# HABITAT USE AND RESPONSES TO ODOURS BY RODENTS IN NEW ZEALAND.

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# ABSTRACT

Four species of introduced rodent live in New Zealand. No more than three species are sympatric here, although all four are in more tropical areas. All are pests for economic, public health and conservation reasons. The factors that might regulate the occurrence and interactions of rodents in New Zealand have not been identified and are poorly understood. A combination of laboratory and field studies was used to examine the interactions between rodents, especially the role that odours play in regulating interspecific interactions. Knowledge of rodent ecology and interactions is required to manage populations of these pests effectively. Snap trapping of Norway rats (*Rattus norvegicus*) and kiore (*R. exulans)* on Kapiti Island indicated that these species were associated with different habitats: most Norway rats were caught in steep, poorly-drained areas with tall vegetation while kiore were associated with flat, well-drained areas of low growing vegetation. Whilst more kiore were caught in grassland and kanuka (*Kunzea ericoides*) forest, kiore caught in kohekohe (*Dysoxylum spectabile*) forest were larger and apparently more productive. Radio-tracking of both species showed that kiore used smaller home ranges and denser habitats than Norway rats, and provided weak evidence that the two species avoided each other when sympatric. In 1996, rats were removed from Kapiti Island by poisoning using Brodifacoum. The ranging behaviour of lethally poisoned radio-carrying rats (n=9) was unaffected by ingestion of poison until shortly before their death when they stopped moving and became unresponsive. Laboratory experiments indicated that kiore might avoid the odours of other rats in a Y maze, but ship rats (*R. rattus*) and Norway rats were less responsive to heterospecific odours. Mice (*Mus musculus*) in laboratory trials could apparently distinguish the odour of rats from their own odour, but did not avoid rat odour. However, when presented with a caged ship rat in a test arena, mice were less active. Pairs of mice that had been exposed to ship rat odour produced larger litters than control mice, but this result needs to be replicated. The results suggest that rodents, particularly kiore, probably avoid heterospecifics, but this behaviour is not mediated by odours alone, rather by more direct interaction. Either competition or predation by larger rodents on smaller ones could explain this avoidance. Future studies should manipulate the presence and abundance of rodents to investigate competitive ability. Such studies would allow a clearer understanding of population regulation and the mechanisms of coexistence, which may in turn allow more efficient control of rodent pests. If rats could be shown to avoid the odour of carnivores, then their behaviour could be manipulated as part of a pest control strategy. Predator-naïve Norway rats showed an aversion to five of the six predator (canid, felid, mustelid) odours they were exposed to in a Y maze. Predator-experienced Norway rats and ship rats, and predator-naïve kiore showed no such aversion. Furthermore, free-living rats did not avoid feeding stations tainted with synthetic carnivore odours. Whilst some rats avoid predator odours, they are unlikely to be suitable for the widespread repellency of rats in New Zealand.

# PREFACE

The following pakiwaitara (folk story) records a discussion between a pouwhaitere (parrot) and a kiore (rat) describing how they climbed trees to feed on certain berries. The story tells of the need for the bird and the kiore to be careful of where they feed lest they be caught in the traps of men. Kiore (Pacific or Polynesian rats) were brought to Aotearoa/New Zealand as a source of food for pre-European Maori voyagers. Kiore may not be blameless in the decline of native species, but ironically, kiore and many native species are currently limited to offshore islands by the spread of humans and their introduced pests, including later arriving rats. It is as necessary today as it was in pre-European times for kiore to watch where, and what, they eat in order to avoid the poisons of mankind.

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|---|---|
| POUWHAITERE | E kio ka piki taua ki runga<br>*Oh kio, let us climb the tree* |
| KIORE | Ki te aha taua i runga?<br>*What shall we do there?* |
| POUWHAITERE | Ki te kaipuarakau<br>*Eat the fruit* |
| KIORE | E aha te puarakau?<br>*What kind of fruit?* |
| POUWHAITERE | He miro, he kahikatea<br>*Miro and kahikatea* |
| KIORE | E tama e ko te wakaruarua ia taua,<br>e tama ra e e haere mai nei te tangata e ronarona<br>nei i te kake torete te wai au, ti mau rawa.<br>*My friend, our kin are diminishing, man comes*<br>*and twists your neck. As for me I shall be*<br>*caught in his snare.* |

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# CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# CHAPTER ONE: INTRODUCTION

*Structure of this Thesis.* The main theme developed in this thesis is one of interactions: interactions between different rat species, between rats and mice, and rat-predator interactions in the New Zealand landscape. I have focused on the role of olfaction in mediating these interactions, but I have also looked at the general ecology of rat species where they coexist. The thesis comprises of seven chapters, one introductory chapter, five experimental chapters, and a concluding chapter. In this introductory section, I provide a theoretical and practical overview of rat management and my research aims. I present a background to the rodent problem in New Zealand, list the species that occur here and the reasons why they are considered pests. I also summarise some of the current knowledge about competition between rodents and the olfactory abilities of rats that led me to develop the experiments that follow as Chapters 2 through 6. In Chapter 7, I have attempted to draw my results together and provide conclusions and implications for rat management and research in New Zealand.

Botanical nomenclature throughout this thesis follows Allen (1961) and Webb, Sykes and Garnock-Jones (1988). Zoological nomenclature follows King (1990) and Heather and Robertson (1996).

*Rodents in a World Setting.* Approximately 42% of all known species of living mammals are rodents (calculated from figures in MacDonald, 1984). This makes the order Rodentia the largest and most successful group of mammals. Rodents are found in almost every habitat and have adapted to practically every terrestrial and freshwater environment. Some species are extremely abundant. The success of the rodent group appears to be due, in part, to the fact that they arose relatively recently in evolutionary history and show some r-selected traits (small body size, early breeding, large litters) that allow them to evolve quickly (MacDonald, 1984). This has made controlling their populations extremely difficult and inefficient (MacDonald, 1984; Berdoy and Smith, 1993). Most rodents eat seeds or vegetation, but some are omnivores and a few have developed close commensal relationships with man. There are three sub-orders of rodents: the Sciuromorpha (squirrels and beavers), the Myomorpha (rats and mice) and the Caviomorpha (the cavies, capybaras, chinchillas etc.). Rats and mice belong to the family Muridae. Murid rodents arose approximately 7 million years ago in Europe and there are now 1082 species found throughout Europe, Australasia, America, Africa and Asia (MacDonald, 1984). Few of these species are economically important (MacDonald, 1984), with the most important being the Norway rat, ship or roof rat and the house mouse (*Rattus norvegicus*, *R. rattus* and *Mus musculus*[1] respectively). These species are commensal with man and cause damage to crops, stored products and man-made structures as well as carrying diseases like bubonic plague, leptospirosis and typhoid (MacDonald, 1984). They have travelled with mankind across the planet and can reach high densities periodically (e.g., 80 000 mice per acre in California in 1941-42; MacDonald, 1984). Existing populations of rodents are most effectively controlled by “second-generation” anticoagulant poisons since biological control and trapping are largely ineffective (MacDonald, 1984). Second-generation poisons are more potent than first-generation poisons (e.g., Warfarin) and usually require only a single feed for an animal to ingest a lethal dose. Furthermore,

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[1] Two separate species of house mouse are recognised: *Mus musculus* and *Mus domesticus*. Mice in New Zealand share morphometric characteristics of both species, but await genetic determination (Murphy and Pickard, 1990).

death is delayed so that bait aversions do not develop in animals that ingest a sublethal dose and survive (MacDonald, 1984).

Ship and Norway rats are widespread on oceanic islands without endemic small mammals (Wace, 1986; Innes, 1990; Amarasekare, 1994). Throughout continental landmasses with indigenous small mammal populations (Australia, America, Asia, Africa and Europe), ship rats are mainly commensal with humans or restricted to disturbed habitats (Innes, 1990). Ship rats declined with the spread of larger Norway rats through Britain, Europe and parts of North America (Innes, 1990; Moors, 1990).

*Rodents in New Zealand.* Four species of rodent exist in New Zealand: three species of rat (ship rat, Norway rat and kiore or Polynesian rat (*R. exulans*)), and house mice. All four species arrived in New Zealand with human immigrants. Kiore arrived first with Maori voyagers (possibly as a source of food) perhaps as long as 2 000 years ago (Holdaway, 1996). By the time the Norway rat arrived in the late 18th Century, kiore were common and widespread. The arrival of the Norway rat, and in the early 19th Century the mouse, may account for the sudden decline in the numbers and range of kiore (Taylor, 1975; Atkinson and Moller, 1990). Kiore populations are now found mainly on offshore islands, but a few populations remain in isolated regions of the South Island (i.e., Westland and Fiordland; Atkinson and Moller, 1990; King and Moller, 1997). In the latter half of the 19th Century, ship rats arrived and they are now the most common and widespread rat on the main islands, having replaced the other three rodent species at many sites (Innes, 1990; King et al., 1996; King and Moller, 1997). Norway rats are more common commensally with humans on both the main (North and South) islands, although isolated populations may still survive in forest (Moors, 1990; King et al., 1996). Mice are periodically abundant in some habitats where rats are usually absent, such as young growth plantation forest or South Island beech (*Nothofagus*) forest (Murphy and Pickard, 1990; King et al., 1996). All four species of rodent are present in varying combinations on offshore islands (Atkinson and Moller, 1990), but apparently do not coexist anywhere in New Zealand, although they do elsewhere (Tomich, 1986). Kiore and/or Norway rats occupy most offshore islands (Atkinson and Moller, 1990). Ship rats and mice are most common on the two main islands and occupy fewer offshore islands. Rodents are ubiquitous in a wide range of New Zealand habitats (Atkinson and Moller, 1990; Innes, 1990; Moors, 1990; Murphy and Pickard, 1990).

Exactly why the later arriving ship rat should be the most common species in New Zealand (but not in Britain), remains unknown, although the two species occupy different habitats in the two countries. Watson (1961) suggested that the ship rats' arboreal nature allowed them to outcompete Norway rats in New Zealand forest, and that forest populations of ship rats were so productive that immigration from them supported less productive populations in adjacent areas.

*Rodents as Pests.* It is generally accepted that the four species of rodent living in New Zealand have had an adverse impact on the native flora and fauna (e.g., Atkinson, 1978; Whitaker, 1978; Veitch and Bell, 1990; Innes and Hay, 1991; Towns, 1991; Innes, 1992; Booth et al., 1996). However, there have been no studies on the direct impact of mice on native species. Mice are found in a variety of habitats including native forest and subalpine tussock, but are apparently more common in disturbed sites than in virgin forest (Murphy and Pickard, 1990). King (1982), Murphy (1992) and Fitzgerald et al. (1996) suggested that mice population irruptions following beech (*Nothofagus*) masting in South Island forests helped drive an increase in stoat numbers in the following year. These stoats born in the year following a mouse irruption may turn to native birds as prey if mice are rare (a "functional response" ; King, 1983; O'Donnell et al., 1996). Alternatively, the sheer numbers of stoats may account for the increased predation on native birds (a "numerical response"; King, 1983). Rat populations may show a similar increase in numbers following beech mast, although they apparently do not reach the high densities of mice populations (King and Moller, 1997). Thus mice and rats may affect native birds directly (by predation) or indirectly by allowing an unsustainable increase in the number of stoats, and possibly other predators, which eat native birds.

In New Zealand, some of the rare and endemic species most at threat by rat predation (e.g., kakapo, *Strigops habroptilus*) are intensively monitored. All nests are closely observed and rats are removed from breeding areas by trapping or poisoning. Many of New Zealand's endemic bird, reptile and invertebrate species are restricted to rat free islands (e.g., South Island saddleback, *Philesturnus carunculatus carunculatus*). There is an emphasis on eradicating rats from more islands for ecological restoration and the translocation of threatened species (Veitch and Bell, 1990; Taylor and Thomas, 1993).

*The Threat of Rodent Invasion on Rodent Free Islands.* Some offshore islands that have been cleared of rats and mice are often visited by boats (e.g., Tiritiri Matangi, an open sanctuary; Craig, 1990), and more islands may receive an increasing number of visitors in the future (Wace, 1986; O'Connor and Simmons, 1990). Every boat that visits a rat free island, and every shipwreck, represents a threat of reinvasion, probably by mice, Norway rats, or the more arboreal ship rat. Ship rats apparently caused the extinction of five species of native land bird, the decline of four other bird species and the greater short-tailed bat (*Mystacina robusta*), and probably the extinction or decline of many invertebrates when they reached the previously rat free Big South Cape Island (off Stewart Island) in 1962 or 1963. The extinctions had occurred within three years of their arrival (Innes, 1990). Wace (1986) concluded that ship rats had been more destructive to bird life on islands than the larger Norway rat, and that more research was needed to help detect the arrival of both species on rat-free islands quickly and to prevent rat invasions.

*Rodent Control.* Introduced rodents are widespread and pose a barrier to the effective conservation of New Zealand's endemic biota because they eat native plants, seeds, invertebrates and vertebrates (Atkinson, 1978; Moors, 1990; Innes, 1990). Thus they may act as predators, competitors, or both for native species in the New Zealand landscape. Rats are conservation pests mainly on oceanic islands (Atkinson, 1985), although they may also compete with native species on continents (Goodyear, 1992). In continental locations, Norway rats are the predominant species and are regarded as pests because they compete with humans for food and carry disease (Berdoy and Smith, 1993). Ship rats represent the biggest rodent problem for conservation on the main islands of New Zealand because they are widespread in forests and readily climb trees (Innes, 1990). Mice may affect native species, especially after ship rat control, when mouse numbers can increase markedly (Innes et al., 1995). The other rodent species may have significant effects on islands where ship rats are not found (e.g., Lovegrove, 1996).

New Zealand's Department of Conservation manages rat populations in two ways: firstly by periodic large scale poisoning, usually during winter and spring, on the main islands (Innes et al., 1995) and secondly, by eradicating rats from offshore islands and trying to prevent their recolonisation.

During winter and spring, rat numbers are low and native birds are beginning to breed. Large scale poison operations at this time often target more than one species (e.g., possums (*Trichosurus vulpecula*) and ship rats), or attempt to maximise the benefits by secondarily poisoning mustelids (Murphy et al., 1998). These poisoning operations have used both aerial drops and poison-filled bait stations (Innes et al., 1995). The aim of these operations is to lower the density of predators during the breeding season of native species and thereby enhance recruitment of young animals at a stage in their life history when they are vulnerable to predation. With improved navigational technology (e.g., Global positioning systems, GPS), large areas of the main islands can be effectively poisoned with second-generation anticoagulants. The main advantage of GPS is that it allows pilots to know with a reasonable degree of certainty that they have covered the whole management area and that a reliable amount of poison has been distributed per unit area. This means that no pockets of land are excluded from poisoning and thus able to act as refugia. Some of these large areas of the main islands are the focus of sustained pest control efforts for all introduced vertebrates, using a variety of techniques and poisons. These areas have become known as “Mainland islands” (Saunders, 1990). Current rat population control by the Department of Conservation relies on this large scale poisoning. New technologies to help control rats are always required since large scale poisoning of this kind only temporarily reduces rat numbers (Innes, 1995) and also kills non-target native species (Spurr, 1979 and 1991). The use of 1080 (sodium monofluoroacetate) as a poison is also controversial because: (a) more non-target bird species are killed when using 1080 to control possums than when trapping or cyanide poisoning are used, and (b) concerns about public health risks of 1080 have not been allayed (Spurr, 1991; Eason et al., 1992; Gough, 1994; Stewart et al., 1994). This has resulted in a high level of publicity and the formation of lobby groups to protest against the use of 1080 in public reserve land and near water supplies. Most seriously, the long term use of second-generation poisons will probably cause rats to evolve resistance by altering either their behaviour, habitat use or physiology as they did in Britain to the first-generation poison Warfarin (Berdoy and Smith, 1993). Second-generation poisons are considered an advance because of their delayed action. Delayed poisoning allows an animal to ingest more than a lethal dose before feeling the first toxic effects (Taylor and Thomas, 1989). This means it is more difficult for animals to develop learned aversions to bait, but changes in habitat use or physiology could still allow rat populations to evolve resistance. In the medium to long term, a variety of techniques are needed to help control rodent populations and thus avoid reliance on a single method that may become less effective over time.

Rat eradication on offshore islands initially relied on bait stations (Taylor and Thomas, 1989; Taylor and Thomas, 1993), but more recently have also relied on helicopters or fixed wing aircraft distributing baits over large areas using GPS navigational equipment. These techniques have been very successful in eradicating rats from islands (Veitch and Bell, 1990) and reducing rat numbers on the main islands (Innes et al., 1995).

With improved monitoring (e.g., King and Edgar, 1977) and poisoning methods (e.g., Taylor and Thomas, 1993; Innes et al., 1995; I. McFadden, Department of Conservation, Auckland, pers. comm.), larger islands are becoming realistic candidates for eradication. New Zealand is at the forefront of rat eradication technology, with many other island nations adopting our techniques (Innes, 1992; T. Casey, United States Geological Survey, Biological Resources Division, Hawaii and I. McFadden, Department of Conservation, Auckland, New Zealand, pers. comm.). Kapiti island (1965 ha) is the largest island where a rodent eradication has been attempted to date (in September 1996; Towns and Ballantine, 1993; R. Empson, Department of Conservation, Wellington, pers. comm.) and had the complicating factors of having two sympatric species (Norway rats and kiore) and multiple landowners. In order to contemplate such an operation, a detailed knowledge of rat ecology was required. I present the results of a five year trapping study designed to characterise the habitat of each rat species and determine the productivity of each species in different habitats in this thesis (Chapter 2).

*Competition and Other Interactions between Rodents.* Interactions between rodents have been widely studied, with the studies falling into one of two broad categories: (1) those concerned with intraspecific behaviours that might affect pest control efforts, particularly feeding habits (Laland and Plotkin, 1991; Galef, 1993; Taylor and Thomas, 1993; Natynczuk and MacDonald, 1994; Galef and

Buckley, 1996), and (2) those that look at microhabitat use and interspecific interactions to explain sympatry of morphologically similar species, (e.g., Goodyear, 1992; Jorgensen et al., 1995; Krasnov and Khoklova, 1996; Morris, 1996; Goldingay and Price, 1997; Tomblin and Adler 1998). The first group have often used laboratory (Norway) rats in small experimental arenas (Galef, 1993; Natynczuk and MacDonald, 1994; Galef and Buckley, 1996) and some authors have assumed that results from laboratory animals will apply to wild rats, but this seems unlikely (Shepherd and Inglis, 1993). Surprisingly few authors (but see Berdoy and MacDonald, 1991; Fenn and MacDonald, 1995, and Buckle et al., 1997) have looked at intraspecific behavioural interactions of pest rodents in the wild, despite the obvious importance of a knowledge of rodent habitat use and behaviour when planning rodent control strategies. Despite the likelihood that the presence of one species will influence other species, even fewer authors have investigated microhabitat use and interspecific interactions of free-living pest species (Goodyear, 1992; King et al., 1996).

In studies of the microhabitat use by sympatric rodents, the study animals have usually been indigenous species, sometimes not from the genus *Rattus*. For example, Goodyear (1992) demonstrated high spatial niche overlap between ship rats and endangered native rice rats (*Orozomys argentatus*) in Florida. In only two published studies that I am aware of, have authors looked at behavioural interactions between introduced species (Storer, 1962; McCartney and Marks, 1973). Storer (1962) and colleagues completed a three year study of rat ecology (principally ship rats and kiore, but also Norway rats and mice) in Micronesia and also conducted trials where ship rats and kiore were placed in the same pens to observe their interactions. McCartney and Marks (1973) observed mixed colonies of Polynesian and ship rats from the Marshall Islands in enclosures. Under these conditions, McCartney and Marks found that Polynesian rats (kiore) became subordinate to ship rats and they hypothesised that in areas of sympatry, reproduction by Polynesian rats would be affected, perhaps leading to exclusion by ship rats. Ship rats and kiore do coexist on some New Zealand islands and elsewhere (Storer, 1962; Atkinson and Moller, 1990; Burwash et al., 1998), but little is known about their ecology on these islands.

While there has been much speculation about interactions between the introduced rodents in New Zealand, in part because all four species do not coexist anywhere here (Watson, 1961; Taylor, 1975; Taylor 1984), there has been limited research in New Zealand on how any of the species might interact behaviourally where they are sympatric. Both studies to date - Dick's (1985) unpublished thesis on the coexistence of kiore and Norway rats on Kapiti Island and Sturmer's (1988) unpublished thesis on the coexistence of kiore, ship and Norway rats on Stewart Island - used trapping studies to infer habitat use of sympatric species and to examine diet to discover niche overlap. Interpretations from such studies are limited because different species probably differ in their trappability (King et al., 1996; King and Moller, 1997) and animals may exclude others from traps. Furthermore, neither author measured the availability of food resources, nor were they able to suggest what limiting factors might act on species that are sympatric to reduce the success of the poorer competitor.

*Olfaction and the Assessment of Predation Risk by Rodents.* Predation is a major selective force in the evolution of animals morphology, physiology, behaviour and life history traits (reviewed by Lima and Dill, 1990, and Kats and

Dill, 1998). Indeed predation has been suggested to account for the disjunct distribution patterns and population dynamics of rodents in New Zealand (Watson, 1961; Taylor, 1984). In behavioural terms, animals may trade-off the risk of predation against feeding or mating. The risk of predation may also be of more importance to animals than any effects of competition (Abramsky et al., 1998). Wild Norway rats in England have been shown to avoid foraging when the risk of predation by red foxes (*Vulpes vulpes*) is high (Fenn and MacDonald, 1995). Furthermore many mammals show an avoidance of predator odours (Dickman and Doncaster, 1984; Jedrzejewski and Jedrzejewska, 1990; Jedrzejewski et al., 1993; Nolte et al., 1994), or decreased feeding on food contaminated with carnivore odours (Sullivan et al., 1985; Heale and Vanderwolf, 1994; Coulston et al., 1993; Mason et al., 1994). Avoidance of mating and a decrease in activity (Ylonen and Ronkainen, 1994), or avoidance of tainted traps (Dickman, 1992; Tobin et al., 1995) have also been recorded in the presence of predators or their odours. Much of this research has been conducted on voles (*Microtus* and *Clethrionomys* spp.). Voles are ideal for such studies because it has been estimated that around 99% of British field voles (*M. agrestis)* born each year are eaten by predators (Dyczkowski and Yalden, 1998). Hence predator avoidance responses would be highly advantageous to voles. Recently some of the studies investigating vole responses to predator odours have been criticised because they have not employed suitable control odours (Mappes et al., 1998). More recent work has failed to demonstrate avoidance of predator contaminated sites or predator-induced breeding suppression in voles, and it now appears likely that early spurious results were due to an artifact of the testing situation (Wolff and Davis-Born, 1997; Mappes et al., 1998).

It remains unknown how important predation is as a selective force for rats and mice. Nonetheless, laboratory rats and mice also show a variety of responses to predator odours including avoidance, freezing, increased defensive behaviours, less time spent in social interactions, physiological arousal, analgesic response, increased vigilance and the inhibition of vocalisations (see Kats and Dill, 1998, for a review). While these behaviours have been documented in laboratory rats and mice, there have been few tests using wild animals that presumably have experience of predators (but see Dickman, 1992; Fenn and MacDonald, 1995, and Burwash et al., 1998). Some authors that have tested wild animals in the presence of predator odours have concluded that animals avoid predators, including those they were unfamiliar with (Burwash et al., 1998). One study that used predator-experienced and predator-naïve mice concluded that the response was learned rather than innate, and unfamiliar odours were not avoided (Dickman, 1992). This was supported by Krasnov and Khoklova (1996) who concluded that the avoidance of jird (*Meriones meridianus*) odours by mice was not innate either. Jirds are desert gerbils that compete with mice in semi-arid grasslands where they coexist.

*The Basis of Rat Olfaction.* Because rats are nocturnal, they could be expected to be under considerable selection pressure to detect predators via cues other than visual ones (Kats and Dill, 1998). Indeed, odours do seem to have great significance to rats and mice for several reasons. Odours function to provoke sexual behaviour (Natynczuk and MacDonald, 1994) and to provide social information about individuals (Hurst and Barnard, 1995; Kavaliers and Colwell, 1995). Odours may allow individual recognition (Gheusi et al., 1997), and may also convey information about foraging sites and what foods are "safe" (Galef, 1993; Galef, 1994; Galef and Buckley, 1996).

The general features of the olfactory system are consistent across all vertebrate groups (Eisthen, 1997). Olfactory systems tend to be highly sensitive; often only very low odour concentrations are required for detection, but despite this sensitivity, habituation to familiar odours is rapid (Nef, 1998). Vertebrates detect odour molecules using a layer of pseudostratified sensory neuroepithelium that is bathed in mucus and located inside the nasal cavity. The epithelium is made up of three main cell types: the olfactory neurons, the supporting cells and the stem cells. The olfactory neurons are bipolar and end in cillia or microvilli that are bathed in the mucus. Intramembranous odour receptor proteins in the olfactory neurons detect odorants dissolved in the mucus and convert the odorous signal into an electrical one that projects directly to the olfactory bulb within the brain (Nef, 1998). Rodents have in the order of $10^6$ olfactory neurons (an order of magnitude more than humans; Nef, 1998), and presumably an acute sense of smell. As well as this main olfactory system, tetrapods possess another accessory olfactory system known as the vomeronasal system because the receptor organs are located in the vomeronasal (or Jacobsen's) organ (Eisthen, 1997). There are three other accessory olfactory systems including the terminal endings of the nervus terminalis, the nervus trigeminalis and the Septal organ of Rudolfo-Masera (Stoddart, 1980; Brown, 1985), but the function of these other accessory systems is unknown.

Portions of the olfactory bulb project into regions of the brain. In the rat, projections of the olfactory bulb have been traced to eight different regions of the brain including the anterior hippocampus (Eisthen, 1997). The vomeronasal system has projections into at least four regions of the rat brain (Eisthen, 1997). It appears, from studies on a range of vertebrates (reviewed in Eisthen, 1997), that the different projections from both regions may carry different sorts of information: the vomeronasal system is implicated in mediating responses to pheromones - both behavioural and physiological responses such as the Bruce effect and Vandenbergh effect - whilst the main olfactory system carries information about foraging and non-reproductive behaviours (Eisthen, 1997). The details of the relative role of the olfactory systems remain obscure (Eisthen, 1997).

Rats exposed to components of weasel (*Mustela erminea*) odour, red fox odour or toluene vapour exhibit fast wave oscillations in the dentate gyrus of the hippocampus of their brains. This response was unique to predator odours and was not observed when rats were exposed to other aversive odours or tail clamping (Heale et al., 1994). However, an intact hippocampus is not necessary for rats to show behavioural changes in response to predator odours (Perrot-Sinal and Petersen, 1997), so the exact location of the brain's processing of predator odours remains unknown.

