals that were not captured, but assumed to be present (captured in sessions prior and post).

Season/survey	Percent Female		Percentage of females breeding		Percent Juvenile		Average weight		
	n	%	N	%	n	%	n	Weight (g) (±SD)	Range (g)
Spring/ Treatment	22	45.5	10	0	22	4.5	21	17.1 (± 2.3)	13 - 21
Summer/Treatment	17	52.9	8	37.5	17	23.5	16	15.8 (± 4.7)	5.5 - 25
Autumn/Treatment	47	38.3	18	55.5	47	44.7	47	14.8 (± 3.3)	9 – 21.5
Treatment combined	**86**	**43**	**37**	**32.4**	**86**	**30.2**	**84**	**15.6 (± 3.5)**	**5.5 - 25**
Spring/Non-treatment	8	25	1	0	8	0	8	17.1 (± 1.6)	14 – 19.5
Summer/Non-treatment	3	33.3	1	100	3	0	3	16 (± 2.3)	14 – 18.5
Autumn/Non-treatment	19	47.4	9	50	19	57.8	19	12 (± 3.1)	8 - 18
Non-treatment combined	**30**	**40**	**11**	**54**	**30**	**36.6**	**30**	**13.8 (± 3.6)**	**8 – 19.5**
Winter (All Non-treatment)	**13**	**46.2**	**5**	**20**	**13**	**23.1**	**11**	**14.7 (± 2.7)**	**9 – 19.5**
Total captures (n = 125)+ mice known to be present, but not captured (n = 4)	**129**	**42.62**	**53**	**35.82**	**129**	**31.3**		**15 (± 3.5)**	**5.5 - 25**
Total individuals	**116**	**44**							

Appendix 6. Break down of mouse population characteristics across years and seasons. Numbers are based on minimum number known alive within sessions. Differences in totals are due to inability to determine breeding state for animals that were not captured, but assumed to be present (captured in sessions prior and post).

Season/survey	% Female		% Females breeding		Percent Juvenile		Average weight		
	n	%	n	%	n	%	n	Weight (g) (±SD)	Range (g)
Spring/ 2009	24	37.5	9	0	24	4.2	24	17.2 (± 2.2)	13 - 21
Spring/2010	6	50	2	0	6	0	5	17 (± 1.9)	14 - 19
Spring/combined	**30**	**40**	**11**	**0**	**30**	**3.3**	**29**	**17.1 (± 2.1)**	**13 - 21**
Summer/2010	13	38.5	5	60	13	23.1	12	15.9 (± 3.5)	11 – 21.5
Summer/2011	7	71.4	4	20	7	14.3	7	15.7 (± 5.8)	5.5 - 25
Summer/combined	**20**	**50**	**9**	**40**	**20**	**20**	**19**	**15.8 (± 4.3)**	**5.5 - 25**
Autumn/2010	37	35.1	13	38.5	37	45.9	37	14.5 (± 3)	10 – 21.5
Autumn/2011	29	48.3	14	64.3	29	51.7	29	13.4 (± 4)	8 – 21.5
Autumn/ combined	**66**	**40.9**	**27**	**51.9**	**66**	**48.5**	**66**	**14 (± 3.5)**	**8 – 21.5**
Winter (data only collected in 2010)	**13**	**46.2**	**5**	**20**	**13**	**23.1**	**11**	**14.7 (± 2.7)**	**9 – 19.5**
Total captures (mice known to be present, but not captured (n = 4) included if appropriate)	**129**	**42.6**	**53**	**35.8**	**129**	**31.3**	**125**	**15 (± 3.5)**	**5.5 - 25**
Total individuals	**116**	**44**							