Some prey species (mountain beaver *Aplodontia rufa*, house mice, deer mouse *Peromyscus maniculatus*, and guinea pig *Cavia porcellus*) were able to discriminate between the urine of coyotes (*Canis latrans*) fed on a meat diet and the urine of those fed on a vegetable diet. This ability indicates that it is probably the sulphurous compounds associated with meat digestion that are used as cues for detecting predators by potential prey, rather than individual species recognition (Nolte et al., 1994). Therefore, one could predict that rats should generalise avoidance responses to predatory animals they have never encountered as long as such sulphurous cues are present.

*Research Objectives.* My primary aim was to conduct experiments to determine the nature and magnitude of the interactions between rodents that live in New Zealand. I was especially interested in those interactions that might affect efforts to control or monitor wild rodent populations. Knowledge of rodent ecology and behaviour in areas of sympatry is necessary to increase our ability to remove rats from offshore islands and control rats effectively and efficiently on the main islands. Better control of rodents will ensure better protection for native species. Hence this research is particularly valuable to wildlife managers. Knowledge of this kind also contributes more generally to an understanding of the evolution of rodent behaviour and an understanding of competition and sympatry of similar species. To achieve this, I had three objectives: (1) to describe the habitat use of two species of rat living on Kapiti Island; (2) to investigate the interactions between species in a laboratory setting; and (3) to determine whether rats avoid predator odours, and whether this could be used as a management tool to repel rats. Each of these objectives is explored more fully below.

*Objective One: To Describe Habitat use by Two Species of Rat Living on Kapiti Island.* Interspecific interactions are likely to affect control or eradication efforts, most obviously because one species may exclude the other from access to poison (at least initially). Interspecific interactions between rats have been little studied in New Zealand, or elsewhere, before. A knowledge of the demography and habitat use of rodents in different habitats is necessary to understand population dynamics of rodents in different areas and ultimately, to manage them efficiently. In order to understand how two species of rat coexisted on Kapiti and whether this coexistence would affect eradication attempts, the Department of Conservation snap trapped rats in different habitats on Kapiti and I collected environmental data at each trap site. I then related rat capture to the environmental variables. These results are presented in Chapter 2. As well as trapping, I used radio-telemetry to document habitat use by rodents in an area where both species were sympatric. Radio-tracking has the advantage that the rats are free to move around their home range and presumably to interact normally; they are also locatable at any time. Radio-tracking of two sympatric species of rodent has not been undertaken in New Zealand before and I expected it to provide information on both temporal and spatial home range use to determine whether or not interspecific overlap occurred.

*Objective Two: Determining Interactions between Species in the Laboratory.* Anecdotal evidence had suggested that kiore might avoid bait stations used by Norway rats (C.R. Veitch, Department of Conservation, Auckland, pers. comm.) and live traps that had been previously occupied by Norway rats (G.N. Bramley, pers. obs.). This avoidance, if it existed, was presumably mediated by odours alone. The avoidance of heterospecific rat odour by kiore is tested for the first time here. I investigated the response of rats to the odour of other rats (both conspecifics and heterospecifics) in a Y-shaped maze, and the results of these experiments are presented in Chapter 3. If rats respond to heterospecifics using odour cues then this will have a bearing on their management, since the same traps or bait stations might not be suitable for both species. A knowledge of whether or not rats respond to odours could also form the basis for more detailed studies on rat interactions.

When ship rats are removed from a forested area, the number of mice tracked in tracking tunnels increases (Clout et al., 1995; Innes et al., 1995; Miller and Miller, 1995; Brown et al., 1996). There are at least two alternative hypotheses for this. One is that mice avoid ship rats and when rats are removed, mice alter their home range in such a way they are more detectable. The other is that when rats are removed, mice increase in number by immigration, reduced mortality and/or reproduction. In order to distinguish between these competing hypotheses, and to understand more about the interactions between the two most common rodents in New Zealand, I conducted three experiments. This is the first time this interaction has been studied in the laboratory and the results are presented in Chapter 4. Mice are not currently the focus of control efforts in New Zealand ecosystems. If it appears that mice adversely affect native species, they will need to be controlled. Because ship rats and mice coexist in many locations, an understanding of how rats and mice interact will be required to allow efficient management of both species simultaneously. This understanding may also help explain the evolution of antipredator responses by mice, since rats may eat mice.

*Objective Three: Determining Whether Rats Avoid Predator Odours.* If wild rats in New Zealand could be shown to reliably avoid predator odours, conservation managers could use predator odours as part of a suite of control methods, including poisoning and trapping, to protect rare species or islands from reinvasion via docking boats. Odours of mustelids have been tested as potential lures for attracting these carnivores to traps (Clapperton et al., 1989), although the results were equivocal. Because it is important that mustelids or other predators not be attracted to conservation areas, smells of predators not found in New Zealand are the best candidates for rodent management, if rats will avoid them. The hypothesis that rats might avoid predators, and that that aversion might be innate and generalised to unfamiliar predators, formed the basis for my experiments detailed in Chapters 5 and 6. By using wild caught animals from islands (with and without predators) in laboratory tests, I was able to avoid any effects of captive breeding (Ralls and Meadows, 1993) but not any effects due to captivity (Ward et al., 1996), hence it was necessary to conduct a field trial (Chapter 6). By testing rats against familiar and unfamiliar predators, I was also able to see if avoidance responses were generalised to other predators. This is the first study to: (a) use wild rats of more than one species tested according to the same method and, (b) use more than one type of experimental situation to provide information on the evolution and importance of olfaction in assessing predation risk. These data contribute to the body of work on the evolution of antipredator responses. I am also able to recommend whether or not predator odours would be useful as part of a suite of techniques to control rodents in New Zealand and elsewhere.

*Format of this Thesis.* Chapters 2-6 are each written as separate papers for publication, thus there is some unavoidable overlap of material presented in each chapter. Each chapter is a discrete unit and has its own abstract and reference section. These chapters are formatted to meet the requirements of the *Journal of Chemical Ecology* although, to save paper, they are presented here as double-sided text. I have also included with each chapter a list of co-authors that have contributed to the research. Chapter 2 includes a section on radio-tracking that was designed and conducted by me. It also includes a section on rat trapping, which was initiated and designed by Raewyn Empson and Colin Miskelly. Julie Alley, Tertia Thurley and Nic Gorman did most of the snap trapping. Collection of the vegetation data was suggested by C.M. King's study at Pureora (King et al., 1996) and conducted by myself and Catherine Beard. Bruce Burns and Mark Kimberley contributed significantly to the direction of the analysis, but I did the analyses myself. For Chapters 3-6, I conducted all of the experimental work. Chapter 3 was designed in consultation with Jane Andrew (a statistician) and conducted and analysed by me. C.M. King and John Innes helped me design the experiments that make up Chapter 4. Joe Waas and Jane Andrew helped design the experiments described in Chapter 5 and Harold Henderson analysed some of the results. Joe Waas also helped design the experiments in Chapter 6. I am responsible for all errors throughout.

## REFERENCES

ABRAMSKY, Z., ROSENWEIG, M.L., and SUBACH, A. 1998. Do gerbils care more about competition or predation? *Oikos* 83:75-84.

ALLEN, H.H. 1961. Flora of New Zealand: Volume I. Government Printer, Wellington, New Zealand.

AMARASEKARE, P. 1994. Ecology of introduced small mammals on Western Mauna Kea, Hawaii. *J. Mamm.* 75:24-38.

ATKINSON, I.A.E. 1978. Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands, pp. 7-30, *in* P.R. Dingwall, I.A.E. Atkinson, and C. Hay (eds.). The Ecology and Control of Rodents in New Zealand Nature Reserves. Department of Lands and Survey Information Series 4.

ATKINSON, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, pp. 35-81, *in* P.J. Moors (ed.). Conservation of Island Birds. International Council for Bird Preservation Technical Publication No. 3.

ATKINSON, I.A.E., and MOLLER, H. 1990. Kiore, pp. 175-192, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

BERDOY, M., and MACDONALD, D.W. 1991. Factors affecting feeding in wild rats. *Acta Oecolog.* 12:261-279.

BERDOY, M., and SMITH, P. 1993. Arms race and rat race: Adaptations against poisoning in the brown rat. *Rev. Ecol. (Terre Vie)* 48:215-228.

BOOTH, A.M., MINOT, E.O., FORDHAM, R.A., and INNES, J.G. 1996. Kiore (*Rattus exulans*) predation on the eggs of the Little Shearwater (*Puffinus assimilis haurakiensis*). *Notornis* 43:147-153.

BROWN, R.E. 1985. The Rodents I.: Effects of odours on reproductive physiology (primer effects), pp. 245-344, *in* R.E. Brown and D.W. MacDonald (eds.). Social Odours in Mammals: Volume One. Oxford University Press, Oxford, United Kingdom.

BROWN, K.P., MOLLER, H., INNES, J.G., and ALTERIO, N. 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. *N.Z. J. Ecol.* 20:271-275.

BUCKLE, A.P., CHIA, T.H., FENN, M.G.P., and VIVASALINGHAM, M. 1997. Ranging behaviour and habitat utilisation of the Malayan wood rat (*Rattus tiomanicus*) in an oil palm plantation in Johore, Malaysia. *Crop Protect.* 16:467-473.

BURWASH, M.D., TOBIN, M.E., WOOLHOUSE, A.D., and SULLIVAN, T.P. 1998. Laboratory evaluation of predator odours for eliciting an avoidance response in roof rats (*Rattus rattus*). *J. Chem. Ecol.* 24:49-66.

CLAPPERTON, B.K., MINOT, E.O., and CRUMP, D.R. 1989. Scent lures from the anal sac secretions of the ferret *Mustela furo* L. *J. Chem. Ecol.* 15:291-308.

CLOUT, M.N., DENYER, K., JAMES, R.E., and MCFADDEN, I.G. 1995. Breeding success of New Zealand pigeons (*Hemiphaga novaeseelandiae*) in relation to control of introduced mammals. *N.Z. J. Ecol.* 19:209-212.

COULSTON, S., STODDART, D.M., and CRUMP, D.R. 1993. Use of predator odors to protect chick-peas from predation by laboratory and wild mice. *J.Chem. Ecol.* 19:607-612.

CRAIG, J.L. 1990. Potential for ecological restoration of islands for indigenous fauna and flora, pp. 156-165, *in* D.R. Towns, I.A.E. Atkinson, and C.H. Daugherty, (eds.). Ecological Restoration of New Zealand Islands. Conservation Sciences Publication No. 2. Department of Conservation, Wellington, New Zealand.

DICK, A.M.P. 1985. Rats on Kapiti Island. Coexistence and diet of *R. norvegicus* (Berkenhout) and *R. exulans* (Peale). Unpublished MSc. thesis, Massey University, Palmerston North, New Zealand.

DICKMAN, C.R. 1992. Predation and habitat shifts in the house mouse, *Mus domesticus*. *Ecology* 73:313-322.

DICKMAN, C.R., and DONCASTER, C.P. 1984. Responses of small mammals to red fox (*Vulpes vulpes*) odour. *J. Zool. (London)* 204:521-531.

DYCZKOWSKI, J., and YALDEN, D.W. 1998. An estimate of the impact of predators on the British field vole (*Microtus agrestis*) population. *Mamm. Rev.* 28:165-184.

EASON, C.T., WRIGHT, G.R., and FITZGERALD, H. 1992. Sodium monofluoroacetate (1080) water-residue analysis after large-scale possum control. *N.Z. J. Ecol.* 16:47-48.

EISTHEN, H.L. 1997. Evolution of Vertebrate Olfactory Systems. *Brain Behav. Evol.* 50:222-233.

FENN, M.G.P., and MACDONALD, D.W. 1995. Use of middens by red foxes: risk reverses rhythms of rats. *J. Mamm.* 76:130-136.

FITZGERALD, B.M., DANIEL, M.J., FITZGERALD, A.E., KARL, B.J., MEADS, M.J., and NOTMAN, P.R. 1996. Factors contributing to fluctuations in house mouse (*Mus musculus*) populations in hard beech (*Nothofagus truncata*) forest. *J. Roy. Soc. N.Z.* 26:237-249.

GALEF, B.G. 1993. Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission. *Anim. Behav.* 46:257-265.

GALEF, B.G. 1994. Olfactory communications about foods among rats: a review of recent findings, pp. 83-101, *in* B.G. Galef, M. Mainardi, and P. Valsecchi (eds.). Behavioral Aspects of Feeding: Basic and Applied Research in Mammals. Harwood Academic Publishers, Chur, Switzerland.

GALEF B.G., and BUCKLEY, L.G. 1996. Use of foraging trails by Norway rats. *Anim. Behav.* 51:765-771.

GHEUSI, G., GOODALL, G., and DANTZER, R. 1997. Individually distinctive odours represent individual conspecifics in rats. *Anim. Behav.* 53:935-944.

GOODYEAR, N.C. 1992. Spatial overlap and dietary selection of native rice rats and exotic black rats. *J. Mamm.* 73:186-200.

GOLDINGAY, R.L., and PRICE, M.V. 1997. Influence of season and a sympatric congener on habitat use by Stephen's Kangaroo rat. *Conserv. Biol.* 11:708-717.

GOUGH, J. 1994. Risk communication and risk management, pp. 39-44, *in* A.A. Seawright, and C.T. Eason (eds.). Proceedings of the Science Workshop on 1080. The Royal Society of New Zealand, Miscelaneous Series 28.

HEALE, V.R., VANDERWOLF, C.J., and KAVALIERS, M. 1994. Components of weasel and fox odors elicit fast wave bursts in the dentate gyrus of rats. *Behav. Brain Res.* 63:159-165.

HEALE, V.R., and VANDERWOLF, C.J. 1994. Toluene and weasel (2-propylthietane) odors suppress feeding in the rat. *J. Chem. Ecol.* 20:2953-2958.

HEATHER, B.D., and ROBERTSON, H.A. 1996. The field guide to the birds of New Zealand. Viking publishers, Auckland, New Zealand.

HOLDAWAY, R. 1996. Arrival of rats in New Zealand. *Nature* 384:225-226.

HURST, J.L., and BARNARD, C.J. 1995. Kinship and social tolerance among female and juvenile wild house mice: kin bias but not kin discrimination. *Behav. Ecol. Sociobiol.* 36:333-342.

INNES, J.G. 1990. Ship rat, pp. 206-225, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

INNES, J.G. 1992. An introduction to rodents in New Zealand, pp. 29, *in* C.R. Veitch, B.M. Fitzgerald, J.G. Innes, and E.C. Murphy (eds.). Proceedings of the National Predator Management Workshop. Threatened species Occasional Publication No. 3. Department of Conservation, Wellington, New Zealand.

INNES, J.G., and HAY J.R. 1991. The interactions of New Zealand forest birds with introduced fauna. *Acta XX IOC Vol. IV*: 2523-2533. New Zealand Ornithogical Congress Trust Board, Wellington, New Zealand.

INNES, J.G., WARBURTON, B., WILLIAMS, D., SPEED, H. and BRADFIELD, P. 1995. Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *N.Z. J. Ecol.* 19:5-17.

JEDRZEJEWSKI, W., and JEDRZEJEWSKA, B. 1990. Effect of a predator's visit on the spatial distribution of bank voles. *Can. J. Zool.* 68:660-666.

JEDRZEJEWSKI, W., RYCHLIK, L., and JEDRZEJEWSKA, B. 1993. Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. *Oikos* 68:251-257.

JORGENSEN, E.E., DEMARAIS, S., and NEFF, S. 1995. Rodent use of microhabitat patches in desert arroyos. *Am. Midl. Nat.* 134:193-199.

KATS, L.B., and DILL, L.M. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361-394.

KAVALIERS, M., and COLWELL, D.D. 1995. Odours of parasitized males induce aversive responses in female mice. *Anim. Behav.* 50:1161-1169.

KING, C.M. 1982. Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*) in relation to seed fall of southern beech. *N.Z. J. Zool.* 9:467-480.

KING, C.M. 1983. The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *J. Anim. Ecol.* 52:141-166.

KING, C.M. 1990. Editor. The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

KING, C.M., and EDGAR, R.L. 1977. Techniques for trapping and tracking stoats (*Mustela erminea*); a review and a new system. *N.Z. J. Zool.* 4:193-212.

KING, C.M., INNES, J.G., FLUX, M., KIMBERLEY, M.O., LEATHWICK, J.R., and WILLIAMS, D.S. 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *N.Z. J. Ecol.* 20:215-240.

KING, C.M., and MOLLER, H. 1997. Distribution and response of rats, *Rattus rattus* and *R. exulans,* to seedfall in New Zealand beech forests. *Pac. Conserv. Biol.* 3:143-155.

KRASNOV, B., and KHOKLOVA, I. 1996. Discrimination of midday jird's odour by house mice. *Anim. Behav.* 52:659-665.

LALAND, K.N., and PLOTKIN, H.C. 1991. Excretory deposits surrounding food sites facilitate social learning of food preferences in Norway rats. *Anim. Behav.* 45:997-1007.

LIMA, S.L., and DILL, L.M. 1990. Behavioral decisions made under the risk of predation: A review and a prospectus. *Can. J. Zool.* 68:619-640.

LOVEGROVE, T.G. 1996. A comparison of the effects of predation by Norway (*Rattus norvegicus*) and Polynesian rats (*R. exulans*) on the Saddleback (*Philesturnus carunculatus*). *Notornis* 43:91-112.

MACDONALD, D.W. 1984. Ed. The Encyclopedia of Mammals: 2. George Allen and Unwin, London.

MAPPES, T., KOSKELA, E., YLONEN, H. 1998. Breeding suppression in voles under predation risk of small mustelids: laboratory or methodological artifact? *Oikos* 82:365-369.

MASON, J.R., EPPLE, G., and NOLTE, D.L. 1994. Semiochemicals and improvements in rodent control, pp 327-346, *in* B.G. Galef, M. Mainardi, and P. Valsecchi (eds.). Behavioral Aspects of Feeding: Basic and Applied Research in Mammals. Harwood Academic Publishers, Chur, Switzerland.

MCCARTNEY, W.C., and MARKS, J. 1973. Inter and Intraspecific aggression in two species of the genus *Rattus*: evolutionary and competitive implications. *Proc. Pa. Acad. Sci.* 47:145-148.

MILLER, C.J., and MILLER, T.K. 1995. Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poison operation. *N.Z. J. Ecol.* 19:19-27.

MOORS, P.J. 1990. Norway rat, pp. 192-206, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

MORRIS, D.W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology* 77:2352-2364.

MURPHY, E.C. 1992. The effects of a natural increase in food supply on a wild population of house mice. *N.Z. J. Ecol.* 16:33-40.

MURPHY, E.C., CLAPPERTON, B.K., BRADFIELD, P.M.F., and SPEED, H.J. 1998. Effects of rat poisoning operations on abundance and diet of mustelids in New Zealand podocarp forests. *N.Z. J. Zool.* 25:315-328.

MURPHY, E.C., and PICKARD, C.R. 1990. House mouse, pp. 225-242, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

NATYNCZUK, S.E., and MACDONALD, D.W. 1994. Scent, sex, and the self-calibrating rat. *J. Chem. Ecol.* 20:1843-1857.

NEF, P. 1998. How we smell: the molecular and cellular bases of olfaction. *News Physiol. Sci.* 13:1-5.

NOLTE, D.L., MASON, J.R., EPPLE, G., ARANOV, E., and CAMPBELL, D.L. 1994. Why are predator urines aversive to prey? *J. Chem. Ecol.* 20: 1505-1516.

O'CONNOR, K.F., and SIMMONS, D.G. 1990. The use of islands for recreation and tourism: changing significance for nature conservation, pp.186-193, *in* D.R. Towns, I.A.E. Atkinson, and C.H. Daugherty (eds.). Ecological Restoration of New Zealand Islands. Conservation Sciences Publication No. 2. Department of Conservation, Wellington, New Zealand.

O'DONNELL, C.F.J., DILKS, P., and ELLIOTT, G.P. 1996. Control of a stoat, *Mustela erminea,* population irruption to enhance mohua (yellowhead), *Mohua ochrocephala,* breeding success in New Zealand. *N.Z. J. Zool.* 23:279-286.

PERROT-SINAL, T., and PETERSEN, K. 1997. Exposure to predator odor reduces locomotor activity levels in adult male rats: lack of effect of hippocampal lesion. *J. Chem. Ecol.* 23:2175-2186.

RALLS, K., and MEADOWS, R. 1993. Breeding like flies. *Nature* 361:689-690.

SAUNDERS, A. 1990. Mapara: island management "mainland" style, pp.147-149, *in* D.R. Towns, C.H. Daugherty, and I.A.E. Atkinson (eds.). Ecological Restoration of New Zealand Islands. Conservation Sciences Publication No. 2. Department of Conservation, Wellington, New Zealand.

SHEPHERD, D.S., and INGLIS, I.R. 1993. Toxic bait aversions in different rat strains exposed to an acute rodenticide. *J. Wildl. Manage.* 57:640-647.

SPURR, E.B. 1979. A theoretical assessment of the ability of bird species to recover from an imposed reduction in numbers, with particular reference to 1080 poisoning. *N.Z. J. Ecol.* 2:46-63.

SPURR, E.B. 1991. Effects of brushtail possum control operations on non-target bird populations. *Acta XX IOC* IV:2534-2545. New Zealand Ornithological Congress Trust Board, Wellington, New Zealand.

STEWART, H., JENKIN, B., MCCARTHY, R., and FLINN, D. 1994. Public versus user perceptions of risks and benefits of plantation forestry in Victoria, Australia, pp. 10-19, *in* A.A. Seawright, and C.T. Eason (eds.). Proceedings of the Science Workshop on 1080. The Royal Society of New Zealand, Miscellaneous Series 28.

STODDART, D.M. 1980. The Ecology of Vertebrate Olfaction. Chapman and Hall, London, United Kingdom.

STORER, T.I. 1962. Editor. Pacific Island rat ecology: Report of a study made on Ponape and adjacent islands 1955-1958. Bernice P. Bishop Museum Bulletin 225. Honolulu, Hawaii.

STURMER, A.T. 1988. Diet and coexistence of *Rattus rattus* (Linnaeus), *R. exulans* (Peale) and *R. norvegicus* (Berkenhout) on Stewart Island, New Zealand. Unpublished MSc. thesis. Massey University, Palmerston North, New Zealand.

SULLIVAN, T.P., NORDSTROM, L.O., and SULLIVAN, D.S. 1985. The use of predator odours as repellents to reduce feeding damage by herbivores. I. Snowshoe hares (*Lepus americanus*). *J. Chem. Ecol.* 11:903-919.

TAYLOR, R.H. 1975. What limits kiore (*Rattus exulans*) distribution in New Zealand? *N.Z. J. Zool.* 2:473-477.

TAYLOR, R.H. 1984. Distribution and interactions of introduced rodents and carnivores in New Zealand. *Acta Zool. Fenn.* 172:103-105.

TAYLOR, R.H., and THOMAS, B.W. 1989. Eradication of Norway rats (*Rattus* *norvegicus*) from Hawea Island, Fiordland, using Brodifacoum. *N.Z. J. Ecol.* 12:23-32.

TAYLOR R.H., and THOMAS, B.W. 1993. Rats eradicated from rugged Breaksea Island (170 ha), Fiordland, New Zealand. *Biol. Conserv.* 65:191-198.

TOBIN, M.E., ENGEMAN, R.M., and SUGIHARA, R.T. 1995. Effects of mongoose odors on rat capture success. *J. Chem. Ecol.* 21:635-639.

TOMICH, P.Q. 1986. Mammals in Hawaii: A synopsis and notational bibliography. Second edition. Bishop Museum Press, Honolulu, Hawaii.

TOMBLIN, D.C., and ADLER, G.H. 1998. Differences in habitat use between two morphologically similar tropical forest rodents. *J. Mamm.* 79:953-961.

TOWNS, D.R. 1991. Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: the kiore (*Rattus exulans*). *J. Roy. Soc. N.Z.* 21:119-136.

TOWNS, D.R., and BALLANTINE, W.J. 1993. Conservation and restoration of New Zealand island ecosystems. *Trends Ecol. Evol.* 8:452-457.

WACE, N.M. 1986. The rat problem on oceanic islands - research is needed. *Oryx* 20:79-86.

WARD, J.F., MACDONALD, D.W., DONCASTER, C.P., and MAUGET, C. 1996. Physiological response of the European Hedgehog to predator and non-predator odour. *Physiol. Behav.* 60:1469-1472.

WATSON, J.S. 1961. Rats in New Zealand: a problem of interspecific competition. *Proc. 9th Pacific Science Congress* 19:15-17.

WEBB, C.J., SYKES, W.R., and GARNOCK-JONES, P.J. 1988. Flora of New Zealand: Volume IV Naturalised pteridophytes, gymnosperms and dicotyledons. Botany Division, Department of Scientific and Industrial Research, Christchurch, New Zealand.

WHITAKER, A.H. 1978. The effects of rodents on reptiles and amphibians, pp. 75-86, *in* P.R. Dingwall, I.A.E. Atkinson, and C. Hay (eds.). The ecology and control of rodents in New Zealand nature reserves, Department of Lands and Survey Information Series 4.

WOLFF, J.O., and DAVIS-BORN, R. 1997. Response of grey-tailed voles to odours of a mustelid predator: a field test. *Oikos* 79:543-548.

VEITCH, C.R., and BELL, B.D. 1990. Eradication of introduced animals from the islands of New Zealand, pp. 137-146, *in* D.R. Towns, C.H. Daugherty, and I.A.E. Atkinson (eds.). The Ecological Restoration of New Zealand Islands. Conservation Sciences Publication No. 2. Department of Conservation, Wellington, New Zealand.

YLONEN, H., and RONKAINEN, H. 1994. Breeding suppression in the bank vole as an antipredatory adaptation in a predicatable environment. *Evol. Ecol.* 8:1-9.

# CHAPTER TWO: INTERSPECIFIC INTERACTIONS BETWEEN KIORE (*RATTUS EXULANS*) AND NORWAY RATS (*R. NORVEGICUS*) BEFORE AND DURING AN ERADICATION ATTEMPT ON KAPITI ISLAND, NEW ZEALAND.

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**Abstract** – Two rat species (*Rattus exulans* and *R. norvegicus*) coexisted on Kapiti Island (1965 ha) until 1996, when they were simultaneously eradicated from this New Zealand island. Between 1992 and 1996, we kill-trapped rats of both species in five different habitats (grassland and four different forest types) to investigate the coexistence of rats on Kapiti. We measured vegetation and microhabitat variables at each trap site and related rat capture to the local environment at each trap. We aimed to describe the associations between each

species of rat and the different habitats. We also quantified the demography and relative productivity of each species in each habitat to determine the distribution and success of rats over the whole island. This information was used in planning the eradication attempt. We also radio-tracked rats of both species from June 1996 until September 1996 when the first poison drop occurred. We aimed to describe the home range and habitat use of both species of rat in an area where they coexisted, and record any changes in habitat use that coincided with poisoning. From 12 202 corrected trap nights we collected 923 rats (391 Norway, 518 kiore, 14 unknown). On a broad scale, kiore were associated with dense, low growing vegetation in well drained, flat areas whilst Norway rats were associated with taller vegetation, growing in steeper areas that were poorly drained. The number of kiore captured varied with year, season and habitat. Kiore were most common in grassland and kanuka (*Kunzea ericoides*) forest. However, kiore were larger and produced more young per female in kohekohe (*Dysoxylum spectabile*) forest than in other forest types or in grassland. This suggests poor recruitment in kohekohe forest relative to other areas. Kiore showed seasonal breeding and most pregnant females were caught in summer. The capture of Norway rats also varied with year and habitat, but was unaffected by season. Norway rats reached similar sizes in different habitats and were equally productive in all habitats. Pregnant female Norway rats were captured in all seasons although few were caught in winter. Radio-tagged kiore occupied overlapping home ranges that varied from 26-89 m in diameter. Six male kiore used an average of 0.14 ha as a home range; females used 0.18 ha on average (n=5). Kiore were found in denser habitat that allowed less light to penetrate

than Norway rats. Norway rats occupied larger home ranges (218-916 m in diameter; average size of 5.78 ha for males (n=7) and 5.13 ha for a single female). Jacob's indices of habitat use indicated that kiore and Norway rats might avoid each other, despite the fact their home ranges overlapped. Following the drop of poison on 19-20 September 1996, rats' use of their home range did not appear to change until shortly before death. However, five rats were discovered lying dead in the open and two diurnally active rats were seen after the poison was spread, suggesting that some rats may have changed their normally secretive nocturnal behaviour. All nine rats carrying radio-transmitters when the poison was dropped died within 10 days of the poison operation. All dead animals recovered had eaten poison. One animal caught in a snap trap on 20 September had also eaten poison. Some Norway rats cached bait (a maximum of 65 g), but no caches were recorded from radio-carrying kiore. Eradication of rats (*Rattus* sp.) from offshore islands like Kapiti is required to allow translocation of threatened species and restoration of island ecosystems. Prior to 1996, eradication operations had only been successful on islands where one species of rat lived. The habitat use, morphology, interactions between species and management of rats on Kapiti Island are discussed.

**Key Words** – coexistence, interspecific interactions, habitat use, rodent management, poisoning, Talon®, Brodifacoum, eradication, Norway rat, Polynesian rat, *Rattus exulans*, *Rattus norvegicus*, Kapiti Island.

## INTRODUCTION

The three main islands of New Zealand (North, South and Stewart Islands) are surrounded by more than 700 smaller islands. Rodents (Genera *Rattus* and *Mus*) are some of the most commonly occurring exotic mammals on New Zealand's islands and many islands support more than one species (Atkinson and Moller, 1990). When two species of morphologically similar rodent coexist, it is likely that the presence of one will influence the ranging behaviour and habitat use of the other (Taylor, 1975; Dueser and Porter, 1986; Dickman, 1991; Ziv et al, 1993). Interspecific interactions have been suggested to account for the disjunct distribution of rodents in New Zealand via competitive exclusion (Watson, 1961; Taylor, 1975 and 1978), but have not been studied in New Zealand before. Exactly which species of rodents coexist on a particular island in New Zealand may be determined, in part, by the competitive interactions between species and the presence or absence of specialist mustelid predators (Taylor, 1984).

Kapiti Island is a nature reserve, and two species of rat existed there. We could not rule out the possibility of interspecific competition between populations of kiore (*R. exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island (Taylor, 1975 and 1978; Dick, 1985, unpubl.). Competition could influence the distribution and abundance of the two species on Kapiti (e.g. Taylor, 1978 and 1984), although we did not know what form any competitive interactions might take.

Intraspecific interactions are also likely to affect the behaviour of resident rodents (Summerlin and Wolfe, 1973; Drickamer, 1995 and 1997). Intraspecific interactions might be important in island rodent populations because they have unusually high densities compared with mainland populations (Gliwicz, 1980). These high densities could lead to increased interaction and competition. However, some authors have considered that the effects of intraspecific competition are reduced on islands (Gliwicz, 1980). This may be because, at high densities, maintaining the competition (e.g. by fighting or scent marking) reduces an individual's fitness (Gray and Hurst, 1998).

New Zealand's Department of Conservation (DoC) is re-establishing self-sustaining populations of certain endemic plant and animal species on offshore islands to protect them from introduced mammals on the main islands. For this to be successful, resident introduced mammals must first be removed in order to allow the successful translocation of rare species (Daugherty et al., 1990; Cowan, 1992). Rats eat native plants and animals and may compete with native species for food (Innes, 1990; Moors, 1990). Eradication of rats from islands is necessary for DoC to achieve its aims of environmental advocacy and protection of endemic and pseudo-endemic species (i.e., those species that once occurred on the main islands, but survive only on island refugia; Daugherty et al., 1990).

The successful eradication of Norway rats from small islands (up to 173 ha) in the late 1980s by poisoning using second-generation anticoagulants was a significant breakthrough in island management and restoration (Taylor and Thomas, 1989; Veitch and Bell, 1990; Towns and Ballantine, 1993). Second-generation anticoagulants kill after a single dose and show delayed side effects, so that rats consuming a sublethal dose do not develop bait aversion (Taylor and

Thomas, 1989). These early eradication efforts relied on poison being distributed in bait stations (Taylor and Thomas, 1993). After these successes, wildlife managers began speculating that eradication from larger islands might be achievable (Empson, 1992; Taylor and Thomas, 1993). Kapiti Island (40°51'S and 174° 56'E) is large (1965 ha), but was seen as a candidate for eradication because it had already been the subject of a successful possum eradication (Cowan, 1992) leaving rodents as the only introduced mammals to be found on the island. Rats were also preventing the establishment of translocated species such as saddleback, *Philesturnus carunculatus* (Lovegrove, 1996).

Kapiti Island represented a more difficult eradication problem than islands cleared of rodents by 1990, not only because of its size, but also because two rat species lived there. Both intra- and inter-specific interference could reduce bait availability to some rats on Kapiti. The effects of both are likely to be similar to intraspecific competition on Hawea and Breaksea Islands, where small Norway rats only got to feed at bait stations or caches once more dominant individuals had left or died (Taylor and Thomas, 1989 and 1993). Despite these intraspecific interactions, allopatric populations of each species had successfully been eradicated from smaller islands (McFadden and Towns, 1991; Taylor and Thomas, 1993). No eradication had been attempted to remove both species at once. It was not known how interspecific interactions between the large Norway rats and smaller kiore would affect an eradication attempt, particularly one that might rely on bait stations. Both competition and habitat use by resident rats are likely to affect an eradication attempt, but little was known about either factor on Kapiti Island. To overcome this lack of knowledge we snap-trapped rats on

Kapiti between 1992 and 1996. Our first two objectives were: (1) to characterise the habitat of each rat species, and (2) to quantify variation in productivity and abundance according to habitat, season and year. This information on rat ecology was required so that as knowledge advanced, the most appropriate eradication techniques could be applied at the most appropriate times and places to ensure the most cost effective eradication. The information was to be used in planning any future eradication attempt, once eradication was thought to be feasible.

By 1995, DoC managers considered that they had accumulated enough knowledge to attempt to eradicate rats from Kapiti Island. This provided us with a unique opportunity to monitor individual rodents through an eradication attempt and further our understanding of complex rodent management situations like the one described. Knowledge of individual rats' fates after the application of poison would also provide us with information that might help explain the outcome of the eradication if it failed. Detailed technical and procedural information about the eradication attempt and its monitoring will be published elsewhere (Empson and Miskelly, in press).

In order to increase the chances of success and decrease the costs of an eradication attempt, it is necessary to know how rats use their habitat. A knowledge of ranging behaviour is important so that bait stations can be placed where all rats will come into contact with them as soon as possible. As rats are removed during an eradication attempt, the home ranges of the remaining rats may expand (Taylor and Thomas, 1993). The possibility then arises that surviving rats will make use of food sources other than poison bait stations as their ranges, and presumably food resources, increase in size. This makes 'the last rat' the most difficult and costly to kill (Taylor and Thomas, 1989). This poses a problem when trying to eradicate two species of rat simultaneously because large individuals may, at least initially, control access to poison and exclude not only small individuals of the same species, but members of another species too. To investigate ranging behaviour by rats on Kapiti we tagged animals with radio transmitters. Our third objective, therefore, was to describe home ranges and habitat use by radio-carrying rats in an area where both species coexisted.

Our final objective was to determine the changes in habitat use and ranging behaviour that coincided with poisoning. Hooker and Innes (1995) showed that radio-carrying, poisoned ship rats did not change their ranging behaviour in broadleaf-podocarp forest on the North Island, but radio-tracking has not been used to study Norway rats or kiore before. If certain rats or species were able to avoid poison and expand their range this might explain observed differences in kill rate and this behaviour could be considered in planning future control or eradication efforts on other islands supporting more than one species of rat.

## METHODS

*Study Area.* Kapiti Island is approximately 5.2 km from the south-western coast of the North Island of New Zealand. Kapiti is approximately 9 km long, 2.3 km wide and reaches 521 m above sea level at its highest point. The western face of the island is steep, with exposed cliffs, but there are small areas of flat land along the eastern side of the island (Figure 1). Esler (1967) and Dick (1985, unpubl.) have described the geology, climate and history of the island. The prevailing winds come from the west and north-west.

Kapiti was designated a nature reserve in 1897. Since then cats (*Felis catus*), sheep (*Ovis aries*), pigs (*Sus scrofa*), goats (*Capra hircus*), cattle (*Bos taurus*), deer (*Axis axis* and *Dama dama*), and brushtail possums (*Trichosurus vulpecula)* have been eradicated from the island (Esler, 1967; Cowan, 1992). The island is home to a wide range of native birds and the native long-tailed bat, *Chalinolobus tuberculatus* (Daniel, 1990). Many native species have been introduced or re-introduced to the island including weka (*Gallirallus australis*), hihi (*Notiomystis cincta*), kokako (*Callaeas cinerea*) and brown teal (*Anas aucklandica*). Private owners retain 15 hectares at the north end of Kapiti; DoC controls the rest. Public access to the island has been restricted since 1949, permits to land are now issued by DoC. Kapiti's prime role is as a bird sanctuary (Esler, 1967). The island has been extensively modified by burning and human occupation (for farming and as a whaling base) in the past, but is now covered by a variety of regenerating forest types (Esler, 1967; Atkinson, 1992).

*Rat Distribution and Abundance.* In 1992, we decided to undertake a monitoring programme of the rodents on Kapiti using a standardised procedure, similar to that of Cunningham and Moors (1983). Snap-trap index lines are a standardised method for the regular sampling of rodents in the same habitat (Cunningham and Moors, 1983). The method has been widely used to obtain information on the distribution and abundance of rodents in New Zealand (e.g., King et al., 1996), but has apparently not been adopted internationally. Index trapping enables an index of abundance to be calculated, which can be used to compare populations in different areas. Eight trapping lines were established in July and September 1992. Trapping began in October 1992 to provide information on rat distribution, abundance, population structure, breeding and habitat use. The trapping lines were distributed from sea level to the summit of the island in a range of habitat types (Figure 1; Table 1). The eight index lines were established so that all major habitat types on the island, identified by Fuller (1985), were represented. Traps were spaced at 25 m intervals on seven of the lines and 50 m on one of the lines (line 6). Line 6 passed through the centre of an area where the aerial application of baits was trialed in 1993 (described by Empson and Miskelly, in press). We did not want to deplete the number of resident rats and affect the outcome of this non-toxic trial operation, so we spaced the traps at 50 m intervals on this line. Line 8 (in the upper grassland) was divided into two shorter lines because there was not enough habitat at either location to have 35 traps spaced 25 m apart.

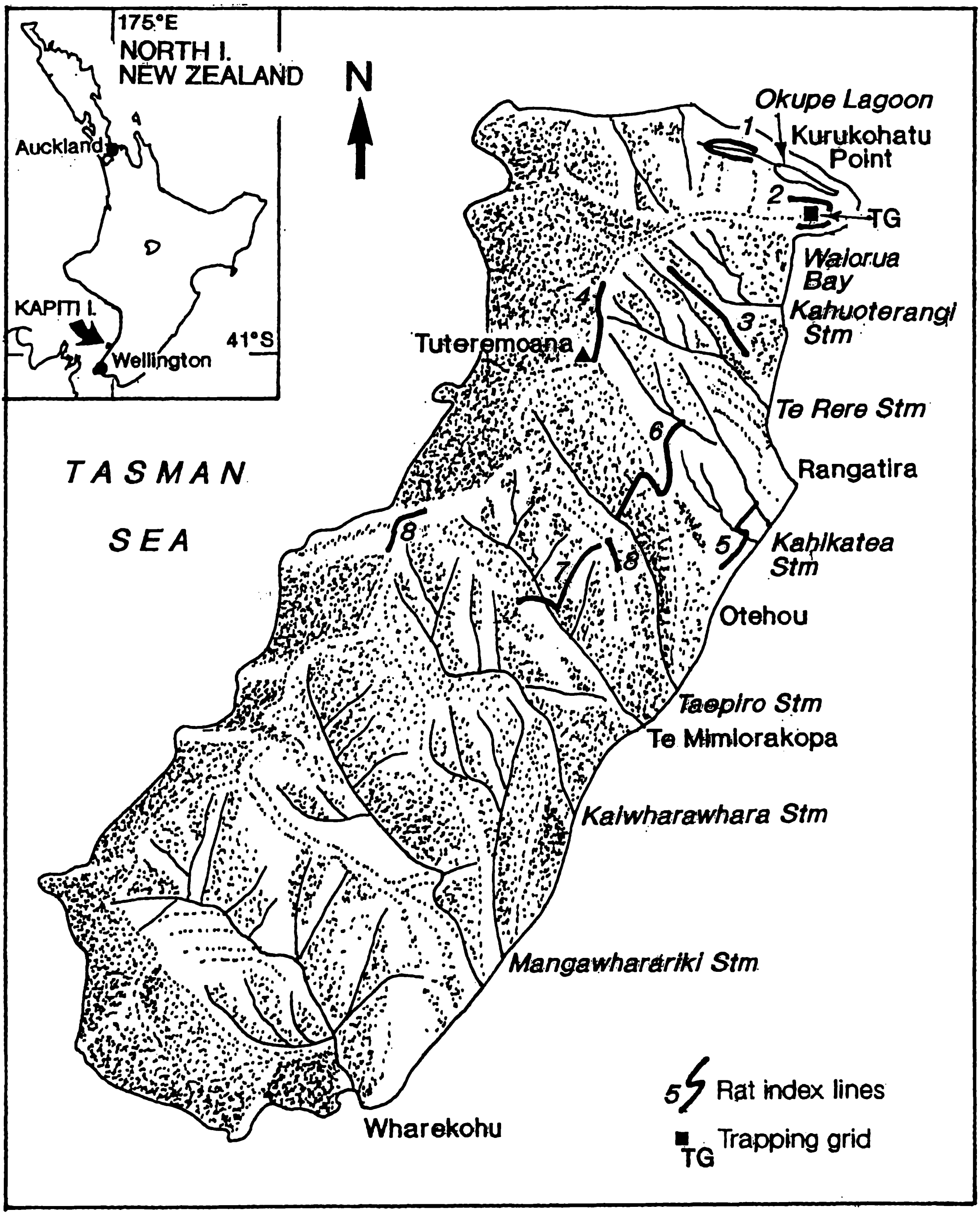


FIG. 1: Map showing location and topography of Kapiti Island, New Zealand, as viewed from the air. Modified from Esler (1967). Not drawn to scale.

TABLE 1: VEGETATION ON THE INDEX TRAPPING LINES, KAPITI ISLAND AS DESCRIBED BY FULLER (1985).

| Line | Vegetation Type | Characteristics |
|---|---|---|
| 1 | Kanuka (*Kunzea ericoides*) forest with a dense canopy and sparse understory of *Coprosma*, *Pseudopanax arborea* and *Olearia paniculata* (akiraho). | Sparse ground cover of *Carex*, *Uncinia* and ferns. Kanuka forest covers 22% of Kapiti. |
| 2 | Coastal shrub/grassland. Rank grass dominated the vegetation with sparse *Coprosma propinqua*, *Cassinia leptophylla* and *Muehlenbeckia*. | The plants are growing in very shallow soils over shingle and boulders. About 15.5% of Kapiti remains in grassland or shrub/grassland, although most of this is on the Western Cliffs. |
| 3 | Diverse young forest with dominant fivefinger (*Pseudopanax arborea*) and common kanuka, hinau (*Elaeocarpus dentatus*), rewarewa (*Knightia excelsa*), tawa (*Beilschmiedia tawa*) and kohekohe (*Dysoxylum spectabile*). | Line 3 was located on a ridge between Te Rere and Te Kahuoterangi catchments (Figure 1). Fivefinger forest covers 25% of Kapiti. |
| 4 | Tawa/hinau forest with other common canopy species being mahoe (*Melicytus ramiflora*), rewarewa, fivefinger and kamahi (*Weinmannia racemosa*). | Line 4 was on the summit ridge, north of the trig. |
| 5 | Diverse forest with dominant fivefinger. kohekohe, akiraho, and lancewood (*Pseudopanax crassifolia*) were also common. | Line 5 was located in the middle of the island (Figure 1). |
| 6 | Mid-altitude tawa/hinau forest with rewarewa, toro (*Myrsine salicina*), matai (*Prumnopitys taxifolia*) and miro (*P. ferruginea*). | The long transect (traps 50 m apart) between Kahikatea and Te Rere catchments. |
| 7 | An almost pure canopy of kohekohe with pukatea (*Laurelia novae-zelandiae*) near streams. | Kohekohe covers about 15% of Kapiti. Line 7 was in the Te Mimi catchment. |
| 8 | Followed the cliff edge grassland at Te Mimi (25 traps) and the grassland around Seismometer Hut (10 traps, Figure 1). Te Mimi grassland is being succeeded by *Hebe*, *Urtica* and bracken. The grass around the hut was more open, with scattered *Hebe* and fivefinger. | The two grasslands were at similar altitude and had similar species, but neither was long enough to have all 35 traps at 25 m spacing. |

Each trapping line consisted of 35 Supreme "Ezeset" rat traps. Initially traps were covered with wire mesh, but there was a high level of interference with the traps by non-target animals. In July 1993 (on lines 4 and 6) and October 1993 (on the other lines), the mesh covers were replaced with aluminium trap covers to reduce this interference. The aluminium trap covers had wire mesh covering each end so that weka and other birds could not enter the traps. Trap covers were held down by two loops of wire embedded in the ground. Each site was marked by a numbered plastic tape, which was attached to adjacent vegetation or a wire marker. Each trap was tied to the trap cover to prevent it being dragged away. Rats were trapped in each season (in January (summer), April (autumn), July (winter) and October (spring)) between October 1992 and July 1996. Trapping was usually conducted in the middle weeks of these months. Thus our method was similar to that recommended by Cunningham and Moors (1983), but differed in that we trapped in different months and used only one trap at each site (rather than two). In addition, we usually spaced our traps more closely (25 m rather than 50 m) than recommended by Cunningham and Moors (1983). Traps were baited with a mixture of peanut butter and rolled oats. They were checked daily and all captures or sprung traps were recorded. Baits were replaced when an animal was caught or if the attractiveness of the bait was reduced (e.g., by hot weather, rain, or consumption by insects). Traps were set for three consecutive nights, so that each trapping line yielded about 100 trap nights per trapping session. One trapping session consisted of approximately 100 trap nights (after adjustment for captures and sprung traps) on each line, in each season of each year. Rats were autopsied as soon as possible after collection and then discarded. The trappers assigned rats an age class (juvenile or adult) based on the rats' body length and weight. Females with plugged vaginas and small males without scrotal testes or visible epididymal tubules were also classed as juveniles.

For the purposes of some analyses, lines were grouped into habitat types as described in Fuller (1985; Table 1). We assigned each habitat type a number as follows: 1=kanuka forest (line1); 2=grassland (lines 2 and 8); 3=fivefinger forest (lines 3 and 5); 4=tawa/hinau forest (lines 4 and 6); 5=kohekohe forest (line7).

*Description of Habitat.* We visited all trap sites in November 1996 to survey the plants present. We used a type of "reconnaissance" plot (Allen, 1992) that was roughly 10m in diameter and centred on the trap location to quantify the vegetation present. We recorded six height tiers: >15 m (emergent); 12-15 m; 5-12 m; 2-5 m; 0.3-2 m; and <0.3m. We also visually estimated the cover abundance for each species in each height tier in one of five classes (using the Braun-Blanquet scale; Kent and Coker, 1992). Epiphytic species were recorded as present but were not assigned a cover value unless cover exceeded 5%. We estimated the mean height of the canopy by eye and also recorded the aspect, slope, physiography, drainage and the relative contribution to the ground cover of live vascular vegetation, bryophytes, forest litter, bare earth and exposed rock. We recorded physiography using Conacher and Dalrymple's (1977) 9-unit classification and drainage according to Taylor and Pohlen's (1970) 6-unit classification.

We used the PC-RECCE suite of programs (Hall, 1992) to create Cornell files suitable for input into the program CANOCO (ter Braak, 1987). Trap site vegetation data was ordinated using the detrended canonical correspondence (DCCA) function of the program CANOCO. Ordination is a method of taking large data sets with measures for a number of variables and condensing them onto one or a few meaningful axes that may or may not be combinations of the variables originally measured. DCCA ordinates data by creating a matrix with species in rows and the trapping sites in columns. Each row and column is totalled and then each species is weighted according to its abundance at a site. The weighted scores are scaled to fit in the range 0-100, and reciprocally averaged in an iterative fashion until the amount of change that occurs with each iteration is minimal. To do this, the largest and the smallest scores are averaged, and the score included for future averaging; this is followed by the second largest and second smallest score etc., until the difference between the values is minimal. An eigenvalue is obtained by taking the range of the unscaled scores for the final iteration and expressing this as a proportion of the range of the scaled values for the previous (scaled to 100) iteration. Second and subsequent axes are derived in a similar manner, but with a new set of initial scores (Kent and Coker, 1992). Thus the eigenvalue is a derived score that summarises information from a number of variables and it may not be strongly related to any one of them. However, similar eigenvalues on any particular axis are closely related to each other and species with similar eigenvalues on all axes occur close to each other on the ground. DCCA is necessary to remove the "arch" caused by moderate species' abundance non-linearities in an ordination plot (i.e., detrending). This arch occurs because data is often collected over a wide range of environmental gradients, where sites occurring at opposite ends of these gradients have few, or no, species in common. Over such a gradient, each individual species' abundance pattern will typically be bell-shaped or non-linear (i.e., most plants will grow in the middle of their physiological range; Ludwig and Reynolds, 1988). The word "canonical" refers to the fact that the first two axes are constrained to be independent so that the second ordination axis is not simply a quadratic distortion of the first. DCCA produces eigenvalues for each species on up to 4 axes. The first two axes are truly independent and usually explain most of the variation in distribution and abundance. The remaining two axes are independent of the first two axes, but may not be independent of each other (Kent and Coker, 1992).

*Relating the Vegetation to Abiotic Features.* The weighted mean species scores for each plot from the DCCA analysis were plotted against the different environmental variables we measured using CANODRAW (Smilauer, 1992). CANODRAW creates a 2-dimensional graph that displays each of the species and sites along the first two axes of the ordination, and superimposes axes to indicate trends in the environmental variables. These ordination plots, along with the correlation coefficients obtained when we correlated the axes with each of the environmental variables we measured, allowed us to interpret each of the two main axes derived from the DCCA output, and explain vegetation patterns in terms of the variables we measured.

*Relating Rat Capture Success to Temporal and Site Factors.* We defined the rat capture rate as the number of rats caught (C) per 100 trap nights (TN) after adjusting for sprung traps (C/100CTN; Cunningham and Moors, 1983). In order to determine whether line, year, habitat or season affected rat capture rate, we used only years when trapping was completed in all seasons to create our models (i.e., 1992 and 1996 were removed). This was necessary to balance the analysis and allow analysis of interaction terms. We investigated the effect of year (1993-1995), season, line (1-8) and habitat type (1-5) on logt(C+1/100CTN) using the General Linear Model procedure of MINITAB (version 12.1). Three measures of rat capture success were used: the total number of rats caught per 100 trap nights (regardless of species), the number of Norway rats caught per 100 trap nights, and the number of kiore caught per 100 trap nights. Our models incorporated year, season and either line or habitat and two-way interactions between these variables. Thus, we created six separate models: two for each measure of rat capture, one using line and one using habitat as a predictor. Those interaction terms and factors that did not significantly affect the models were progressively removed. Hence the final models included only significant predictors. We also used post-hoc Tukey's tests to compare pairwise combinations of samples.

To specifically consider the effect of abiotic site factors on rat capture, we compared the total (uncorrected) number of rats caught at each trap with the ordination scores obtained from the first two axes of the DCCA ordinations and with each of the environmental variables we measured. We used a Pearson correlation of ranked data in MINITAB to achieve this. Ranked data were used since the data were not normally distributed. Conducting a Pearson correlation on ranked data is equivalent to conducting a Spearman non-parametric correlation in most cases (Conover, 1980). We used a sequential Bonferroni test to correct our *P*-value to account for the large number of correlations (Rice, 1989). We then conducted backwards stepwise elimination regression analysis using the number of rats caught as the response, and the habitat variables as predictors (n=12, including the first two ordination axes). As well as relating the overall habitat at a trap site to the total number of rats caught there, we also correlated the number of rats caught with the understory habitat. We defined understory habitat as the vegetation less than two metres in height (i.e., from the three lower vegetation tiers we recorded). We also conducted backwards elimination regression on this understory vegetation data. Because both Norway rats and kiore rarely climb trees, they probably came into direct contact with these lower plants more often when moving about their range than they did the upper vegetation tiers.

*Population Parameters in Different Habitat Types.* The C/100CTN of pregnant females of each species from each habitat type was compared using a Friedman Two-way ANOVA by rank in MINITAB to investigate the hypothesis that females in some habitats were more likely to be pregnant. We assumed that the distribution of rat ages was the same in all habitats and that traps in one area were not age-biased in their capture rates. Captured rats were weighed and their head and body length measured using the protocol outlined in Cunningham and Moors (1983). We investigated the effect of habitat, season and year on female productivity by comparing the number of uterine scars and embryos (summed together) per female with each of these variables using a Generalised Linear Model. In creating the model we used habitat, season and year as predictors and specified body weight and length as covariates to account for the fact that larger females could have been older and had more opportunities to reproduce. We used Tukey's tests to detect significant pairwise differences.

*Determination of Home Ranges.* Descriptive kill-trapping studies are necessary to understand the distribution and population dynamics of rats and make poison control operations more efficient (Miller and Miller, 1995), but are not helpful in determining ranging behaviour. Live-trapping can be of use in understanding what factors allow the coexistence of two or more species, how those species interact (Dickman, 1991; Haering and Fox, 1995; Tomblin and Adler, 1998), and for understanding spatial behaviour (Fitzgerald et al., 1981; Innes and Skipworth, 1983). However, trap capture can be affected by the social status of the previous trap occupant (Drickamer, 1995 and 1997) and larger individuals might be more likely to spring some types of trap than smaller animals (C.M. King, University of Waikato, Hamilton, pers. comm.). Also, kiore appear to avoid bait stations that have been visited by Norway rats (C.R. Veitch, DoC, Auckland, pers.comm.). Thus the species of the previous occupant might affect capture success in areas where species are sympatric. Furthermore, when animals are trapped they are immobilised at the point of capture and their normal ranging behaviour is disrupted while they remain in the trap. Radio-telemetry has the advantage that, after initial capture, animals are free to move (Wilson et al., 1992) and potentially unbiased information can be gathered about resource selection (Aebischer et al., 1993). To derive home range estimates, numbered pegs marked with reflective tape were positioned in a 15 by 15m grid system over the 150 by 150m study area (Figures 1 and 2). Four lines with reflective markers every 10m extended the grid 100m in each direction (Figure 2). We recorded all fixes on aerial photographs (scale 1:2000). We were able to measure distances moved by rats that had left the grid using these photographs.

Rats were captured in live capture cage traps set at the grid-markers in the centre of the study area (Figure 2). We placed most of our traps in the centre of the grid to capture as many of the animals that lived there as possible. The trapping grid was asymmetric because we had a limited number of traps.

Traps were baited with a segment of apple coated with peanut butter and were opened at dusk and closed near dawn to prevent capture of weka. Traps were checked at least three times a night. Trapping was carried out between 18-28 June 1996, again between 27 July and 4 August 1996, again between 25 August and 1 September 1996, and finally between 18-26 September 1996.

Captured rats were released into a large plastic bag, then weighed and sexed. The rats were then anaesthetised using a pad of cotton wool soaked in laboratory grade di-ethyl ether. While each rat was sedated, it was fitted with a single-stage radio transmitter. The radios were attached using replaceable non-release cable tie collars around the rat's neck. Twenty six rats (eight Norway and 18 kiore) carried radios during the study. Fourteen radio transmitters were used. Seven of the radios (weighing 5.1 g each) emitted pulses at a rate of 40 pulses per minute and were fitted with 1 mm stainless steel whip-type aerials. The remaining seven transmitters (5.7 g each) pulsed at 36 pulses per minute and had a lighter gauge whip-type aerial. Transmission frequencies were set between 160 and 162 MHz (Sirtrack Telemetry Electronics, Havelock North, New Zealand). Rats were released at the site of their capture when they awoke.

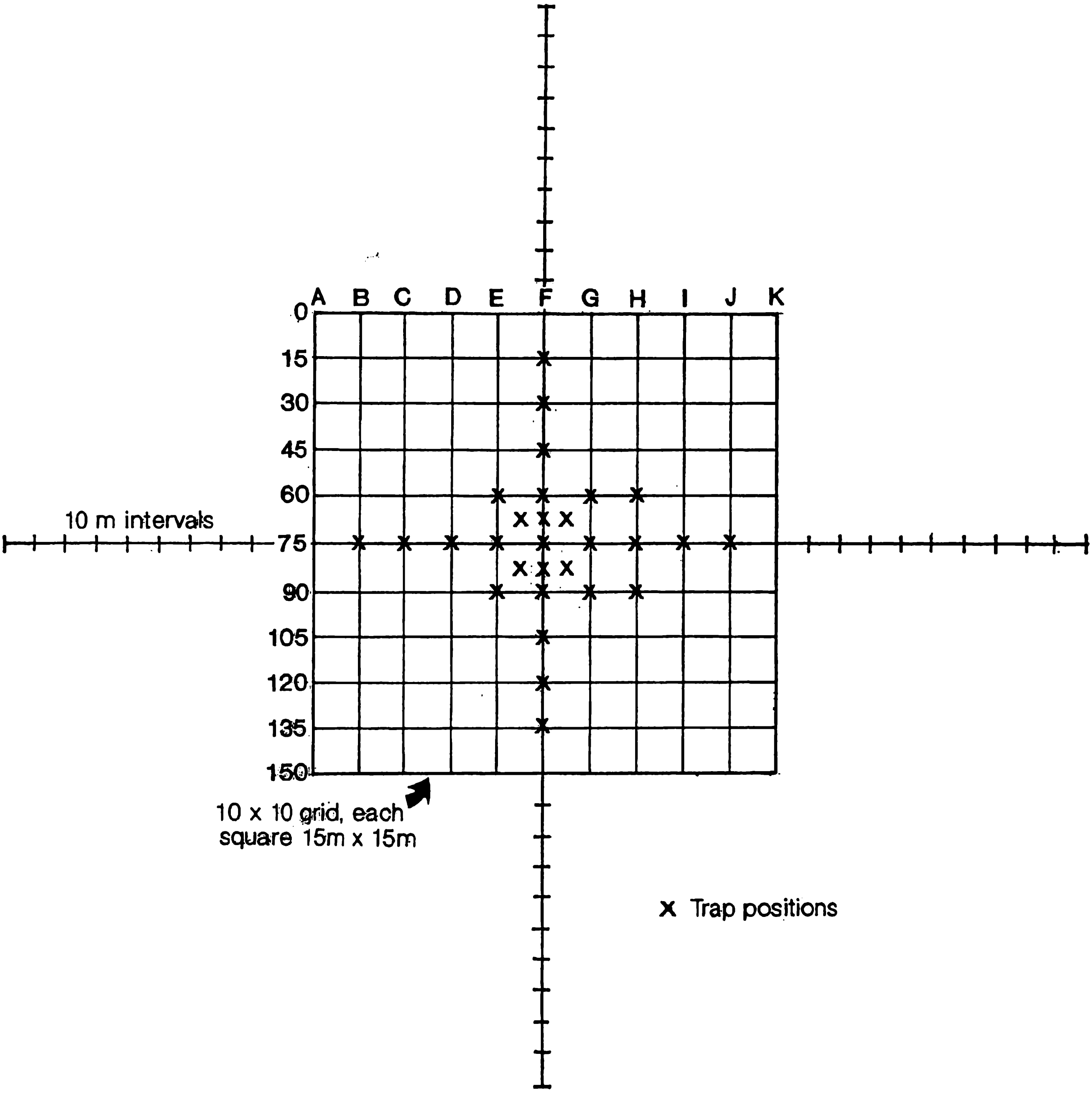


FIG. 2. Grid layout of radio-tracking study area. A pole marked each intersecting point on the grid with a numbered reflective marker attached.

A Telonics TR-4 receiver combined with a hand-held 3-element Yagi antenna was used to locate the rats. The transmitter signals were generally detectable over a distance of more than 100m but the range decreased in strong winds. We determined the position of each rat in rotation during either the first or the second half of the night. This meant that at least 30 minutes separated each individual rat location and most locations were more than an hour apart. Each rat was also located at least once each day during daylight to locate daytime nests. We estimated positions of rats from a distance of less than 10 metres and positions were measured relative to two grid markers. We left a numbered marker pole in place near where the rat was thought to have been. We found no evidence that rats were disturbed by this procedure and rats were commonly seen. During the next day, we returned to each pole and measured the light intensity above and below any vegetation using a portable hand-held incident light meter. We measured incident light in W $m^{-2}$ using a LiCor Li200SB Pyranometer (University of Waikato Electronics, Hamilton, New Zealand and LiCor Electronics, United States of America) or in lux, using a Gossen Lunasix 3 incident light meter (Berlin, West Germany). All measurements were converted to W $m^{-2}$ for analysis. We only made light measurements on sunny days between 1200 and 1700 hrs. We assumed that by doing this, and by converting the measurements to a proportion, that there would be less variability due to conditions on any one day. The proportion of light that penetrated the vegetation gave us an estimate of the density of the cover provided to the rats by the habitat they were using. For each rat (including only those with few fixes) we calculated an average value for the proportion of light penetrating in the sites they frequented. These averages were grouped into two samples – one for

Norway rats and one for kiore, and were compared using a Mann-Whitney U test. Radiolocation data were analysed using the "RANGES" computer package (version 5.02, Institute of Terrestrial Ecology, Wareham, United Kingdom).

*Home Range Analysis.* One hundred percent minimum convex polygons (MCPs) were used to calculate home ranges, along with a cluster analysis to calculate 95% harmonic means. Cluster analysis is useful for eliminating outlying fixes and separating range cores (Kenward and Hodder, 1996). For cluster analysis, we used the "nearest neighbour distance" joining method, which determines that the distance between fix clusters must be larger than the distance within a fix cluster. Convex polygons are then constructed around each cluster of fixes and the total area summed (Kenward and Hodder, 1996). We also calculated range diameter and the distance moved between locations by each rat. The distance moved between fixes was averaged for each animal and then averaged across animals to yield the estimates we present. We examined autocorrelations in our data to determine the length of time necessary between fixes for the same animal to make them statistically independent and examined spatial overlap of ranges between rats. We used the autocorrelation function of RANGES 5.02, with fixes set at 30-minute intervals and tracking sessions set 30 hours apart, to determine the time to independence between fixes (i.e., the optimal time between locations to collect data). Independence was reached in a period of one hour (mean=234 minutes, s.d=218 minutes) by 5 of the10 rats that met the autocorrelation criteria. Two of these were Norway rats (one male and one female) and three were kiore (one female and two males). This indicates that, at least for those rats, a period of one hour between fixes was adequate to ensure independence. Rooney et al. (1998) sub-sampled a large set of location data for Irish mountain hares (*Lepus timidus*) and bank voles (*Clethrionomys glareolus*) and concluded that the best way to estimate range size and use was to collect repeated fixes as close together as possible, for as long as possible. We attempted to do this and believe that our estimates of rat home range are reliable.

We were able to calculate Jacob's index of cohesiveness from our data using the "dynamic interactions" procedure of RANGES based on geometric means to determine if pairs of rats (kiore-kiore, Norway-kiore or Norway-Norway) tended to be closer together or further apart than expected by chance. The Jacob's index value ranges between –1 (avoidance) and +1 (cohesiveness) for each pair of rats. We compared values for Norway-Norway, Norway-kiore and kiore-kiore pairs using a Wilcoxon-signed rank procedure in MINITAB with two-tailed tests. Although we were unable to get simultaneous fixes on different rats we considered that fixes up to one hour apart for different animals were collected at the same time. We then repeated the analysis but considered that fixes collected up to 12 hours apart for different animals (i.e., from the same night) were collected at the same time.

*Poison Operation.* On 19 and 20 September 1996, the Department of Conservation carried out a poison drop on Kapiti Island designed to eradicate the rats living there. More poison was dropped on the island on 15 October 1996 (Miskelly and Empson, in press). The attempt used an aerial drop of cereal baits impregnated with 20 ppm Brodifacoum (Talon® 7-20 baits, Animal Control Products, Private Bag, Wanganui, New Zealand) and died green according to the national standard for poison baits. One helicopter equipped with an underslung auger bucket was used to distribute bait. Pilots relied on differential global positioning using satellite (DGPS) navigation to ensure the majority of the island was covered. At sites of cultural or other significance (e.g., human water sources), baits were hand-spread by volunteers at 25 m intervals on a grid marked out before the operation. Three small offshore islands were also included in the eradication operation, with toxic bait distributed in bait stations on a 25 m grid. Nine rats (four Norway and five kiore) were wearing radios when the poison was dropped.

## RESULTS

*Rodent Distribution and Abundance.* We achieved a total of 12 202 corrected trap nights. We caught a total of 923 rats (and three rats' tails), of which 518 (56.12%) were kiore and 391 (42.36%) were Norway rats. Fourteen rats (1.52%) had been scavenged to the point where we could not determine what species they were.

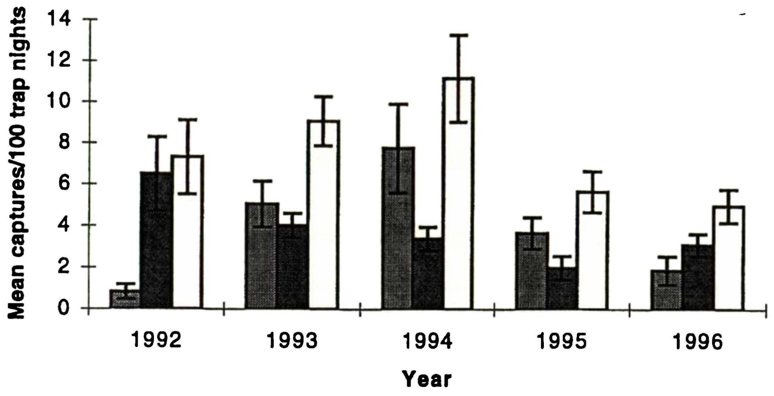
*Habitat Description.* Because our classifications are somewhat arbitrary and were decided *a priori*, we also present an analysis of rat capture by line to indicate differences between lines within a habitat type. This comparison should be interpreted cautiously since there was no replication of lines and only partial replication of habitats. Thus, it may be inappropriate to generalise these results to other, similar, forests. Furthermore, we consider it likely that we have underestimated the number of Norway rats since large rats may be able to escape from Supreme Ezeset traps (King and Moller, 1997; C.M. King, University of Waikato, Hamilton, pers. comm.).

*Temporal and Spatial Variability in Rat Capture.* A peak capture rate for kiore of 55.1/100CTN was recorded in grassland (on line 2) during the July 1994 trapping session. Kiore numbers fluctuated more across years than Norway rat numbers did, with kiore being generally more common in 1994 (Figure 3a). The total number of rats captured did not differ significantly across season (Figure 3b), although kiore showed more seasonal variation in capture rate than Norway rats. Rats were distributed across all lines and habitats with most rats, regardless of species, being caught on lines 1 (kanuka) and 2 (grassland) at the northern end of the island (Figures 3c and 3d). The high total capture rates in the grassland and kanuka (Figure 3c) were mainly due to the large numbers of kiore caught there. Norway rats were never caught in such abundance in any habitat type, but were most common in kanuka forest and grassland too (Figure 3c). On lines where capture rates of Norway rats were high, kiore capture rates tended to be low and vice versa (Figure 3d), but this correlation was not significant at the 0.05 level ($r=0.148$, $P=0.096$).

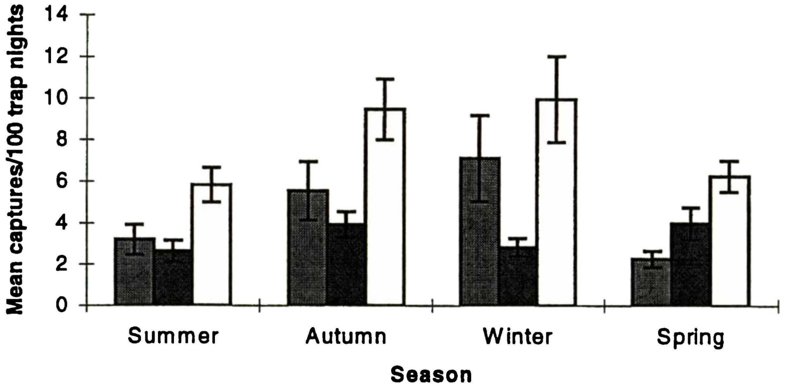
According to our linear models, kiore capture varied with season, line and habitat (Table 2). Norway rat capture varied with year, habitat and a year by season interaction (Table 2). Total rat capture was affected by year, season, line and the interaction terms year by season and year by line (Table 2).

FIG. 3. (facing page) Rat capture on Kapiti Island, New Zealand, by year, season, habitat and line. Dark bars represent the number of Norway rats, light bars the number of kiore and white bars the total rat capture (regardless of species). Errors are shown as ± 1 standard error of the mean. (a) Annual variation in rat captures per 100 trap nights for each species of rat (b) Seasonal variation in rat captures per 100 trap nights for each species of rat. (c) The mean number of rat captures per 100 trap nights for each species in each habitat. (d) The mean number of rat captures per 100 trap nights for each species on each line.

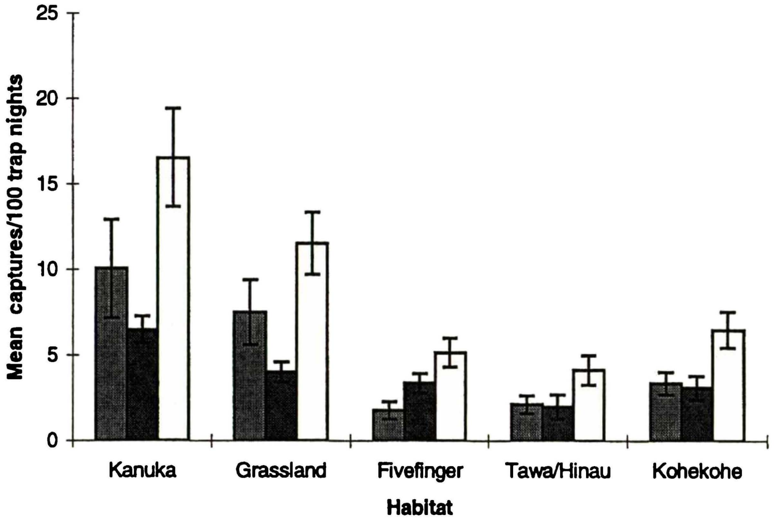
(a)


Mean captures/100 trap nights
14
12
10
8
6
4
2
0
1992
1993
1994
1995
1996
Year

(b)


Mean captures/100 trap nights
14
12
10
8
6
4
2
0
Summer
Autumn
Winter
Spring
Season

(c)


Mean captures/100 trap nights
25
20
15
10
5
0
Kanuka
Grassland
Fivefinger
Tawa/Hinau
Kohekohe
Habitat

(d)

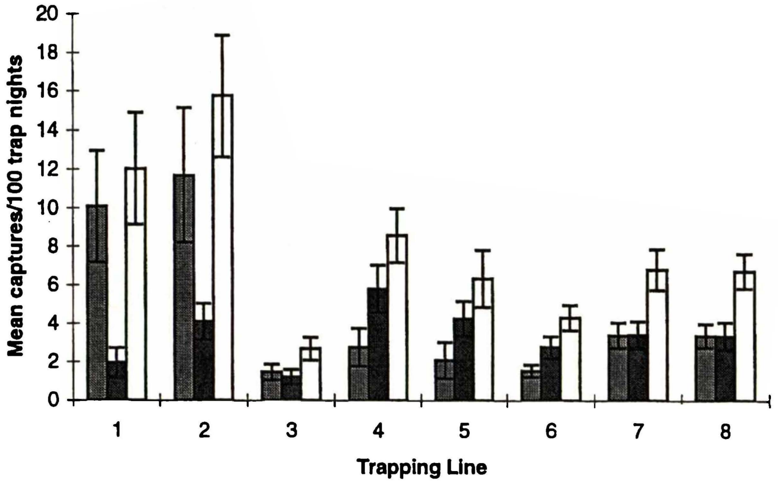

Mean captures/100 trap nights
20
18
16
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
Trapping Line

TABLE 2: F-STATISTICS FOR LINEAR MODELS DESIGNED TO INVESTIGATE THE EFFECT OF TEMPORAL AND SPATIAL VARIABLES ON RAT CAPTURE ON KAPITI ISLAND, NEW ZEALAND.*

| Model | Degrees Of Freedom | Norway rats | kiore | Total Rat capture |
|---|---|---|---|---|
| Year | 2 | 5.77** | 1.18 | 9.96** |
| Season | 3 | 1.60 | 4.79* | 3.83* |
| Line | 7 | 4.00* | 5.18** | 6.26** |
| Habitat | 4 | 3.13* | 11.14** | 6.32** |
| Year x Season | 6 | 2.04* | 2.11 | 3.03* |
| Year x Line | 21 | 0.86 | 1.99* | 1.42 |
| Year x Habitat | 14 | 0.69 | 1.09 | 1.35 |
| Season x Line | 21 | 1.16 | 1.49 | 1.74* |
| Season x Habitat | 12 | 1.55 | 0.7 | 1.66 |

* F-Statistics marked with an asterix were significant at $P$=0.05. Two asterixes indicates significance at $P$=0.01. Separate models were created to look at interactions between line and habitat with the other variables and non-significant factors were removed to calculate final models.

*Correlates between Capture and the Vegetation and Abiotic Features.* When all top story vegetation was considered and ordinated together, it became clear that on a broad scale, kiore and Norway rats were associated with different kinds of habitat (Figure 4). Mann-Whitney tests showed a significant difference between ordination scores on axis 1 for traps that were successful at catching kiore and those that were successful at catching Norway rats (W=590.0, $P$=0.0001) but not on axis 2 (W=825.5, $P$=0.153). Also, traps that were successful at catching kiore were different on axis 1 from those that did not catch kiore (W=11146.5, $P$<0.001). Successful kiore traps may have also differed on axis 2 (W=8741.5, $P$=0.06). When all traps are considered (i.e., regardless of species caught), traps that were successful were different to unsuccessful traps on axis 1 (W=9526.0, *P*<0.001) but not on axis 2 (W= 7893.5, *P*=0.09). These differences suggest that kiore were associated with low growing vegetation on flat; well-drained foot slopes and alluvial toeslopes (Figure 4). Norway rats were associated with steeper, more open and poorly drained sites with taller vegetation. This is consistent with the number of captures shown on each line and habitat in Figures 3c and 3d. Traps that were successful (regardless of species) tended to be those that had caught several kiore. This is reflected in the similar ordination scores of "successful total traps" and "successful kiore" traps in Figure 4.

Across all five habitats, there appears to be no general trend associated with Norway rat capture (Table 3). Sequential Bonferroni tests indicated that a *P*-value of 0.00028 was required to indicate significant correlations between rat capture and trap site attributes at the 0.05 level. None of the variables we measured were significantly correlated with Norway rat capture in any habitat. Backwards elimination regression produces a different result because it takes all the variables into account, whereas correlation considers each variable on its own, ignoring the others. Since our environmental variables were not independent of each other, the same outcome from both methods is unlikely.

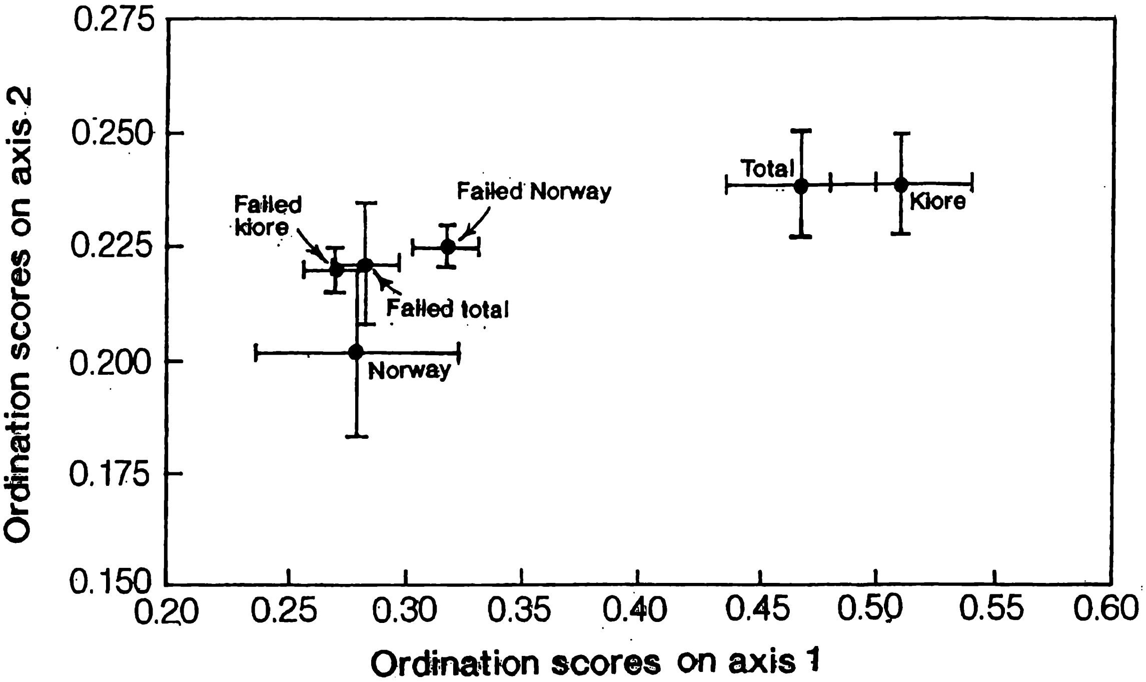


FIG. 4. Ordination plot for successful and unsuccessful traps on Kapiti Island, New Zealand. The mean value ± 1 standard error of the mean are shown. A successful trap was defined as one that caught ≥ 4 rats of a given species or ≥ 6 rats in total between October 1992 and July 1996. Unsuccessful traps were those that did not catch this many rats and are labelled "failed" traps with the species they failed to capture.

Backwards stepwise elimination regression (Table 3) indicates that the abundance of Norway rats in a habitat appears to be influenced by a number of environmental factors. On the other hand, kiore are affected by fewer of the habitat variables we measured. Backwards elimination regression indicated that in five-finger forest, Norway rat capture was related with a high score for physiography, implying that Norway rats were associated with stream edges and alluvial toeslopes. However, in tawa-hinau forest, Norway rat captures showed an increase with axis 1. We interpret axis 1 to increase as the mean top height declines and the physiography and drainage scores decrease (Table 4). This implies that Norway rats in tawa-hinau forest are associated with ridge-tops and convex creep slopes, although perhaps rather poorly drained and possibly ponded ones rather than water channels. Norway rats in grassland were associated with more open areas, again ridge-tops and convex creep slopes, with taller vegetation (our interpretation of axis 1, Table 4). In grassland, Norway rats were also related to axis 2, which did not correlate with any of the variables we measured. More Norway rats were caught on line 8 than line 1 (Figure 3d). Line 8 was steeper and at higher altitude, and succession was more advanced there than at line 1. Line 8 was likely to be fog-covered more often because of its altitude (Fuller, 1985) and also to be less fertile with nutrients leaching to lower slopes. Parts of line 8 were also more exposed to the westerly weather and salt spray. In kanuka forest, Norway rats were associated with axis 2, which correlated negatively with physiography. This implies that Norway rats were caught more often on ridge-tops and less often on lower slopes in kanuka forest. In kohekohe forest, Norway rats were associated with areas low in ground cover (and high in bare soil) and areas that were well drained (Table 3).

TABLE 3: SIGNIFICANT PREDICTORS OF RAT CAPTURE ON KAPITI ISLAND DETERMINED BY BACKWARDS ELIMINATION REGRESSION ON ENVIRONMENTAL VARIABLES.*

| Species caught | Grassland (n=70) | Kanuka forest (n=35) | Five finger forest (n=70) | Tawa-Hinau forest (n=70) | Kohekohe forest (n=35) |
|---|---|---|---|---|---|
| Norway | Exposed soil (T=-0.68)<br>Physiography (T=-2.67)<br>Drainage (T=4.91)<br>Axis 1 (T=-2.85)<br>Axis 2 (T=-2.09)<br>S=1.38, R-Sq=32.84 | Aspect (T=2.59)<br>Axis 2 (T=-2.04)<br>S=0.679, R-Sq=33.65 | Slope (T=-2.87)<br>Vegetation (T=-2.44)<br>Litter (T=-6.05)<br>Exposed soil (T=-3.09)<br>Physiography (T=2.66)<br>S=1.01, R-Sq=45.66 | Axis 1 (T=2.14)<br>S=1.49, R-Sq=16.40 | Vegetation (T=3.4)<br>Moss (T=3.35)<br>Litter (T=3.45)<br>Exposed soil (T=3.75)<br>Exposed rock (T=2.65)<br>Drainage (T=3.07)<br>S=0.86, R-Sq=74.25 |
| Kiore | Axis 1 (T=5.09)<br>S=2.13, R-Sq=27.63 | Axis 1 (T=3.26)<br>S=2.38, R-Sq=31.42 | Vegetation (T=-4.07)<br>Moss (T=-2.78)<br>Litter (T=-3.75)<br>Axis 1 (T=2.75)<br>S=1.02, R-Sq=24.21 | S=0.987, R-Sq=0.0 | Axis 1 (T=2.97)<br>S=1.34, R-Sq=22.72 |
| Percentage kiore | Axis 1 (T=2.77)<br>S=33.6, R-Sq=10.57 | Aspect (T=-3.09)<br>Exposed soil (T=2.32)<br>Mean top ht (T=2.18)<br>Axis 2 (T=3.49)<br>S=16.1, R-Sq=51.47 | Exposed soil (T=2.70)<br>Axis 1 (T=2.78)<br>S=36.2, R-Sq=23.65 | Aspect (T=2.25)<br>Exposed rock (T=-2.03)<br>S=34.0, R-Sq=9.63 | Vegetation (T=3.12)<br>S=30.6, R-Sq=32.18 |

*Captures are divided by habitat and rat species. Note that R-Sq is presented as a percentage and that S is the standard deviation of Y about the regression line

## TABLE 4: CORRELATIONS BETWEEN THE AXES DERIVED FROM DETRENDED CANONICAL CORRESPONDENCE ANALYSIS (DCCA) AND THE ENVIRONMENTAL VARIABLES WE MEASURED FOR HABITATS ON KAPITI ISLAND.*

| Habitat | Grassland | | Kanuka | | Five-Finger | | Tawa-Hinau | | Kohekohe | |
|---|---|---|---|---|---|---|---|---|---|---|
| DCCA axis | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Aspect | -0.22 | -0.13 | -0.16 | 0.06 | 0.20 | 0.17 | -0.24 | -0.20 | -0.06 | -0.35 |
| Slope | -0.46* | -0.09 | 0.35 | 0.12 | 0.35 | 0.11 | -0.12 | 0.04 | -0.48* | 0.18 |
| Vegetation cover | 0.02 | 0.09 | -0.2 | -0.19 | -0.10 | 0.16 | -0.21 | -0.09 | 0.09 | -0.19 |
| Moss cover | 0.60* | -0.09 | 0.10 | -0.11 | 0.22 | 0.02 | -0.21 | 0.08 | -0.05 | 0.03 |
| Litter cover | -0.66* | 0.16 | -0.00 | 0.23 | -0.13 | -0.37 | 0.19 | 0.07 | -0.13 | 0.03 |
| Exposed soil | -0.21 | -0.12 | 0.31 | -0.09 | 0.35 | 0.10 | 0.08 | -0.01 | -0.25 | 0.10 |
| Exposed rock | 0.09 | -0.20 | 0.17 | 0.20 | 0.08 | 0.38 | -0.33 | -0.15 | -0.42 | -0.41 |
| Mean top height | -0.41* | -0.14 | -0.21 | 0.24 | -0.01 | 0.26 | -0.67* | -0.22 | -0.14 | 0.12 |
| Physiography | 0.76* | -0.22 | -0.19 | -0.43 | 0.23 | 0.13 | -0.44* | -0.04 | -0.57* | -0.09 |
| Drainage | 0.79* | -0.23 | -0.00 | 0.02 | 0.05 | -0.06 | -0.44* | -0.11 | -0.53* | -0.01 |

*An asterix indicates significance at $P=0.05$ after correction using sequential Bonferroni tests (Rice, 1989).

There are few trends across habitats for kiore (Table 3). Correlation showed that kiore capture in grassland correlated with an increasing amount of moss cover (r=0.42, *P*=0.0001) and a decreasing amount of litter cover (r=-0.39, *P*=0.0001). Kiore capture also increased with physiography and drainage (r=0.47, *P*=0.0001 and r=0.51, *P*=0.0001 respectively). Kiore capture also varied in grassland according to axis 1. We interpreted axis 1 to be a combination of decreasing slope and mean top height, and increasing ground cover, physiography and drainage (Table 4). Thus most kiore were caught in flat, well-drained areas with abundant low vegetation. This may reflect the fact that line 1 caught more kiore than line 8, and line 1 fitted that description. Backwards elimination regression (Table 3) showed that kiore were associated with axis 1 in grassland which, from our understanding of axis 1, also indicates most kiore were caught in flat, well drained areas with abundant low growing ground cover. Kiore were associated with axis 1 in kanuka forest, which did not correlate with any of the variables we measured (Table 4). Kiore capture was unrelated to the variables we measured in tawa-hinau forest (Table 3), but related to axis 1 in kohekohe forest (again, axis 1 did not correlate with our variables; Table 4). It appears kiore in five-finger forest live in areas with little cover (Table 3).

*Understory Vegetation.* Table 5 shows the correlation between the understory axes and the environmental variables we measured. When we examined only the understory vegetation, there were no trends that appeared across all habitats (Table 6). There were no significant correlations between Norway rats and the variables we measured, but in grassland, kiore were related to the proportion of bryophyte cover (r=0.42, *P*=0.0001), the physiography (r=0.47, *P*=0.0001), the drainage (r=0.51, *P*=0.0001), and axis 1 (r=0.51, *P*=0.0001). Axis 1 is a combination of decreasing slope, vegetation height and litter cover and increasing moss, physiography and drainage (Table 5). This implies that kiore in grassland are associated with flat, mossy, well-drained areas with low vegetation. This was reiterated in the backwards elimination analysis where kiore capture was related to axis 1 (indicating the same type of habitats; Table 6). The backwards elimination regression showed that Norway rats were negatively associated with axis 1 in grassland, thus Norway rats tended to be caught in steeper, barer, taller, more poorly drained areas. In tawa-hinau forest, Norway rats were associated with both ordination axes (Table 6). Axis 1 was a combination of decreasing physiography and mean top height. Axis 2 was not strongly correlated with any variables we recorded.

Table 5: Correlations Between the Axes Derived from Detrended Canonical Correspondence Analysis (DCCA) and the Environmental Variables we Measured for Understory Habitat on Kapiti Island.*

| Habitat | Grassland | | Kanuka | | Five-Finger | | Tawa-Hinau | | Kohekohe | |
|---|---|---|---|---|---|---|---|---|---|---|
| DCCA axis | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Aspect | -0.23 | -0.14 | -0.31 | 0.27 | -0.14 | 0.19 | -0.30* | -0.20 | 0.07 | 0.15 |
| Slope | -0.46* | -0.16 | 0.11 | 0.57* | -0.37 | 0.34 | -0.11 | 0.00 | -0.39 | 0.37 |
| Vegetation cover | 0.02 | 0.11 | -0.18 | 0.31 | 0.31 | 0.00 | -0.22 | -0.02 | 0.22 | -0.19 |
| Moss cover | 0.61* | -0.02 | 0.15 | -0.08 | -0.04 | 0.03 | -0.09 | 0.27 | -0.13 | -0.02 |
| Litter cover | -0.66* | 0.03 | 0.01 | -0.24 | 0.09 | -0.21 | 0.17 | 0.05 | -0.05 | 0.27 |
| Exposed soil | -0.20 | -0.12 | 0.17 | 0.09 | -0.33 | 0.09 | 0.10 | -0.01 | -0.29 | 0.37 |
| Exposed rock | 0.09 | -0.16 | 0.10 | 0.00 | -0.54* | 0.42* | -0.27 | -0.16 | 0.00 | 0.45 |
| Mean top height | -0.42* | -0.20 | -0.2 | 0.10 | -0.66* | 0.42* | -0.60* | 0.12 | -0.04 | 0.43 |
| Physiography | 0.76* | -0.13 | 0.16 | -0.51 | -0.54* | 0.38 | -0.42* | -0.03 | -0.35* | 0.39 |
| Drainage | 0.78* | -0.12 | -0.14 | 0.17 | 0.06 | -0.19 | -0.35 | 0.05 | -0.32 | 0.54 |

*An asterix indicates significance at $P$=0.05, after correction using sequential Bonferroni tests (Rice, 1989).

TABLE 6: SIGNIFICANT VARIABLES FROM A BACKWARDS ELIMINATION REGRESSION OF RAT CAPTURE AGAINST ENVIRONMENTAL VARIABLES FOR VEGETATION LESS THAN TWO METRES HIGH IN A RANGE OF HABITATS ON KAPITI ISLAND.

| Species caught | Grassland (n=70) | Kanuka Forest (n=35) | Five finger forest (n=70) | Tawa-Hinau forest (n=70) | Kohekohe forest (n=35) |
|---|---|---|---|---|---|
| Norway | Exposed soil (T=-2.25)<br>Physiography (T=-2.62)<br>Drainage (T=5.22)<br>Axis 1 (T=-2.86)<br>S=1.4, R-Sq=30.42 | Exposed soil (T=-3.44)<br>Mean top ht (T=-3.95)<br>S=0.64, R-Sq=43.44 | Slope (T=-2.86)<br>Litter (T=-5.02)<br>Mean top ht (T=3.35)<br>S=1.01, R-Sq=45.64 | Axis 1 (T=2.51)<br>Axis 2 (T=2.19)<br>S=1.49, R-Sq=15.69. | Vegetation (T=3.35)<br>Moss (T=3.37)<br>Litter (T=3.4)<br>Exposed soil (T=3.60)<br>Exposed rock (T=3.01)<br>Drainage (T=2.44)<br>Axis 2 (T=3.26)<br>S=0.917, R-Sq=70.74 |
| Kiore | Axis 1 (T=4.99)<br>S=2.14, R-Sq=26.82 | Slope (T=2.01)<br>S=2.67, R-Sq=10.91 | Exposed soil (T=3.32)<br>S=1.06, R-Sq=13.98 | S=0.987, R-Sq=0.987 | Vegetation (T=2.39)<br>S=1.39, R-Sq=14.73 |
| Percentage kiore | Axis 1 (T=2.78)<br>S=33.6, R-Sq=10.6 | S=21.6, R-Sq=0.0 | Litter (T=2.34)<br>Exposed soil (T=3.61)<br>S=37.0, R-Sq=20.58 | Exposed rock (T=-2.28)<br>S=32.9, R-Sq=16.69 | Vegetation T=2.78<br>S=32.5, R-Sq=21.06 |

*Captures are divided by habitat and rat species. Note that R-Sq is presented as a percentage and that S is the standard deviation of Y about the regression line

*Population Parameters in Different Habitats.* We were able to sex and assign an age class to 859 rats (373 Norway and 486 kiore). Fourteen rats (1.52%) had been almost completely scavenged, and the remaining 50 (18 Norway and 32 kiore, 5.42% of total) had been partially scavenged, which meant we were able to assign species, but not sex or age. We were able to measure the head and body length of some of these scavenged animals, but we did not weigh any of them. This data is summarised in Table 7.

TABLE 7: SUMMARY OF RAT CAPTURE DATA FROM KAPITI ISLAND, NEW ZEALAND.*

| Species | Norway rat | | kiore | |
|---|---|---|---|---|
| Sex | Male | Female | Male | Female |
| % of species capture | 46.05 | 53.95 | 45.12 | 54.88 |
| Average weight (g) | 223.9±5.6 | 200.9± 4.8 | 80.4 ± 1.4 | 74.3± 1.1 |
| | (168) | (197) | (247) | (235) |
| Head-body length (mm) | 181.9± 2.0 | 174.7 ± 1.9 | 133.6± 0.9 | 129.0±0.9 |
| | (198) | (198) | (252) | (236) |
| Percentage reproductive | | 28 (164) | | 16 (180) |
| Average litter size | | 8.9± 1.1 (28) | | 5.6± 0.3 (21) |

*The number of animals from which the statistics are calculated (n) is shown in brackets.

Male kiore were heavier than females (T=-3.41, *P*=0.0007). The head and body length (i.e., length of the head plus the body) of male kiore was longer than that of female kiore (T=3.69, *P*=0.0003). Male Norway rats were heavier than females (T=-3.12, $P$=0.002). Male Norway rats were also longer than females (T=-2.62, $P$=0.0092).

Twenty-one pregnant kiore had from 3-9 embryos (Table 7), whereas twenty-eight pregnant Norway rats ranged from 2-32 embryos. Two of the pregnant Norway rats appeared to be in the early stages of pregnancy and had large numbers of embryos (32 and 18). It is unlikely that they could have successfully reared this many offspring and when these two rats are removed from the data set, Norway rats averaged 7.6 embryos (s.e.=0.5, range 2-12). Reproductive female rats were caught in all seasons, but there was a summer peak in the number of pregnant females of both species and very few of either species were collected in winter (Table 8). Only a few reproductive female kiore were caught in spring (October). Reproductive female Norway rats were trapped in all habitats, but no reproductive female kiore were caught in five-finger forest (lines 3 or 5). The proportion of reproductive females caught in each line blocked by season did not vary according to line (kiore S=6.82, $P$=0.45; Norway S=4.5, $P$=0.72).

The number of uterine scars and embryos found in female kiore adjusted for weight and length varied with year ($F_{4,230}$=2.92, $P$=0.022; Table 9). Females were most productive in 1996 (mean=6.54 scars per female caught, s.d.=6.72, n=28). The number of scars also varied with habitat and most scars and embryos were observed in October and January ($F_{3,230}$=3.18, $P$=0.025). The habitat was also a significant predictor of scar and embryo number for kiore ($F_{4,230}$=3.83, $P$=0.005). More scars and embryos were recorded per female in kanuka and kohekohe forest (mean=5.9 and 4.8 respectively) than in the other three habitat types (range 1.8 in five-finger forest to 3.9 in tawa-hinau forest; Table 9). The number of uterine scars and embryos found in Norway females did not vary with year ($F_{4,194}$=0.23, *P*=0.919) nor with the habitat ($F_{3,194}$=0.84, *P*=0.504). However, it did vary seasonally ($F_{3,194}$=4.38, *P*=0.005), with animals caught in July having fewer scars and embryos than those caught in other months. Most pregnant female rats were caught in the January trapping session although there were not significantly more rats caught then than in other seasons (Friedman test: for kiore S=7.13, *P*=0.068; for Norway rats S=6.72, *P*=0.08). The weight of female kiore, when adjusted for body length, varied according to the year ($F_{4,232}$=28.44, *P*=0.0001), the season ($F_{3,232}$=13.86, *P*=0.0001) and the habitat ($F_{4,232}$=4.25, *P*=0.002; Table 9). Female kiore were: (1) heavier in summer and lightest in winter; (2) heaviest in 1992; and (3) heavier in kohekohe forest (Table 9).

The weight of male kiore, when adjusted for length, also varied with year ($F_{4,245}$=14.72, *P*=0.0001; Table 9). Male rats were, on average, heavier in 1992 and 1996 and those that lived in kohekohe forest were heavier than rats from other habitats ($F_{4,245}$=3.44, *P*=0.009). The weight of male kiore, corrected for length, varied with habitat ($F_{4,245}$=3.44, *P*=0.009) and year ($F_{4,245}$=14.72, *P*=0.0001), but not season ($F_{3,245}$=2.15, *P*=0.09; Table 9). The weight of male Norway rats varied with year ($F_{4,165}$=9.82, *P*=0.0001) but not with season or habitat. Length-adjusted female Norway rat weights varied according to year ($F_{4,191}$=6.16, *P*=0.0001) with rats being heaviest in 1992, and season ($F_{3,191}$=6.34, *P*=0.0001) with heavier rats captured in October. The weight of female Norway rats did not vary with the habitat in which they were trapped ($F_{4,191}$=2.12, *P*=0.08; Table 9). Male Norway rat weights varied with year ($F_{4,165}$=9.82,

$P$=0.0001) but were unaffected by season ($F_{3,165}$=1.48, $P$=0.223), or the habitat ($F_{2,165}$=0.84, $P$=0.502).

TABLE 8: THE PROPORTION OF PREGNANT OR LACTATING (I.E., “REPRODUCTIVE”) FEMALES OF EACH SPECIES OF RAT CAUGHT ON KAPITI ISLAND BETWEEN OCTOBER 1992 AND JULY 1996 IN EACH HABITAT AND SEASON.

| Season | Summer | | Autumn | | Winter | | Spring | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|
| | kiore | Norway | kiore | Norway | kiore | Norway | kiore | Norway | kiore | Norway |
| Grassland | 0.29 (14) | 0.71 (7) | 0 (16) | 0 (9) | 0 (20) | 0.14 (7) | 0 (13) | 0 (2) | 0.06 (63) | 0.24 (25) |
| Kanuka | 0.78 (18) | 0.6 (5) | 0.12 (25) | 0 (3) | 0 (12) | 0 (8) | 0 (9) | 0.6 (7) | 0.27 (64) | 0.3 (23) |
| Five finger | 0 (3) | 0.67 (3) | 0 (7) | 0.36 (14) | | 0.11 (9) | 0 (2) | 0.25 (8) | 0 (12) | 0.35 (34) |
| Tawa-Hinau | 0(3) | 0.4 (10) | 0.17 (6) | 0.21 (14) | 0.2 (5) | 0.33 (3) | 0 (7) | 0.11 (27) | 0.10 (21) | 0.20 (54) |
| Kohekohe | 0.33 (6) | 0.71 (7) | 0.43 (7) | 0 (4) | 0 (2) | 0 (5) | 0.2 (5) | 0.42 (12) | 0.3 (20) | 0.36 (28) |
| Total | 0.45 (44) | 0.59 (32) | 0.11 (61) | 0.18 (44) | 0.03 (39) | 0.09 (32) | 0.03 (36) | 0.29 (56) | 0.16 (180) | 0.28 (164) |

* The total number of females caught is shown in brackets. When no females were caught in a given habitat and season the cell is left empty.

Table 9: Weight and Productivity Variables in each Habitat, Season and Year for Rats Caught on Kapiti Island.

| | | Weight of female rats (g) | | Uterine scars and embryos | | Weight of male rats (g) | |
|---|---|---|---|---|---|---|---|
| Predictor | | Kiore | Norway | Kiore | Norway | Kiore | Norway |
| | 1992 | 79.7±12 (3)$^{a}$ | 222.7±7.8 (26)$^{a}$ | 5.0±2.9 (3)$^{ab}$ | 9.6±1.3 (29)$^{a}$ | 90.0±4.9 (3)$^{ab}$ | 217.2±10.1 (16)$^{b}$ |
| | 1993 | 73.8±1.6 (63)$^{a}$ | 192.1±8.7 (60)$^{b}$ | 3.4±0.6 (66)$^{ab}$ | 7.5±1.3 (62)$^{a}$ | 87.8±2.4 (74)$^{a}$ | 229.0±9.9 (50)$^{b}$ |
| Year | 1994 | 72.9±1.0 (88)$^{a}$ | 201.3±10.8 (50)$^{b}$ | 4.6±0.6 (89)$^{ab}$ | 10.7±1.7 (50)$^{a}$ | 74.1±2.4 (103)$^{b}$ | 213.8±11.4 (49)$^{a}$ |
| | 1995 | 77.0±2.1 (53)$^{b}$ | 198.9±13.7 (33)$^{a}$ | 2.9±0.5 (53)$^{a}$ | 6.9±1.2 (34)$^{a}$ | 78.5±2.5 (50)$^{b}$ | 229.7±19.2 (70)$^{b}$ |
| | 1996 | 74.1±2.5 (28)$^{a}$ | 201.4±10.2 (28)$^{b}$ | 6.5±1.3 (28)$^{b}$ | 8.4±1.4 (28)$^{a}$ | 90.2±4.7 (17)$^{a}$ | 230.9±12.3 (33)$^{ab}$ |
| | Grassland | 71.6±1.5 (91)$^{a}$ | 180.5±9.7 (39)$^{a}$ | 3.0±0.5 (91)$^{a}$ | 6.1±1.0 (40)$^{a}$ | 78.0±1.8 (99)$^{b}$ | 217.4±13.5 (34)$^{a}$ |
| | Kanuka | 75.1±1.8 (75)$^{a}$ | 190.8±14.5 (31)$^{a}$ | 5.9±0.7 (76)$^{b}$ | 4.5±1.0 (33)$^{a}$ | 75.4±3.4 (66)$^{b}$ | 196.2±16.4 (22)$^{a}$ |
| Habitat | Five-finger | 70.5±4.8 (21)$^{a}$ | 230.1±10.5 (37)$^{a}$ | 1.8±0.6 (21)$^{ac}$ | 11.1±1.7 (38)$^{a}$ | 83.0±4.1 (32)$^{b}$ | 254.7±6.9 (34)$^{a}$ |
| | Tawa-Hinau | 75.6±3.6 (24)$^{a}$ | 193.2±8.9 (62)$^{a}$ | 3.9±0.9 (25)$^{abc}$ | 10.1±1.4 (64)$^{a}$ | 85.7±3.5 (27)$^{ab}$ | 211.3±10.8 (56)$^{a}$ |
| | Kohekohe | 84.2±3.5 (24)$^{b}$ | 219.8±7.8 (28)$^{a}$ | 4.9±0.9 (26)$^{abc}$ | 10.0±1.6 (28)$^{a}$ | 95.3±4.6 (23)$^{a}$ | 246.0±12.0 (22)$^{a}$ |
| | Summer | 84.3±2.3 (45)$^{a}$ | 181.5±13.5 (44)$^{a}$ | 5.4±0.7 (47)$^{a}$ | 8.0±1.2 (44)$^{ab}$ | 92.2±1.8 (47)$^{a}$ | 200.9±14.5 (32)$^{a}$ |
| Season | Autumn | 76.3±2.2 (67)$^{a}$ | 198.6±9.0 (52)$^{b}$ | 5.8±0.7 (68)$^{a}$ | 9.3±1.4 (53)$^{ab}$ | 78.6±2.2 (82)$^{a}$ | 215.9±9.7 (54)$^{a}$ |
| | Winter | 68.0±1.6 (86)$^{b}$ | 200.7±9.3 (39)$^{b}$ | 2.7±0.5 (88)$^{a}$ | 4.5±1.1 (39)$^{a}$ | 74.8+2.8 (89)$^{a}$ | 253.7±9.9 (40)$^{a}$ |
| | Spring | 73.2±1.8 (37)$^{b}$ | 216.8±6.7 (62)$^{b}$ | 2.7±0.7 (36)$^{a}$ | 10.8± 1.3 (67)$^{b}$ | 83.7±4.3 (29)$^{a}$ | 223.2±10.5 (42)$^{a}$ |

*The mean value ± 1 standard error of the mean are shown. Values in brackets are the number of individuals contributing to the data set and vary because some rats were partially scavenged and were unable to be weighed. Note that rows in the same column marked with different letters are significantly different from each other at *P*=0.05.

*Radio-Tracking and Home Range Analysis.* Home range data from 11 kiore and eight Norway rats are presented here. By graphing incremental range area against the number of fixes we found that an asymptote for mean range area was reached after approximately 25 fixes, although the confidence limits at 25 fixes were approximately 40%. Therefore, only animals from whom more than 30 fixes were obtained, or those who were tracked during the poison drop, are presented here. On average, 40.5 (s.d.=19.1, range =21-76) fixes were used to estimate the home ranges of male kiore (n=6) and a mean of 35.2 (s.d.=8.6, range 28-48) to estimate the home ranges of female kiore (n=5). A mean of 37.9 (s.d.=24.1, range=25-82) fixes were used to calculate the male Norway rat home ranges (n=7). We used 19 fixes to estimate the home range of one female Norway rat.

*Home Range Size and Length: Minimum Convex Polygons (MCPs).* Norway rats used much larger home ranges than kiore (Table 10). Male kiore moved an average of 15.5 m between fixes (s.d.=7.7 m). Female kiore moved an average of 17.5 m between fixes (s.d.=4.3). Male Norway rats moved 80.3 m between fixes on average (s.d.=34.59). The single female Norway rat moved an average of 115.7 m between fixes.

TABLE 10: HOME RANGE DESCRIPTORS FOR NORWAY RATS AND KIORE ON KAPITI ISLAND, NEW ZEALAND.*

| | kiore | | Norway rats | |
|---|---|---|---|---|
| | Male (n=6) | Female (n=5) | Male (n=7) | Female(n=1) |
| Size (ha, MCP method) | 0.14± 0.04<br>(0.03-0.3) | 0.18±0.05<br>(0.05-0.31) | 5.78±3.25<br>(1.59-21.01) | 5.13 |
| Length (m) | 51.8 ±3.8<br>(26-77) | 67.2±8.2<br>(40-89) | 438.7±95.3<br>(218-916) | 459 |
| Size (ha, Harmonic mean method) | 0.04±0.008 | 0.08±0.03 | 1.75±0.79 | 3.52 |
| Number of nuclei | 3.20 | 0.84 | 2.6 | 1 |

*Values are shown as means ± 1 standard error of the mean. Numbers in brackets indicate the range of values.

*Overlap of Home Ranges.* There were a total of 342 potential pairwise overlaps in home ranges from the 19 home ranges we estimated using the harmonic mean method (Table 11). Of those, 124 did not overlap. For the 218 overlapping ranges, the average overlap was 33.87%. The proportion of overlap appears to be largely a function of the fact that Norway rat ranges were large and overlapping. Therefore, they may overlap many small kiore ranges and parts of some Norway rat ranges. Kiore ranges overlapped both the ranges of other kiore and the ranges of Norway rats. Because they were much smaller, kiore home ranges made up a very small percentage of Norway rat ranges.

Wilcoxon signed rank tests on Jacob's indices of habitat use (when fixes up to one hour apart were treated as simultaneous) showed that kiore and Norway rats may avoid each other (Wilcoxon statistic =229.0, $P$=0.07, n=25). Norway rats showed no avoidance or cohesion with other Norway rats (Wilcoxon statistic=33.0, *P*=0.24). Likewise, kiore distribution appeared to be random with respect to other kiore (Wilcoxon statistic= 42.0, *P*=0.834). When fixes from the same night were considered simultaneous, none of the three pair-wise interactions were significant.

TABLE 11: HOME RANGE OVERLAP OF RATS ON KAPITI ISLAND*

| | kiore | Norway rat |
|---|---|---|
| kiore | 43/110 | 66/88 |
| | (26<20%) | (66<20%) |
| Norway rat | 64/88 | 42/56 |
| | (34>90%) | (21<30%) |

*From the 19 home ranges we recorded, a maximum of 19x18 (or 342) overlaps could have been recorded if all ranges had overlapped with all others. This table presents overlapping species in rows, and overlapped species in columns. For example, 66/88 (top right) indicates that 88 cases may have occurred where kiore overlapped Norway rat home ranges. 66 instances of overlap were recorded. All of these overlaps were less than 20%.

*Cover Provided by Habitat Used by Each Species.* Norway rats used vegetation that allowed an average of 8.3% of incident light to penetrate it (s.e.=1.6%, range=2.4-13.9%, n=7). Kiore used denser vegetation that allowed only 2.6% of incident light to penetrate it (s.e.=0.5%, range=0.2-7.5%, n=15; W=119.0, *P*=0.007). In other words, kiore used habitat that provided more cover. On 30 July 1996, we excavated an underground tunnel to find a radio-carrying male kiore that had not moved for two days. The radio-carrying kiore and another one (of unknown sex) were found together (alive) in an underground tunnel that consisted of at least two entrances and two leaf-filled nests. The tunnel was up to 25 cm deep, more than 1.5 m long and had a diameter of approximately 2.5-3.0 cm (i.e., it was too small to have been excavated or inhabited by Norway rats). It is not known how the hole arose, but reports of kiore using underground shelters together are rare (Atkinson and Moller, 1990) and thus worth reporting.

*Post-poisoning Behaviour of Rats.* All the dead rats we collected after the poison drop (5 Norway and 6 kiore) had poison bait in their stomachs and had extensive internal bleeding. We also snap trapped one kiore on the night immediately after the poison drop (20 September 1996) and it too had cereal bait in its stomach. We did not accumulate enough fixes after the poison drop to accurately estimate home range size, but no rat ventured outside the previously calculated range area. Rats moved similar distances between fixes before and after poisoning (Table 12). The first two rats (one of each species) were collected dead on 22 September and all except one kiore had been collected by the 25 September (6 days post-drop). The remaining kiore was found dead on 29 September (10 days post-drop).

Two of the five Norway rats we discovered dead after the drop were found lying in the open (i.e., not within their daytime nests or under any kind of cover). The remaining three died under cover. We also saw two rats active during the day on 23 September; we had seen no diurnally active rats previously. One male Norway rat wearing a radio was discovered curled up in a small grass nest with a second (female) Norway rat that had been dead longer than he had. The female had been partially scavenged. Three of the six kiore (including one not wearing a radio) and one Norway rat were found alive, and out in the open, before they died. When these rats were found they were unresponsive to our presence and their breathing was laboured. We checked them hourly until they died, between three and eight hours later. The remaining three kiore were found in grass nests. When we searched daytime dens that had been occupied by the rats since the poisoning, none of the kiore dens contained baits. We found three bait caches from two of the five Norway rats we followed. The amount of bait in each cache was 62.05 g, 2.05 g (10 baits and 2 baits respectively, both cached by presumably the same animal), and 11.95 g (2 large baits).

TABLE 12: MOVEMENTS BETWEEN FIXES BY RADIO-CARRYING RATS BEFORE AND AFTER AN ERADICATION ATTEMPT ON KAPITI ISLAND, NEW ZEALAND.*

| | | Before Poison drop | After Poison drop |
|---|---|---|---|
| kiore | Male (n=3) | 19.7±16.6 | 20.3±5.4 |
| | Female (n=2) | 23.2±0.3 | 15.7±2.2 |
| Norway rats | Male (n=4) | 65.6±49.1 | 69.06±36.5 |

* The poison drop occurred on 19 September 1996. Fixes from before the drop are those collected between 1-19 September 1996. Those collected after the poison drop were between 19 September and when each animal died (a maximum of 10 days later).

# DISCUSSION

In our study, Norway rats appeared to be influenced more by the microhabitat variables we measured than kiore were, but the exact relationship between capture and environment varied across habitats. At a broad level, when we ordinated all plots on the same axes, kiore were caught in habitats that were quantitatively different from that of Norway rats in terms of physiography, slope, drainage and vegetation height. Norway rats were also more widespread than kiore on Kapiti. Their size and productivity did not appear to vary across habitats but did across seasons and years. Kiore were larger and more productive in kanuka and kohekohe forest than they were in other habitats; their size and productivity also varied with season and year. Norway rats appeared to breed in all seasons, whilst most kiore apparently bred in summer. The productivity of rats in each habitat was not necessarily related to the number of rats caught there, for example, most kiore were caught in grassland, yet kiore were more productive in kanuka forest. In the grassland where we radio-tracked rats, the two species may have avoided direct contact with each other, but they showed no evidence of prolonged avoidance of jointly used areas. Kiore used habitat that was denser than that occupied by Norway rats. Kiore also used much smaller home ranges than Norway rats did. After poisoning, approximately half the radio-carrying rats returned to daytime dens to die, while the other half died out in the open. All radio-carrying rats were killed by the aerial operation, with the last rat (a kiore) dying 10 days after the first drop. This information is of use to wildlife managers worldwide in planning and conducting rat eradication on uninhabited islands for the conservation of rare, endemic species.

*Coexistence and Interactions.* Dick (1985, unpubl.) had studied the distribution of rodents on Kapiti in 1983/84 using kill trapping to investigate broad scale habitat associations and diet. He found that Norway rats were most common in most habitats he sampled, but kiore predominated in high altitude tawa-hinau forest and kanuka forest. Dick's study was relatively short in duration (one year) and used different trap layouts and methods in different habitats and at different times of the study, making effective comparisons difficult.

Dueser and Porter (1986) reported that competition between rodents on Assateague Island was "ubiquitous" and statistically significant but concluded that habitat structure was more important in determining habitat use. Because the capture rates of the two species we caught in kill traps were only weakly related to each other, and the home ranges of kiore and Norway rats overlapped, we consider it likely that habitat structure was also more important than competitive interactions in determining local abundance on Kapiti Island. Norway rats seemed to be influenced by many of the microhabitat variables we measured, whilst kiore were influenced by fewer. Our calculations of Jacob's index were significant at the 0.1 level, indicating that the two species may have avoided each other. It is possible, therefore, that Norway rats distribute themselves according to habitat and kiore distribute themselves according to the abundance of Norway rats. This is supported by anecdotal evidence that kiore avoid bait stations that Norway rats have used (C.R. Veitch, Department of Conservation, pers. comm.) and avoid live traps that have captured Norway rats (G.N. Bramley unpublished data). Furthermore, Dick (1985, unpubl.) showed that Norway rat captures were negatively correlated with kiore captures. It is possible that larger sample sizes are necessary to detect any small competitive effects on Kapiti (Gliwicz, 1980; Dueser and Porter, 1986).

During our radio-tracking, we observed what we believe to be an incidence of predation by a Norway rat upon a kiore: a kiore was moving about its range normally in the early evening, and then recorded with a male Norway rat on two occasions about an hour apart. The following day the kiore was collected dead and mostly eaten, with fresh Norway rat faeces near the body. Thus the nature of the Norway rat-kiore interaction may be more complex than competition alone. In order to separate the relative impacts of interspecific competition and habitat structure in determining population abundance, species removal experiments of the kind conducted by Brown and Munger (1985) are needed. They created large natural enclosures and either removed species of rodent or added supplementary food. They concluded that interspecific interactions were important in structuring Chihuahuan desert rodent communities, but they did not specifically consider habitat structure as an alternative hypothesis. Habitat structure can influence such factors as predation risk (Schooley et al., 1996) and food availability (Guerra and Vickery, 1998) so the interactions are likely to be complex, but they require investigation, perhaps in large enclosures, since two species of free living rats are hard to manipulate independently.

The diet of both species, in New Zealand and elsewhere, has been documented often and summarised by Atkinson and Moller (1990) and Moors (1990). Both species are omnivorous and opportunistic, eating mostly invertebrates, with kiore surviving on larger amounts of vegetation at some times of year (Bunn and Craig, 1989). No New Zealand study, that we are aware of, has measured resource availability and use by one or more species of rodent and inferred from that, competitive advantage.

In order to understand the interaction of the two rat species, it is necessary to understand their diet, since interactions are likely to be over food. It is also necessary to know more about the feeding behaviours, foraging efficiency and energetic requirements of both species to determine if one species is a more efficient forager than the other, and thus is able to spend less time gathering food. If kiore proved to be more efficient than Norway rats, then this might explain why kiore persist in the presence of Norway rats (Guerra and Vickery, 1998).

*Habitat Associations.* It appears from our kill trapping data that the two species of rat living on Kapiti island did partition habitat to some extent and that kiore were more successful in some habitats (kohekohe, kanuka and grassland) than they were in others (tawa-hinau and five finger forest). This is consistent with previously published accounts of kiore habitat use (Atkinson and Moller, 1990). Radio-tracking showed the kiore we studied were usually associated with dense groundcover, and kill trapping showed they were found in areas of low growing vegetation, whereas Norway rats were apparently equally successful in all the habitats we sampled. Furthermore, Norway rats did not show a particular breeding season on Kapiti, whilst kiore did, breeding predominantly during the summer (Dick, 1985, unpubl.; this study). This suggests that the habitat, overall, is more suitable for Norway rats since they are able to live everywhere on the island and breed at all times of the year.

The vegetation on Kapiti has been studied often (Esler, 1967; Fuller, 1985; Atkinson, 1992) and succession on the island has been well documented. The usual process of succession is grassland followed by *Cassinia* then manuka (*Leptospermum scoparium*), followed quickly by kanuka or more slowly by five-finger (Esler, 1967). Kanuka is long lived and can be followed either by five-finger, when canopy kanuka dies prematurely, or by more terminal species (Esler, 1967). Five-finger slows the succession process, with late seral species such as kohekohe and tawa appearing later. Kanuka frequently persists into late seral forests as a component of the canopy (Esler, 1967). The nature of this succession would appear to have an influence on the rat community present because kiore are more successful in kanuka forest than in five-finger forest. Kanuka forest is common on Kapiti (Table 1) and its presence may help explain the continuing coexistence of the two rat species.

Morris (1996) determined that generalist species responded to habitats at a larger scale than specialists. Seamon and Adler (1996) agreed that habitat generalists should exhibit little preference for microhabitat gradients within a single habitat and exist in a range of habitats. On the other hand, specialists would inhabit fewer habitats and experience microhabitats in a coarse grained-manner with population performance linked to particular gradients in microhabitat structure. If this were true, it implies that Norway rats could be regarded a more generalist species since they exist in a range of habitats, whilst kiore are more specialised and are only able to persist in some habitats without immigration. However, Seamon and Adler (1996) thought that specialists should also show less variation over time in their associations since they are adapted to the best predictors of resource availability in a habitat. Generalists would fluctuate more, in part because they move habitats when conditions become unsuitable. This does not appear to be true for the kiore we studied, since the number of kiore caught fluctuated both annually and seasonally. Furthermore, variations in capture rate across time in each habitat do not indicate that rat numbers are increasing in one habitat and decreasing in another. It may be that the relatively recent arrival of both rats in New Zealand has given them insufficient time to adapt to the habitats and competitors here. It also raises the question of scale, since Norway rats may successfully switch to other microhabitats within the habitats we recognised. That is to say, Norway rats are less specific in their preferences of microhabitats and swap according to larger gradients (for example, interactions that determine food supply) than kiore, which might be more responsive to microhabitat gradients and less likely to change habitat preference. This would explain why there is no overall trend in Norway rat microhabitat use in all the habitats we measured.

Our trapping sites were located randomly with respect to microhabitat and, in some cases, ranges of microhabitats were not available for all habitats. This means that some microhabitats are not represented at all while small numbers of trap sites may represent others. This may also explain why Norway rats did not show the same trends across all habitats. Sturmer (1988, unpubl.) found the greatest degree of habitat separation between Norway rats and kiore living sympatrically with ship rats on Stewart Island. It seems likely that both are generalist species but that

Norway rats have a wider niche than kiore and thus may be better competitors in more marginal habitat (Sturmer, 1988, unpubl.).

Our data suggest that Norway rat populations were stable and about as successful in all habitats. Kiore populations were not: they fluctuated more across time, space and habitat – perhaps dependent on food (Bunn and Craig, 1989) or food and shelter (Roberts and Craig, 1990) in each environment. Rat capture rates in particular habitats did not reflect the productivity of rat populations in those habitats. For example, surprisingly few pregnant kiore were collected from lines 2 and 8 (grassland), despite the fact that most kiore were caught along these two lines. It appears the most productive areas for kiore are lines 1 and 7 (kanuka and kohekohe forest respectively). Not only did kiore produce larger litters in these two habitats, they also achieved larger sizes. It is possible that young kiore are produced in these habitats and disperse into the adjacent grasslands. They might then be caught in grassland when they are slightly larger and more likely to set off the traps (King et al., 1996; C.M. King, University of Waikato, Hamilton, unpublished data).

*Rat Morphology and Breeding*. The size of the Norway rats we captured falls within the range of values reported by Moors (1990) and is similar to those reported on Kapiti by Dick (1985, unpubl.). However, Dick reported a larger average size for female rats than we recorded and found no significant difference in weight between the sexes. Litter size is also well within the previously reported range of 6-8 for Norway rats (Moors, 1990). Dick (1985, unpubl.) found that Norway rats on Kapiti bred in all seasons of the year and that was also true in the years of our study, and at Pureora between 1982 and 1987 (C.M. King, University of Waikato, Hamilton, pers. comm.), although we recorded few pregnancies in winter. The average litter size of the kiore we caught was larger than the average of 4.7 reported by Dick (1985, unpubl.) but still smaller than that on many other New Zealand islands (e.g., average of 6.7 on Tiritiri Matangi Island; Moller and Craig, 1986). Kiore were similar in size and weight to those recorded by Atkinson and Moller (1990), being most similar to those from Macauley Island in the Kermadec group and somewhat smaller than those reported by Dick (1985, unpubl.). Atkinson and Moller (1990) believed that kiore breeding in grassland habitat consisted of a short spring and summer pulse, whilst on forested islands breeding was more prolonged. We only caught pregnant kiore in grassland in January; most pregnant kiore (from all habitats) were caught in summer and autumn. Thus, on the same island, some habitats allowed longer breeding than others, which suggests that there are differences in habitat quality for kiore. Better kiore habitats would be those where kiore achieved larger sizes and reproduced either more often or more successfully. They may also be those with the most kiore. If there are better habitats, and they are not the ones with the most kiore, then it is possible that some kiore are being excluded from better habitats by the larger and possibly predatory Norway rat. Dick (1985, unpubl.) suggested that both species of rat prefer grassland habitat but that Norway rats exclude kiore from it, since he caught predominantly Norway rats on 2 of the 3 grasslands he sampled. Kiore dominated both grasslands we studied, but were not most productive there. Dick (1985, unpubl.) suggested that kiore reach highest densities in sub-optimal refuge forest habitat on Kapiti. Taylor (1984) and Atkinson and Moller (1990) considered that grassland is sub-optimal habitat for kiore, with forest providing better resources. We agree that kiore are probably most common in sub-optimal habitat on Kapiti, but disagree with Dick (1985, unpubl.) that kanuka forest is sub-optimal. Grassland probably provides better cover and more escape opportunities for kiore; this might explain their apparent abundance in this habitat (Roberts and Craig, 1990; this study). King et al. (1996) similarly suggested that mice (*Mus musculus*) were most abundant in grass and disturbed habitat at Pureora because it was there that they could escape predation by ship rats (*Rattus rattus*). Food has been shown to be limiting for kiore in grassland areas (Bunn and Craig, 1989; Craig and Bunn, 1989) and our data suggests that whilst kiore can live in grassland, they are more successful in other areas.

Atkinson and Moller (1990) suggested, partly on the basis of Dick's (1985, unpubl.) yearlong study in 1983/84, that the density of kiore fluctuated less on predominantly forested islands such as Kapiti than it does on grass-covered islands. This does not appear to be the case since kiore captures (and presumably density) fluctuated during our (longer) study with numbers varying strongly with season, habitat and year (i.e., forested areas experienced fluctuations in just the same way as grassland ones did). Dick (1985, unpubl.) concluded that seasonal weight changes were greater for kiore than Norway rats, which is supported by our data. Very few of the female kiore (6 of 65) caught by Dick (1985, unpubl.) were pregnant. We also caught few pregnant kiore and the reason for this is unclear. More pregnant Norway rats were caught than kiore, despite the fact more kiore were caught. It is unclear why this should be, since many juveniles of both species were caught. This implies very good recruitment of kiore, but it is impossible to check this since we did not collect age data. It is possible that pregnant kiore avoid traps or use microhabitats we did not sample. The shorter breeding season of kiore may also have provided fewer opportunities to catch pregnant individuals. More small kiore were caught in winter. There are at least two possible reasons for this: one is that more young animals were caught in winter and the other is that larger animals lost body mass during the winter because food was limiting. Given that most breeding occurs in summer and autumn, it seems most likely that individuals caught in winter are younger animals. There could be a natural cohort progression reflected in our trapping data, but it was not possible to check this as we did not collect precise data on age.

Differences in litter sizes from different habitat types have been recorded for rodents (e.g., Hispid cotton rats, *Sigmodon hispidus*; Slade et al., 1996), but not in New Zealand. Litter size in Hispid cotton rats is correlated to maternal size. By specifying both length and weight as covariates we were able to statistically adjust for body size and exclude the possibility that our result is due to the different size of females in different habitats. Slade et al. (1996) suggested that dispersal or habitat selection should occur at small sizes (i.e., early in life) so that females might maximise their growth rate and thereby achieve larger sizes and higher fitness. Nothing is known about size or age specific dispersal in rodents in New Zealand and this could be a suitable area for future research.

*Home Range Use*. The home range diameters we recorded for kiore were outside the range of 37-60 m across previously reported in Atkinson and Moller's (1990) review of kiore worldwide, and less than the maximum reported dispersal of

268 m. The only study of Norway rat home ranges in New Zealand reported a maximum length of 330 m (Moors, 1985). Norway rats on Kapiti used much longer ranges than this and are perhaps more similar to Norway rats in Britain (i.e., they travel several hundred metres to feed; Taylor and Quy, 1978).

Glass and Slade (1980) concluded that Hispid cotton rats had a negative effect on the voles (*Microtus ochrogaster*) that they coexisted with and that coexistence relied on the seasonality of the interaction, habitat heterogeneity and the wider niche of the voles. A similar phenomenon appears to be operating on Kapiti, where coexistence of the rats we studied occurs because Norway rats have a wider niche and there are some habitats in which kiore are very successful. The seasonality of kiore-Norway rat interactions is unknown and should be examined.

Island populations of rodents appear to be unique in many ways, including a relaxation of home range or territorial defence (Gliwicz, 1980; Gray and Hurst, 1998). Rat home ranges on Kapiti overlapped, regardless of species, in an area where kill trapping had shown that both rats were relatively abundant over a five-year period. Goldingay and Price (1997) found that spatial segregation occurred between two species of kangaroo rat (*Dipodomys*) when the rats were at high density, and that the spatial distribution was temporally stable where both species were relatively abundant. This may not have been the case on Kapiti, where the relative abundance of rats in each habitat varied over time. We do not know the density of rats on Kapiti, although it is likely to be higher than mainland sites (Gliwicz, 1980). Furthermore, we still do not understand the nature of the interaction between Norway rats and kiore that could lead to the kind of reciprocal variation and habitat segregation shown in this study and that of Dick (1985, unpubl.). Future studies should address this issue by manipulating pairs of species in controlled settings to examine behaviour (e.g., McCartney and Marks, 1973), resource selection (e.g., Goodyear, 1992), seasonality (e.g., Glass and Slade, 1980) and competitive efficiency (e.g., Guerra and Vickery, 1998).

*Management Implications.* It appears from our study, that if bait stations had been used on Kapiti, they would have had to be very closely spaced to ensure all kiore came into contact with poison. Spacings of 20-25 m would have been recommended, but this would have required a huge labour effort to position and stock the bait stations. This problem was removed by the use of an aerial poison drop. Furthermore, bait stations may have proven inappropriate for another reason - we could not rule out the possibility that kiore would be excluded from bait stations by Norway rats. Because Norway rats cached baits, a larger than necessary amount of poison was probably required to reduce rat numbers quickly and hence maximise the chances of success. This would also increase the chances of non-target poisoning. Kiore used dense areas of habitat, which suggests that they may not have come into contact with surface-spread bait immediately. This may explain why one kiore remained alive for 10 days: if it normally inhabited tunnels of vegetation in the grassland and seldom ventured out to the surface of the grass, it would not have encountered poison. Since kiore do not breed until summer months and kiore numbers are lowest in winter, late winter and early spring would appear to be the best time to attempt an eradication because numbers are lowest and there is presumably less food available. At this time of year kiore are also lighter in weight and will presumably require less poison to kill them. The number of pregnant Norway rats is low in winter so dependent or newly independent young rats do not need to be factored into the method of poison delivery. Both species of rat were commonly found in the open after poisoning, especially when they were near death. This behaviour was not recorded for either species of rat prior to the poison drop. Rats that were active in open areas will have been available to be eaten by weka, morepork (*Ninox novaezelandiae*) and other species (e.g., gulls) thus, secondary poisoning would be unavoidable.

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## REFERENCES

AEBISCHER, N.J., ROBERTSON, P.A., and KENWARD, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.

ALLEN, R.B. 1992. RECCE. An inventory method for describing New Zealand vegetation. FRI Bulletin No. 181. Forest Research Institute, Ministry of Forestry, Christchurch, New Zealand.

ATKINSON, I.AE. 1989. The value of New Zealand islands as biological reservoirs, pp. 1-16, *in* A. Burbidge (ed.), Australian and New Zealand Islands: Nature Conservation Values and Management. Occasional Paper 2/89, Department of Conservation and Land Management, Western Australia.

ATKINSON, I.A.E. 1992. Effects of possums on the vegetation of Kapiti Island and changes following possum eradication. DSIR Land Resources Contract Report No. 92/52, Department of Scientific and Industrial Research Land Resources, Lower Hutt, New Zealand.

ATKINSON, I.A.E., and MOLLER, H. 1990. Kiore, pp. 175-192, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

TER BRAAK, C.J.F. 1987. CANOCO – a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis (Version 2.1.) TNO Institute of Applied Computer Science, Wageninen, Netherlands.

BROWN, J.H., and MUNGER, J.C. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology* 66:1545-1563.

BUNN, T.J., and CRAIG, J.L. 1989. Population cycles of *Rattus exulans*: population changes, diet and food availability. *N.Z. J. Zool.*16:409-418.

CONACHER, A.J., and DALRYMPLE, J.B. 1977. The nine unit landsurface model. An approach to pedogeomorphic research. *Geoderma* 18:1-154.

CONOVER, W.J. 1980. Practical Nonparametric statistics (Second edition). John Wiley and Sons, New York, USA.

COWAN, P.E. 1992. The eradication of introduced Australian brushtail possums, *Trichosurus vulpecula*, from Kapiti Island, a New Zealand nature reserve. *Biol. Conserv.* 61:217-226.

CRAIG, J.L., and BUNN, T.J. 1989. The effects of experimental manipulation of food supplies on a population of *Rattus exulans*. *N.Z. J. Zool.* 16:419-425.

CUNNINGHAM, D.M., and MOORS, P.J. 1983. A guide to the identification and collection of New Zealand rodents. New Zealand Wildlife Service Occasional Publication No. 4. New Zealand Wildlife Service, Wellington, New Zealand.

DANIEL, M.J. 1990. New Zealand long-tailed bat, pp.117-123, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

DAUGHERTY, C.H., TOWNS, D.R., ATKINSON, I.A.E., and GIBBS, G.W. 1990. The significance of the biological resources of New Zealand islands for ecological restoration, pp. 9-21, *in* D.R. Towns, C.H. Daugherty, and I.A.E. Atkinson (eds.). Ecological Restoration of New Zealand Islands. Conservation Sciences Publication No. 2. Department of Conservation, Wellington, New Zealand.

DICK, A.M.P. 1985. Rats on Kapiti Island. Coexistence and diet of *R. norvegicus* (Berkenhout) and *R. exulans* (Peale). Unpublished MSc. thesis, Department of Botany and Zoology, Massey University, Palmerston North, New Zealand.

DICKMAN, C.R. 1991. Mechanisms of competition among insectivorous mammals. *Oecologia* 85:464-471.

DRICKAMER, L.C. 1995. Odors in traps: does most recent occupant influence capture rates for house mice? *J. Chem. Ecol.* 21:541-555.

DRICKAMER, L.C. 1997. Responses to odors of dominant and subordinate house mice (*Mus domesticus*) in live traps and responses to odors in live traps by dominant and subordinate males. *J. Chem. Ecol.* 23:2493-2506.

DUESER, R.D., and PORTER, J.H. 1986. Habitat use by insular small mammals: relative effects of competition and habitat structure. *Ecology* 67:195-201.

EMPSON, R.A. 1992. Kapiti Island – Proposed rat eradication, p. 34, *in* C.R. Veitch, B.M. Fitzgerald, J.G. Innes, and E.C. Murphy (eds.). Proceedings of the National Predator Management Workshop. Threatened Species Occasional Publication No. 3. Department of Conservation, Wellington, New Zealand.

EMPSON, R.A., and MISKELLY, C.M. in press. The risks, costs and benefits of using Brodifacoum to eradicate rats from Kapiti Island, New Zealand. *N.Z. J. Ecol.*

ESLER, A.E. 1967. The vegetation of Kapiti Island. *N.Z. J. Bot.* 5:353-394.

FITZGERALD, B.M., KARL, B.J., and MOLLER, H. 1981. Spatial organisation and ecology of a sparse population of house mice (*Mus musculus*) in a New Zealand forest. *J. Anim. Ecol.* 50:489-518.

FULLER, S.A. 1985. Kapiti Island Vegetation. Report on a vegetation survey of Kapiti Island, 1984/85. Department of Lands and Survey, Wellington, New Zealand.

GLASS, G.E., and SLADE, N.A. 1980. The effect of *Sigmodon hispidus* on spatial and temporal activity of *Microtus ochrogaster*: Evidence for competition. *Ecology* 61:358-370.

GLIWICZ, J. 1980. Island populations of rodents: Their organisation and functioning. *Biol. Rev.* 55:109-138.

GOLDINGAY, R.L., and PRICE, M.V. 1997. Influence of season and a sympatric congener on habitat use by Stephen's Kangaroo rat. *Conserv. Biol.* 11:708-717.

GOODYEAR, N.C. 1992. Spatial overlap and dietary selection of native rice rats and exotic black rats. *J. Mamm.* 73:186-200.

GRAY, S.J., and HURST, J.L. 1998. Competitive behaviour in an island population of house mice, *Mus domesticus*. *Anim. Behav.* 56:1291-1299.

GUERRA, B., and VICKERY,W.L. 1998. How do red squirrels, *Tamias hudsonicus*, and eastern chipmunks, *Tamias striatus*, coexist? *Oikos* 83:139-144.

HAERING, R., and FOX, B.J. 1995. Habitat utilization patterns of sympatric populations of *Pseudomys gracilicaudatus* and *Rattus lutreolus* in coastal heathland: A multivariate analysis. *Aust. J. Ecol.* 20:427-441.

HALL, G.M.J. 1992. PC-RECCE: Vegetation inventory data analysis. Forest Research Institute Bulletin No. 182. Landcare Research, Christchurch, New Zealand.

HOOKER, S., and INNES, J.G. 1995. Ranging behaviour of forest-dwelling ship rats, *Rattus rattus*, and effects of poisoning with Brodifacoum. *N.Z. J. Zool.* 22:291-304.

INNES, J.G. 1990. Ship rat, pp. 206-225, *in* C.M. King (ed.). The Handbook of New Zealand Mammals, Oxford University Press, Auckland, New Zealand.

INNES, J.G., and SKIPWORTH, J.P. 1983. Home ranges of ship rats in a small New Zealand forest as revealed by trapping and tracking. *N.Z. J. Zool.* 10:99-110.

KENWARD, R.E., and HODDER, K.H. 1996. RANGES V: An analysis system for biological location data. Institute of Terrestrial Ecology, Wareham, Dorset, United Kingdom.

KENT M., and COKER, P. 1992. Vegetation description and analysis: a practical approach. CRC Press, Boca Raton.

KING, C.M., INNES, J.G., FLUX, M., KIMBERLEY, M.O., LEATHWICK, J.R., and WILLIAMS, D.S. 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *N.Z. J. Ecol.* 20:215-240.

KING, C.M., and MOLLER, H. 1997. Distribution and response of rats, *Rattus rattus*, *R. exulans*, to seedfall in New Zealand beech forests. *Pac. Conserv. Biol.* 3:143-155.

LUDWIG, J.A., and REYNOLDS, J.F. 1988. Statistical Ecology. John Wiley and Sons, New York, USA.

LOVEGROVE, T.G. 1996. A comparison of the effects of predation by Norway (*Rattus norvegicus*) and Polynesian rats (*R. exulans*) on the Saddleback (*Philesturnus carunculatus*). *Notornis* 43:91-112.

MCCARTNEY, W.C., and MARKS, J. 1973. Inter and Intraspecific aggression in two species of the genus *Rattus*: evolutionary and competitive implications. *Proc. PA. Acad. Sci.* 47:145-148.

MCFADDEN, I., and TOWNS, D.R. 1991. Eradication campaigns against kiore (*Rattus exulans*) on Rurima rocks and Korapuki, northern New Zealand.

Department of Conservation Science and Research Internal report no. 97. Department of Conservation, Wellington, New Zealand.

MILLER, C.J., and MILLER, T.K. 1995. Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poisoning operation. *N.Z. J. Ecol.* 19:19-27.

MOLLER, H., and CRAIG, J.L. 1986. The population ecology of *Rattus exulans* on Tiritiri Island, and a model of comparative population dynamics in New Zealand. *N.Z. J. Zool.* 14:305-328.

MOORS, P.J. 1985. Norway rats on the Noises and Motukawao Islands, Hauraki Gulf, New Zealand. *N.Z. J. Ecol.* 8:37-54.

MOORS, P.J. 1990. Norway rat, pp. 192-206, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

MORRIS, D.W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology* 77:2352-2364.

ROBERTS, M., and CRAIG, J.L. 1990. The demography of kiore, *Rattus exulans*, in three habitats. *N.Z. J. Zool.* 17:43-53.

ROONEY, S.M., WOLFE, A., and HAYDEN, T.J. 1998. Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mamm. Rev.* 28:89-98.

RICE, W.R. 1989. Analysing tables of statistical tests. *Evolution* 43:223-225.

SCHOOLEY, R.L., SHARPE, P.B., and VAN HORNE, B. 1996. Can shrub cover increase predation risk for a desert rodent? *Can. J. Zool.* 74:157-163.

SEAMON, J.O., and ADLER, G.H. 1996. Population performance of generalist and specialist rodents along habitat gradients. *Can. J. Zool.* 74:1130-1139.

SLADE, N.A., MCMURRY, S.T., and LOCHMILLER, R.L. 1996. Habitat differences in mass-specific litter sizes of hispid cotton rats. *J. Mamm.* 77:346-350.

SMILAUER, P. 1992. CANODRAW v 3.0 Users guide. Microcomputer Power. Ithaca, New York, United States of America.

STURMER, A.T. 1988. Diet and coexistence of *Rattus rattus* (Linnaeus), *Rattus exulans* (Peale) and *Rattus norvegicus* (Berkenhout) on Stewart Island, New Zealand. Unpublished MSc. thesis, Department of Botany and Zoology, Massey University, Palmerston North, New Zealand.

SUMMERLIN, C.T., and WOLFE, J.L,. 1973. Social influences on trap response of the cotton rat, *Sigmodon hispidus. Ecology* 54:1156-1159

TAYLOR, N.H. and POHLEN, I.J. 1970. *Soil Survey Method.* Soil Bureau Bulletin 25. New Zealand Department of Scientific and Industrial Research. Wellington, New Zealand.

TAYLOR, R.H. 1975. What limits kiore (*Rattus exulans*) distribution in New Zealand? *N.Z. J. Zool.* 2:473-477.

TAYLOR, R.H. 1984. Distribution and interactions of introduced rodents and carnivores in New Zealand. *Acta Zool. Fenn.* 172:103-105.

TAYLOR, R.H. 1978. Distribution and interactions of rodent species in New Zealand, pp. 135-141, *in* P.R. Dingwall, I.A.E. Atkinson, and C. Hay (eds.). Ecology and control of rodents in New Zealand nature reserves. Department of Lands and Survey Information Series, No. 4.

TAYLOR, R.H., and THOMAS, B.W. 1989. Eradication of Norway rats (*Rattus norvegicus*) from Hawea Island, Fiordland, using brodifacoum. *N.Z. J. Ecol.* 12:23-32.

TAYLOR, R.H., and THOMAS, B.W. 1993. Rats eradicated from rugged Breaksea Island (170 ha), Fiordland, New Zealand. *Biol. Conserv.* 65:191-198.

TAYLOR, K.D., and QUY, R.J. 1978. Long distance movements of a common rat (*Rattus norvegicus*) revealed by radio-tracking. *Mammalia* 42:63-71.

TOMBLIN, D.C., and ADLER, G.H. 1998. Differences in habitat use between two morphologically similar tropical forest rodents. *J. Mamm.* 79:953-961.

TOWNS, D.R., and BALLANTINE, W.J. 1993. Conservation and Restoration of New Zealand island ecosystems. *Trends Ecol. Evol.* 8:452-457.

VEITCH, C.R., and BELL, B.D. 1990. Eradication of introduced animals from the islands of New Zealand, pp. 137-146, *in* D.R. Towns, C.H. Daugherty, and I.A.E. Atkinson (eds.). Ecological Restoration of New Zealand Islands. Conservation Sciences Publication No. 2. Department of Conservation, Wellington, New Zealand.

WATSON, J.S. 1961. Rats in New Zealand: a problem of interspecific competition. *Proc. 9th Pacific Science Progress* 19:15-16.

WILSON, W.L., MONTGOMERY, W.I., and ELWOOD, R.W. 1992. Range use in female woodmice (*Apodemus sylvaticus*) in deciduous woodland, pp. 549-560, *in* I.G. Priede and S.M. Swift (eds.). Remote monitoring and tracking of animals. Ellis Horwood Ltd, Chichester, England.

ZIV, Y., ABRAMSKY, Z., KOTLER, B.P., and SUBACH, A. 1993. Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos* 66:237-246.

# CHAPTER THREE: RATS (*RATTUS RATTUS, R. NORVEGICUS* AND *R. EXULANS*) RESPONSES TO THE ODOUR OF OTHER RAT SPECIES IN LABORATORY TRIALS.

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**Abstract** – Little is known about how rat species interact where they coexist. Behavioural interactions may be mediated by odours. I measured the behavioural responses of male and female ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*) and kiore (*R. exulans*) to the odour of other rats and house mice (*Mus musculus*) in five trials using the same experimental protocol. Wood shavings that had been used as bedding by rats or mice provided the odours. Tests were conducted in a Y-shaped maze to determine: (1) whether rats would distinguish between odours of conspecifics and heterospecifics, and (2) if they avoided heterospecific odours compared to the odours of conspecifics. Rats that were tested included Norway rats from Kapiti Island and the North Island, ship rats from the North Island and kiore from the Hen and Chicken Islands, New Zealand. Norway rats from Kapiti Island were tested against the odours of ship rats and mice; all other rats were tested against the odours of heterospecific rats. Test odours were presented in one arm of the Y maze with the animals' own soiled bedding in the other arm. To test the hypothesis that prior experience in the Y maze apparatus affected rats responses to odours, experimentally naïve kiore were compared to a similar group of kiore that had experienced the apparatus in other experiments. I recorded five measures of rats' use of the maze: time to visit each arm, number of visits to each arm, time spent in each arm, distance travelled down each arm, and a total activity score. Experimentally experienced kiore visited the odour of other kiore more than they visited the odour of Norway rats. Experimentally naïve kiore were less likely to explore the maze than kiore who had spent time in the maze before. There was no difference in responses between male and female kiore. I recorded few statistically significant results, perhaps because the sample sizes were too small to counter the large individual variation. Female ship rats were more active during tests and approached odours more quickly than male ship rats. Norway rats showed no consistent trend in their responses to the odour of other rats. Female Norway rats were generally more active and explored the maze more than male Norway rats. The potential role of odours in mediating interspecific interactions in New Zealand is discussed.

**Keywords -** interspecific interactions, odours, ship rat, kiore, Polynesian rat, Norway rat, communication, Y maze.

## INTRODUCTION

Three cosmopolitan species of introduced rat live on New Zealand's islands (*Rattus norvegicus*, *R. rattus*, and *R. exulans*; Atkinson and Moller, 1990;

Innes, 1990; Moors, 1990). However, there are few places where all three species currently coexist in the same locality (Taylor, 1984; Atkinson and Moller, 1990). Norway rats (*R. norvegicus*) and kiore (*R. exulans*) are mostly restricted to offshore islands. Norway rats are also common in some urban areas on the main islands (Moors, 1990). Ship rats (*R. rattus*) are the most abundant rat in forested areas of the main islands (Innes, 1990). Parasitological evidence suggests that ship rats and Norway rats may have existed on more offshore islands in the past (Roberts, 1991), but sympatric populations did not persist. Interspecific competition has been suggested to account for the present distribution of rodents in New Zealand (Watson, 1961). However, the interactions between combinations of the three species have not often been studied (but see Bramley et al., Chapter 2, and Sturmer (1988) unpubl.), so it remains unknown whether rats compete or not.

In order for competition between species to exist, the species must use some of the same resources and at least one of those resources must be limiting (Begon et al., 1990). Individuals of species that are competing may respond to the level of the resources (exploitation competition; Begon et al., 1990) or to physical encounters with their competitor (interference competition; Begon et al., 1990). Animals may also use indirect cues such as territorial scent marks deposited by competitors who then leave the area (Herrera and MacDonald, 1994). Scent marking can also be regarded as a kind of interference competition, since an animal leaves evidence of its presence, which then affects the behaviour of later-arriving animals. Competitive effects may determine the time and duration of foraging or they may shift the activity of less competitive species to more marginal microhabitats in the same way that predation might (Bouskila, 1995; Abramsky, 1998), thereby diminishing any overlap in resource use.

Assessing whether competition occurs requires a knowledge of each species' potential and realised niches on a range of fronts (e.g., ecology, behaviour and physiology), and a knowledge of the abundance of resources as the animals perceive them (Goodyear, 1992). The existence of competition is difficult to prove since, if the competition is strong, natural selection could be expected to decrease it (for example, by divergence leading to niche separation). Weak competition is difficult to detect because it may cause only subtle changes in the organisms under study. Over time, competition could cause habitats and resources to be partitioned in such a way that competition is not obvious to human observers. Since rodents are small, nocturnal, wide-ranging and secretive, interactions between them would be difficult to directly observe in the wild.

Nonetheless, rodents have been observed in many investigations of competitive interactions (e.g., McCartney and Marks, 1973; Glass and Slade, 1980; Brown and Munger, 1985; Dueser and Porter, 1986; Goodyear, 1992; Ziv et al., 1993; Gray and Hurst, 1998). Rodents are particularly suitable for such studies because they are widespread, small, and easy to maintain in captivity. Furthermore, different combinations of rodent species, including native and introduced species, live sympatrically at different localities. Some species are locally abundant and easy to trap in certain areas. Rodents in New Zealand provide a unique opportunity to study competitive interactions because the coexisting species are ecologically and morphologically very similar. They are the most internationally widespread and abundant rat species (MacDonald, 1984), and there are no native species of rodent with which they might compete. Furthermore, the three species have only recently (within the last 200 years) come into contact, and the historical distribution of each species has been documented (Atkinson and Moller, 1990; Innes, 1990; Moors, 1990) or can be inferred (Roberts, 1991). This recent association means it is unlikely that niche separation has happened, and any initial competitive interactions may still be detectable when species meet in the laboratory or in the wild (Glass and Slade, 1980).

Exactly why ship rats should be the prevalent species on the main islands of New Zealand is unknown. Watson (1961) thought it might be because they successfully inhabit forest in New Zealand and outcompete the less agile Norway rat in the forest environment. He went on to suggest that ship rats in forest might produce enough young to provide a source of immigrant ship rats for rural and some urban situations, but this assertion has not been verified. Ship rats may have contributed to the extinction or decline of endemic rodents in areas such as the Florida Keys, the Antilles and the Galapagos Islands (Goodyear, 1992), but the details of their interactions are unknown. Furthermore, Norway rats are a more widespread and successful species than the localised endemics that Goodyear studied, and are therefore probably better equipped to deal with competition from ship rats. In continental sites, such as the United States of America, the spread of Norway rats may have caused the decline of ship rats (Ecke, 1958); the same is true in Britain (Watson, 1961). All three species of rat found in New Zealand live sympatrically at many tropical locations (e.g., Hawaii and New Caledonia; Tomich, 1986; Innes, 1990). They also coexist on Stewart Island and nearby

Pearl Island, New Zealand, where mice (*Mus musculus*) are absent (Atkinson and Moller, 1990).

Knowledge of interactions between ship rats, Norway rats and kiore in New Zealand might indicate the nature of interactions between these pest species and endangered endemic rodents where they coexist in other countries. In addition, all three species found in New Zealand are economic and public health pests subject to control in many parts of the world. Knowledge of which species are behaviourally dominant (and in which circumstances), which species avoid others, and how avoidance is mediated may improve management efforts in areas where they coexist. This is particularly important in New Zealand where only one attempt has been made to simultaneously eradicate more than one species of rat from an island (Bramley et al., Chapter 2).

House mice are also widespread in New Zealand (Murphy and Pickard, 1990, Atkinson and Moller, 1990). In areas where they are sympatric, rats appear to occupy different habitats to mice (King et al., 1996). Despite this, competition remains to be demonstrated between the rats or between rats and mice in New Zealand. Taylor (1984) suggested that predation by mustelids and cats (*Felis catus*) may have been more important than interspecific competition in determining rodent distribution in New Zealand. These two hypotheses are not mutually exclusive, but are difficult to separate experimentally, particularly if one species of rat is not only a competitor, but a predator too (for example, Norway rats may eat kiore; Bramley et al., Chapter 2).

Competition may act, at least in part, to regulate rodent populations (Taylor,1984; Abramsky et al., 1998), hence it has potentially important implications for the management of rats. A complete knowledge of the mechanisms of population control is required so that natural mortality can be augmented by imposed mortality (e.g., poisoning) at critical times. Scents are important in rodent social behaviour and responses may vary according to which part of the body produced the scent, the social status of the donor, the donor's physiological state and a similar range of factors to do with the receiver (Brown, 1985). It is possible that rodents use scents to mediate inter- and intra-specific competitive interactions, with rodents avoiding the scent deposits of more efficient or dominant competitors of another species (Krasnov and Khoklova, 1996) or conspecifics (Drickamer, 1997). I tested the choice behaviour of wild-reared rats in captivity when presented with scents from the urine and faeces of other rat species. I compared rats responses to heterospecifics with their responses when presented with the odour of a conspecific stranger, and with bedding tainted by their own urine and faeces. I also compared Norway rats responses to the scent of mice in one trial. If rats show an aversion or preference for other species' odours, this may suggest the strength and direction of interactions between rats and suggest which species should be closely studied in the wild to detect competitive effects.

## METHODS

*Animals.* A total of 45 animals was used in these trials: 18 kiore (10 females and 8 males), 18 Norway rats (8 females, 10 males), and 9 ship rats (4 females and 5 males). The rats were divided into five mixed-sex groups of nine for testing. The kiore were wild-caught using traditional Maori pitfall traps on islands from the Hen and Chickens group and supplied to me by the Ngati Wai Trust Board (Whangarei, New Zealand). Kiore are the only rat known to live on the islands where these kiore were caught (Atkinson and Moller, 1990), but ship rats or mice may have reached the islands in the past (Roberts, 1991). Nine of the kiore had been used in other trials to investigate their responses to odours of predators and herbivores (Bramley and Waas, Chapter 6); the other nine were experimentally naïve. All 30 kiore were caught at different times, but were transported to Hamilton in one large cage and housed in the same room upon arrival; thus the kiore were probably familiar with one another's odours. The remaining 27 rats were caught from the wild in live capture cage traps baited with peanut butter and apple. All of these (ship and Norway) rats had been used in trials similar to the ones the nine kiore had experienced (Chapters 5 and 6 in this thesis). Nine of the Norway rats were caught on Kapiti Island (40°51'S and 174°56'E), where they coexisted with kiore. The cage traps were washed before and after use on Kapiti Island by soaking them in boiling water, scrubbing them and then leaving them to air dry. The remaining nine Norway rats were caught around the Waikato region and north of Auckland on the North Island (Chapter 5), where they presumably coexisted with ship rats and mice. The ship rats were caught along the banks of the Waikato River at Tamahere, south of Hamilton City, and likewise could have been in contact with both Norway rats and mice. The cage traps were not cleaned between captures at a site and could have caught more than one species of rat or other animals such as possums

(*Trichosurus vulpecula*, on the North Island) or weka (*Gallirallus australis*, on Kapiti), but were cleaned between sites.

Ship and Norway rats were housed individually in plastic bottomed, wire cages (46 x 24 x 20 cm high). Kiore were housed, either individually or in same-sex pairs, in plastic tubs with wire tops (40 x 27 x 15 cm deep). Kiore were separated a week before testing and were housed singly until the tests were completed. All cages were provided with an empty can and either a hard plastic or cardboard tube to act as retreats. Rats of different species were kept in separate rooms and checked on alternating days so as not to introduce smells on clothing or skin. The same cages were used for housing Norway and ship rats, but between occupants they were cleaned with hot water and "Vircon", a low foaming, low odour detergent, and then air dried. All animals had *ad libitum* access to water and food (Sharpes Diet 86 rat chow, occasional seed mixes and pieces of apple; kiore were also given fresh grass seed heads). Wood shavings covered the bottom of the cages as bedding material. Bedding was changed weekly. The rats were kept on a constant 12:12 light schedule, with lights on at 2200 hrs, and maintained at temperatures between 15 and 24°C during the trials. Four different rooms were used to house rats, although kiore were housed in a room formerly occupied by Norway rats. The surfaces of the room were wiped with hot, soapy water before the kiore were housed there.

*Donor Odours.* Bedding was collected from a total of 75 animals of both sexes (30 kiore, 21 ship rats, 24 Norway rats) weekly for two weeks. This bedding was tainted with urine and faeces and was used as the odour source for the trials. The bedding of three randomly chosen, same sex, conspecific individuals was mixed together in plastic bags, sealed, and stored frozen for periods of up to one year in the same freezer. Norway rats from Kapiti were tested first (on 18-19 March 1997). I used laboratory mouse bedding from white mice at the Ruakura Agricultural Centre's (Hamilton, New Zealand) small animal colonies as a donor odour in tests with Kapiti rats. Norway rats from the North Island were tested on 10 and 11 June 1997, ship rats on 12 and 13 of July 1997, and kiore were tested between 14 and 17 July 1997.

*Trials.* Animals were collected, one at a time, from the animal rooms and transported in their cages, in darkness, to a separate trial room. They were then transferred into an experimental arena illuminated with red light. When the animals were in the arena, the red light was turned off and all observations were completed using infra-red light sources. Tests were videoed using a Videotronic Tri-Q CCD camera and Panasonic AG5260 video recorder. After each test the animals were returned to their cages and then to the animal rooms.

I used a 10 cm diameter, semi-round Y maze made of PVC to examine the responses of rats to the odours of other rats (Figure 1). Each choice arm of the maze was ducted at the beginning. Each duct was connected to an extractor fan that drew air along the maze and out the ducts. This was designed to remove odours from each arm of the maze. The extractor fan removed air to outside the trial room.

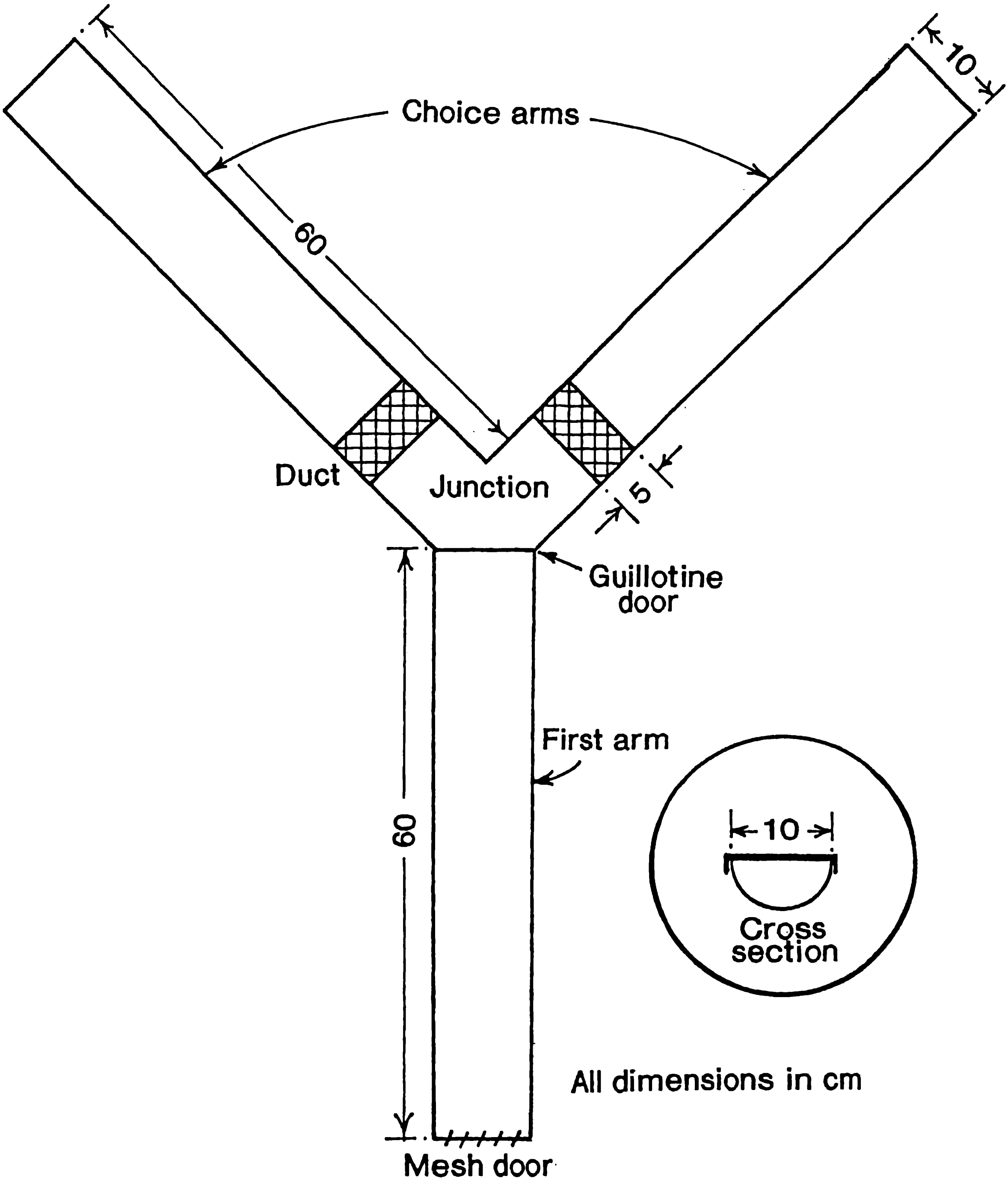

FIG. 1: The Y maze apparatus used to test the choice behaviour of rats when presented with odours of other rats or mice.

Approximately 10 g of thawed bedding from donor rats was placed in one choice arm of the maze. Around 10 g of the animals' own (fresh) bedding was placed in the other choice arm to act as a control. The position of the donor bedding (left or right) was alternated between tests. I washed my hands using hot water and soap between handling each donor odour. The position of the donor bedding and the species of donor were recorded on the videotape after the trial. Three identical mazes were used and after each test, the maze was washed using Vircon soap powder then dried with a towel.

Each sample of nine rats was tested in a trial using the same randomised incomplete block design. Each sample of nine rats was tested against the bedding odours of three donors: ship and Norway rats and either kiore or mice (i.e., conspecifics and two other species). This represents an "incomplete" design because collectively all nine rats were tested against three odours, but each rat was tested only twice. For each sample, tests with conspecific bedding used material from unfamiliar individuals (i.e., caught in different locations and housed at different times or in different rooms), except for the kiore.

There were five trials; each trial lasted two days. Odours were randomly assigned to three positions in each of two blocks. One block was tested per day. Each of the nine rats in the five trials was randomly allocated to a position (and odour) in each block, with the proviso that a rat did not receive the same odour twice. This meant that each (randomly chosen) individual was tested twice, against two different (randomly chosen) odours. Each species odour was used six times in each two-day trial, three times for each sex, with different bedding being used each time. The position of each odour within each block was re-randomised for every trial. Tests began one hour after the lights in the colony had gone off (1100 hrs) and continued sequentially until all animals had been tested. Prior to the start of each test, the rat was placed in the first arm, with the guillotine door shut, for a five-minute acclimation period. The video recorder was then turned on and I left the room. When the guillotine door was opened, from outside the room, the rats were free to explore the maze for fifteen minutes. I recorded: (1) the time until the rat visited each of the arms (a visit occurred when the rat's head was more than 5 cm down the arm); (2) the number of visits to the donor and control arms; (3) the time spent in each arm, as a percentage of the 15 minute test; (4) the distance travelled down each arm, and (5) a total activity score for each rat, which was the number of visits to each arm summed together. The odour being tested and the position of the odour were unknown to me when I scored the rats' behaviour.

*Data Analysis.* I used the Generalised Linear Model (GLM) procedure in MINITAB (version 12.1) to construct models for each of the measures listed above. For Norway rats and kiore, the trial (trial 1 or 2) and the donor odour were specified as predictors. In cases where the trial proved to be a significant predictor, the trials were subsequently analysed separately. If responses did not vary with the trial, they were lumped together for further analysis. I also created separate models to test the effect of the sex of the test animal and the sex of the donor animal. In subsequent analyses, I specified the individual subject as a random effect and the donor odour as a fixed predictor. The animal's sex is an implicit characteristic of the individual and hence is partially accounted for in these models. Tukey's tests were used to elucidate significant pairwise differences. Because ANOVAs are relatively robust, even when their assumptions are violated (Underwood, 1981), I was able to use this type of analysis despite the fact my data did not meet all the assumptions required (the data were not normal and had unequal variances). Furthermore, the ANOVAs, the residual maximum likelihood models and nonparametric methods all yielded very similar results when used on a similar data set (Bramley et al., Chapter 5).

## RESULTS

Exploratory data analysis showed that the data I recorded for the treatment (other rat bedding) and control (own bedding) were very similar for all the variables I measured (Tables 1-4). This may have been because the ducts at the beginning of each arm were not removing the odours from the arms as I expected. For this reason, the bedding of conspecifics was used as a control for the other two odours in all analyses.

*Kiore.* Kiore from the two different trials (those that had completed other experiments and those that had not) were significantly different for all measures I recorded ($F_{1,35} \geq 6.53$, $P \leq 0.016$) except for the amount of time spent in the odour and control arms ($F_{1,35}=0.33$, $P=0.57$ and $F_{1,35}=0.17$, $P=0.69$, respectively). Experimentally naïve animals were less active (mean activity=3.5, s.e.=1.0) than experienced kiore (mean activity=14.4, s.e.=2.8), and took longer to approach the odour arm (mean=4.6%, s.e.=2.4% for experienced animals and mean=61.1%, s.e.=10.1% for naïve animals). Naïve kiore also took longer to approach the control arm tainted with their own odour (mean=11.3%, s.e.=5.6% for experienced animals and mean=61.2%, s.e.=10.2% for naïve animals). Hence each trial was considered separately in subsequent analyses.

The measures I recorded for kiore did not differ significantly according to the sex of the test animal or the donor animal for either trial. The number of visits to the odour arm made by experimentally naïve kiore did not differ for the three donor species I used, nor were any of the other variables that I measured significantly different (Table 1). For kiore that had completed other experiments, the number of visits did vary according to odour, with kiore visiting kiore odours more than Norway rat odours, but not more than the odour of ship rats ($F_{2,17}$=5.15, *P*=0.04; T=-3.08, *P*=0.04 for Norway rats and T=-2.31, *P*=0.12 for Ship rats, Table 2). There were other observable trends in the kiore data set (Tables 1 and 2) that were consistent across the two trials, although the magnitude of the responses varied.

*Ship Rats.* None of the variables I recorded for ship rats differed according to the donor odour (Table 3). Some ship rat responses varied with the sex of the individual being tested: (1) the number of visits to the odour ($F_{1,17}$= 11.94, *P*=0.004); (2) the number of visits to the control ($F_{1,17}$= 8.67, *P*=0.011); (3) the time in the control arm ($F_{1,17}$= 9.82, *P*=0.008), and (4) the activity ($F_{1,17}$= 11.38, *P*=0.005). Female rats made more visits to both arms, spent longer in the control arm and were more active. The sex of the donor was not a significant predictor for any of the variables I recorded.

Table 1: Mean Responses (± 1 s.e. of mean) of Experimentally Naïve kiore (n=6) to the Odour of Other Rat species in a Y Maze.*

| Donor species | Visits to odour | Time in odour arm (% of test) | Distance towards odour (cm) | Visits to control arm | Time in control arm (% of test) | Distance towards control (cm) | Activity | Time to approach odour (% of test) | Time to approach control (% of test) |
|---|---|---|---|---|---|---|---|---|---|
| Kiore | 2.3±1.3 | 24.1±12.5 | 30.0±13.4 | 1.7±1.3 | 3.4±2.6 | 19.3±12.2 | 4.0±2.5 | 59.1±19.3 | 82.1±14.2 |
| Ship rat | 1.5±0.8 | 5.1±2.4 | 36.7±11.8 | 1.8±0.7 | 22.4±14.6 | 37.3±11.8 | 3.5±1.5 | 59.7±19.1 | 49.7±21.2 |
| Norway rat | 1.7±0.7 | 14.1±7.4 | 30.0±13.4 | 1.3±0.6 | 30.2±15.8 | 40.0±12.6 | 3.0±1.1 | 64.5±17.5 | 51.8±16.7 |

* Time measures are shown as the mean percentage of six 15 minute tests.

TABLE 2: MEAN RESPONSES (± 1 S.E. OF MEAN) OF EXPERIMENTALLY EXPERIENCED KIORE (N=6) TO THE ODOUR OF OTHER RAT SPECIES IN A Y MAZE.*

| Donor species | Visits to odour | Time in odour arm (% of test) | Distance towards odour (cm) | Visits to control arm | Time in control arm (% of test) | Distance towards control (cm) | Activity | Time to approach odour (% of test) | Time to approach control (% of test) |
|---|---|---|---|---|---|---|---|---|---|
| Kiore | 10.0±3.6$^{a}$ | 25.8±11.6 | 52.1±2.8 | 7.5±3.3 | 8.6±2.9 | 43.0±8.9 | 17.5±6.7 | 2.0±0.7 | 18.6±16.3 |
| Ship rat | 7.3±2.2$^{ab}$ | 21.7±13.3 | 56.8±3.0 | 6.5±1.8 | 11.4±3.7 | 53.4±2.3 | 13.8±3.7 | 3.2±1.2 | 4.4±1.5 |
| Norway rat | 6.2±2.0$^{b}$ | 9.0±2.3 | 52.9±1.2 | 5.8±2.0 | 25.7±13.4 | 57.6±1.1 | 12.0±3.9 | 8.5±7.1 | 10.8±5.9 |

Values marked with different letters are significantly different at $P$=0.05. Unmarked values are statistically indistinguishable from others in the same column. Time measures are shown as the mean percentage of six 15 minute test.

*Norway Rats.* The video recorder failed to operate for one test where a female Norway rat from Kapiti Island was exposed to a Norway donor, so this reduced my sample size to 11 for Norway rat donors. In the other tests, none of the variables I measured for Norway rats that received ship rat or Norway rat odours were significantly different between the two trials (rats from Kapiti Island and rats from North Island), so they were pooled for further analysis. None of the measures varied with the donor odour (Norway and ship rat, kiore and mice; Table 4) although the activity of rats bordered on significance ($F_{3,34}$=2.55, *P*=0.09). There was no consistent trend evident in Table 4. Most Norway rat responses varied with sex: (1) the number of visits to the odour ($F_{1,34}$= 23.8, *P*=0.0001); (2) the time spent in the odour arm ($F_{1,34}$= 5.62, *P*=0.025); (3) the number of visits to the control arm ($F_{1,34}$= 12.21, *P*=0.002); (4) the distance travelled down the control arm ($F_{1,34}$= 4.39, *P*=0.045); (5) the overall activity ($F_{1,34}$= 19.77, *P*=0.0001); (6) the time taken to approach the odour arm ($F_{1,34}$= 9.52, *P*=0.004), and (7) the time taken to approach the control arm ($F_{1,34}$= 7.26, *P*=0.012). The distance travelled down the odour arm may have differed according to the sex of the test animal ($F_{1,34}$= 3.86, *P*=0.059). In general, female rats were more active and left the first arm earlier. The sex of the donor animal was not significant in predicting any of the responses by Norway rats.

TABLE 3: MEAN RESPONSES (± 1 S.E. OF MEAN) OF SHIP RATS (N=6) TO THE ODOUR OF OTHER RAT SPECIES IN A Y MAZE.*

| Donor species | Visits to odour | Time in odour arm (% of test) | Distance towards odour (cm) | Visits to control arm | Time in control arm (% of test) | Distance towards control (cm) | Activity | Time to approach odour (% of test) | Time to approach control (% of test) |
|---|---|---|---|---|---|---|---|---|---|
| Kiore | 13.0±4.5 | 33.7±10.3 | 54.8±2.3 | 14.8±6.8 | 16.0±2.6 | 53.2±3.4 | 27.8±11.3 | 3.1±1.2 | 1.6±0.8 |
| Ship rat | 21.2±6.6 | 29.7±8.2 | 53.6±2.2 | 19.7±5.4 | 14.6±3.1 | 53.0±3.0 | 40.8±11.4 | 7.4±4.4 | 4.4±3.6 |
| Norway rat | 16.2±5.1 | 21.9±7.3 | 58.2±1.1 | 18.5±7.2 | 15.1±3.4 | 53.1±2.7 | 34.7±12.1 | 3.8±1.6 | 0.9±0.3 |

* Time measures are shown as the mean percentage of six 15 minute tests.

TABLE 4: MEAN RESPONSES (± 1 S.E. OF MEAN) OF NORWAY RATS TO THE ODOUR OF OTHER RODENT SPECIES IN A Y MAZE.*

| Donor species | Visits to odour | Time in odour arm | Distance towards odour(cm) | Visits to control arm | Time in control arm | Distance towards control (cm) | Activity | Time to approach odour (% of test) | Time to approach control (% of test) |
|---|---|---|---|---|---|---|---|---|---|
| House mouse (n=6K) | 3.3±0.7 | 22.9±12.4 | 42.5±6.1 | 3.2±1.2 | 20.8±13.6 | 52.0±5.8 | 6.5±1.8 | 5.4±6.8 | 6.4±5.7 |
| Kiore (n=6N) | 2.3±0.8 | 10.2±4.4 | 46.3±10.0 | 1.8±0.5 | 4.6±1.7 | 50.0±10.0 | 4.2±1.2 | 44.2±29.7 | 43.7±34.2 |
| Ship rat (n=6K, 6N) | 4.1±0.9 | 24.4±8.7 | 49.3±4.9 | 3.2±0.9 | 15.7±7.2 | 49.0±6.7 | 7.3±1.7 | 15.2±32.3 | 22.7±37.3 |
| Norway rat (n=5K, 6N) | 3.5±0.6 | 33.2±9.6 | 52.9±5.4 | 3.3±0.5 | 8.5±2.3 | 50.3±5.7 | 6.8±1.1 | 14.1±29.7 | 15.1±29.5 |

* Norway rats were from two sources (six from Kapiti Island and six from North Island, New Zealand). The number of Norway rats used in each trial and the source (K=Kapiti, N=North Island) is shown in brackets. Time measures are shown as the mean percentage of six 15 minute tests.

# DISCUSSION

*The Role of Odours.* Odours are thought to mediate some intraspecific competitive interactions (e.g., Summerlin and Wolfe, 1973) and may also function in interspecific interactions (Krasnov and Khoklova, 1996). My study however, demonstrates no clear or common pattern of rat responses to heterospecific odours, although heterospecific odours might modify the behaviour of kiore. Nonetheless, it seems likely that all rats tested could discriminate between the odours tested (Stoddart, 1980; Nef, 1998). Further experiments are needed to confirm my results using kiore that have coexisted with other rat species. Stapp and Van Horne (1996) used odour-scented traps to capture a range of rodents in North American short-grass prairie. The animals they caught did not avoid traps scented with heterospecific odour, and they concluded that odours did not help to explain rodent distribution in short-grass prairie. Gurnell and Little (1992), using similar methods, reached the same conclusion for woodland rodents in Britain. Live trapping studies using traps tainted with the odour of competitors could also be used to investigate the effect of the residual odours of one species on the trapping rate of another species in New Zealand. In order to accumulate data, such studies rely on an animal entering a trap. Trapping studies can be unreliable because there are many possible reasons why an animal might not enter a trap, regardless of whether it is tainted with odour or not. For example, the bait might be unattractive, the animal might be trap shy, it might be neophobic, it may not encounter the trap, or the animal may fail to correctly spring the trap's mechanism and escape. Dickman (1992) used tainted traps to detect predator avoidance in mice (*Mus domesticus*) and then verified his results by introducing both predator-naïve and predator-experienced mice to areas with predators and measured their survival. A similar approach would indicate the relative advantages of detecting competitors for rats in New Zealand.

I found that kiore that had experienced the maze before, in other experiments, were more likely to explore it, and inexperienced animals were less likely to. Since both groups of rats I studied showed the same trend, but experienced kiore were generally more active, I consider it unlikely that the use of the other rats in prior experiments has seriously affected their ability to respond normally to the odours in these experiments. The neophobia (or new place aversion) shown by the kiore I studied was not recorded by Cowan (1977), who reported that the three rat species he studied readily investigated new places, but avoided new objects in familiar places. Cowan's study did not include kiore.

The overall activity of ship and Norway rats varied with sex. The other significant differences between sexes (e.g., in the number of visits to the odour, the time spent in the odour arm or the time taken to approach the odour arm), that I recorded are likely to be a function of this difference in activity. I cannot explain why male ship and Norway rats should be less active.

*Intraspecific Interactions in the Wild.* How rodents respond to the odour of conspecifics in their habitat has not been widely studied. Atkinson and Moller (1990) reported that kiore avoided each other except during the mating season, when males were attracted to females. They also concluded that kiore did not associate with members of their family after weaning. Thus, on the basis of Atkinson and Moller's (1990) review, one might predict that the adult kiore I studied would avoid the odour of other kiore in my trials. However, I recorded radio-tagged adult kiore together on several occasions in autumn and winter (outside breeding season) and could find no evidence that adult kiore of either sex avoided each other under natural conditions (Bramley et al., Chapter 2). I do not know if the radio-carrying kiore I followed were related or not. The kiore I used in these experiments arrived in one cage and were kept in same-sex pairs prior to testing. I saw no evidence of aggressive encounters and neither did Barbehenn and Strecker (1962) who observed wild kiore. Strecker and Jackson (1962) kept kiore in captivity and reported that there might be "momentary antagonistic behaviour" between a resident and a newly introduced kiore in a cage, but henceforth there was no aggression noted. Strecker and Jackson (1962) also caged kiore with ship rats without difficulty.

Norway rats are colonial, with colonies consisting of females and a resident male. At high densities, strangers are readily tolerated (Moors, 1990). Thus Norway rats could be expected to readily associate with other Norway rats, possibly even those that are foreign to them, in my trials. Odours are important to Norway rats who seem to recognise other individuals by smell alone (Gheusi et al., 1997). Laboratory Norway rats also use olfactory stimuli for accurate orientation in open environment tests (Lavenex and Schenk, 1998). It is likely that Norway rats recognise the social status of other rats based on odour cues alone, as some other rodents do (e.g., Hispid cotton rats (*Sigmodon hispidus*); Summerlin and Wolfe, 1973; and laboratory mice; Drickamer, 1997).

McCartney and Marks (1973) kept colonies of both ship rats and kiore. They reported that ship rats were less aggressive to other individuals than kiore were. Ship rats are apparently evenly dispersed through habitat (Hooker and Innes, 1995). Home ranges of radio-carrying female ship rats at Rotoehu (North Island, New Zealand) were contiguous and did not overlap, whilst male home ranges were larger, and overlapped those of both females, and other males (Hooker and Innes, 1995). Ship rats appear to know their neighbours, because they recognise their absence and take over their ranges quickly if the neighbour is removed (Innes, 1990). Therefore, ship rats might be expected to investigate readily the smell of other ship rats to acquire information about the other rat.

*Interspecific Competition and Coexistence.* A characteristic feature of the ecology of the three species under consideration in this study is the variation in their degree of association both in New Zealand (Taylor, 1984; Atkinson and Moller, 1990) and throughout the Pacific region (Marshall, 1962; Jackson and Strecker, 1962; Tomich, 1986). Competition has been demonstrated in other rodent populations (e.g., Dueser and Porter, 1986) and could explain the observed rat distribution, although there may be other factors, such as the distribution of predators, involved (Taylor, 1984).

It is possible that the different sizes of the three species (kiore being the smallest; Norway rats the largest) might explain the apparent sensitivity of kiore to odours since body size is likely to affect habitat use and predation risk. However, Vasquez (1996) argued that larger (not smaller) animals might be more sensitive to the risk of predation because they could escape less easily. Competitive ability might also be affected by body size, but in the opposite way: smaller rodents might be more sensitive to the odour of other rats since they have only their agility to rely on to escape from a physical encounter with a larger, more powerful rat of another species. This might explain any differential sensitivity since the benefits of identifying competitors could be higher than the costs for small species, but not for larger ones.

McCartney and Marks (1973) reported that ship rats dominated kiore in behavioural tests and speculated that this subordination of kiore might lower the reproductive rate of kiore in areas where they were sympatric with ship rats. Although it remains to be tested, it seems likely that the larger Norway rat would behaviourally dominate over both the other species. However, Norway rats might be outcompeted ecologically by the ship rat in some areas. The only field studies to investigate coexistence have used kill-trapping and have examined diet and microhabitat use between Norway and kiore on Kapiti (Dick 1985 unpubl.; Bramley et al., Chapter 2), and habitat use and diet of all three species on Stewart Island (Sturmer 1988, unpubl.). Dick (1985, unpubl.) and I (Chapter 2) disagreed over the statistical significance of the reciprocal distribution in both time and space revealed by kill-trapping on Kapiti Island. Nonetheless, both authors reported habitat differences and concluded it was likely that competition, rather than habitat preferences, caused this segregation. Sturmer (1988, unpubl.) caught the three species of rat in different areas on Stewart Island and noted dietary differences between them. He concluded that interference competition, particularly between kiore and Norway rats, might be a factor influencing rat distribution there. Sturmer

(1988, unpubl.) did not measure food availability at the sites so was unable to demonstrate food shortages.

The detectability of interference competition is often lessened in dense populations (such as those on islands; Gliwicz 1980; Gray and Hurst, 1998), perhaps because fewer competitive interactions happen. There may be fewer interactions because the costs incurred by animals maintaining the interference at high densities are prohibitive (Gray and Hurst, 1998). Paradoxically, one might expect more visible competitive interactions in denser populations because animals are more likely to come into contact with each other when there are more animals. The simplest way around this paradox would be to conduct experiments in large enclosures where the density and species composition could be manipulated to determine the relative effects of density and competition on behaviour. It should also be possible to test the relative efficacy of odours as cues in large enclosures by applying odours to areas and measuring visitation rate and behaviour. This would allow authors to interpret whether odours moderate interactions or not (e.g., Drickamer, 1997).

## REFERENCES

ABRAMSKY, Z., ROSENWEIG, M.L., and SUBACH, A. 1998. Do gerbils care more about competition or predation? *Oikos* 83:75-84.

ATKINSON, I.A.E., and MOLLER, H. 1990. Kiore, pp. 175-192, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

BARBEHENN, K.R., and STRECKER, R.L. 1962. Intra- and Interspecific Behavior A. Field data, pp. 166-172, *in* T.I. Storer (ed.). Pacific Island rat ecology: Report of a study made on Ponape and adjacent islands 1955-1958. Bernice P. Bishop Museum, Bulletin 225. Honolulu, Hawaii.

BEGON, M., HARPER, J.L., and TOWNSEND, C.R. 1990. Ecology: Individuals, Populations and Communities. Second edition. Blackwell Scientific Publications. Melbourne, Australia.

BOUSKILA, A. 1995. Interactions between predation risk and competition: A field study of kangaroo rats and snakes. *Ecology* 76:165-178.

BROWN, R.E. 1985. The rodents II: Suborder Myomorpha, pp. 345-457, *in* R.E. Brown and D.W. MacDonald (eds.). Social Odours in Mammals, Volume 1. Oxford University Press, Oxford, United Kingdom.

BROWN, J.H., and MUNGER, J.C. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology* 66:1545-1563.

COWAN, P.E. 1977. Neophobia and Neophilia: New object and new place reactions of three *Rattus* species. *J. Comp. Physiol. Psych.* 91:63-71.

DICK, A.M.P. 1985. Rats on Kapiti Island. Coexistence and diet of *R. norvegicus* (Berkenhout) and *R. exulans* (Peale). Unpublished MSc. thesis, Department of Botany and Zoology, Massey University, Palmerston North, New Zealand.

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

DRICKAMER, L.C. 1997. Responses to odors of dominant and subordinate house mice (*Mus domesticus*) in live traps and responses to odors in live traps by dominant and subordinate males. *J. Chem. Ecol.* 23:2493-2506.

DUESER, R.D., and PORTER, J.H. 1986. Habitat use by insular small mammals: relative effects of competition and habitat structure. *Ecology* 67:195-201.

ECKE, D.H. 1958. Analysis of populations of the roof rat in southwest Georgia. *United States Public Health Monograph* 27:1-18.

GHEUSI, G., GOODALL, G., and DANTZER, R. 1997. Individually distinctive odours represent individual conspecifics in rats. *Anim. Behav.* 53:935-944.

GLASS, G.E., and SLADE, N.A. 1980. The effect of *Sigmodon hispidus* on spatial and temporal activity of *Microtus ochrogaster*: evidence for competition. *Ecology* 61: 358-370.

GLIWICZ, J. 1980. Island populations of rodents: Their organisation and functioning. *Biol. Rev.* 55:109-138.

GOODYEAR, N.C. 1992. Spatial overlap and dietary selection of native rice rats and exotic black rats. *J. Mamm.* 73:186-200.

GRAY, S.J., and HURST, J.L. 1998. Competitive behaviour in an island population of house mice, *Mus domesticus*. *Anim. Behav.* 56:1291-1299.

GURNELL, J., and LITTLE, J. 1992. The influence of trap residual odour on catching woodland rodents. *Anim. Behav.* 43:623-632.

HERRERA, E.A., and MACDONALD, D.W. 1994. Social significance of scent marking in capybaras. *J. Mamm.* 75:410-415.

HOOKER, S., and INNES, J.G. 1995. Ranging behaviour of forest-dwelling ship rats, *Rattus rattus*, and effects of poisoning with Brodifacoum. *N.Z. J. Zool.* 22:291-304.

INNES, J.G. 1990. Ship rat, pp. 206-225, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

JACKSON, W.B., and STRECKER, R.L. 1962. Ecological distribution and relative numbers, pp. 45- 63, *in* T.I. Storer (ed.). Pacific Island rat ecology: Report of a study made on Ponape and adjacent islands 1955-1958. Bernice P. Bishop Museum, Bulletin 225. Honolulu, Hawaii.

KING, C.M., INNES, J.G., FLUX, M., and KIMBERLEY, M.O. 1996. Population biology of small mammals in Pureora Forest Park: 2. The feral house mouse (*Mus musculus*). *N.Z. J. Ecol.* 20:253-269.

KRASNOV, B., and KHOKLOVA, I. 1996. Discrimination of midday jird's odour by house mice. *Anim. Behav.* 52:659-665.

LAVENEX, P., and SCHENK, F. 1998. Olfactory traces and spatial learning in rats. *Anim. Behav.* 56:1129-1136.

MARSHALL, J.T. 1962. Geographic distribution and colour phases of Micronesian rodents, pp. 39-43, *in* T.I. Storer (ed.). Pacific Island rat ecology: Report of a study made on Ponape and adjacent islands 1955-1958. Bernice P. Bishop Museum, bulletin No. 225. Honolulu, Hawaii.

MACDONALD, D.W. 1984. Editor. The Encyclopedia of Mammals: Volume 2. George Allen and Unwin. London, United Kingdom.

MCCARTNEY, W.C., and MARKS, J. 1973. Inter and intraspecific aggression in two species of the genus *Rattus*: evolutionary and competitive implications. *Proc. PA. Acad. Sci.* 47:145-148.

MOORS, P.J. 1990. Norway rat, pp. 192-206, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

MURPHY, E.C., and PICKARD, C.R. 1990. House mouse, pp. 225-242, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

NEF, P. 1998. How we smell: The molecular and cellular bases of olfaction. *News Physiol. Sci.* 13:1-5.

ROBERTS, M. 1991. Parasitological evidence for the presence of other rodent species on "kiore only" islands. *J. Roy. Soc. N.Z.* 21:349-356.

STAPP, P., and VAN HORNE, B. 1996. Do olfactory cues mediate interactions between rodents on northern shortgrass prairie? *Can. J. Zool.* 74:226-232.

STODDART, D.M. 1980. The Ecology of Vertebrate Olfaction. Chapman and Hall. London, United Kingdom.

STRECKER, R.L., and JACKSON, W.B. 1962. Intra- and interspecific behavior B. Data from captive rats, pp. 173-176, *in* T.I. Storer (ed.). Pacific Island rat ecology: Report of a study made on Ponape and adjacent islands 1955-1958. Bernice P. Bishop Museum, Bulletin 225. Honolulu, Hawaii.

STURMER, A.T. 1988. Diet and coexistence of *Rattus rattus* (Linnaeus), *R. exulans* (Peale) and *R. norvegicus* (Berkenhout) on Stewart Island, New

Zealand. Unpublished MSc. thesis, Department of Botany and Zoology, Massey University, Palmerston North, New Zealand.

SUMMERLIN, C.T., and WOLFE, J.L. 1973. Social influences on trap response of the cotton rat *Sigmodon hispidus*. *Ecology* 54:1156-1159.

TAYLOR, R.H. 1984. Distribution and interactions of introduced rodents and carnivores in New Zealand. *Acta Zool. Fenn.* 172:103-105.

TOMICH, P.Q. 1986. Mammals in Hawaii: A synopsis and notational bibliography. Second edition. Bishop Museum Press, Honolulu, Hawaii.

UNDERWOOD, A.J. 1981. Techniques of Analysis of Variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.* 16:513-605.

VASQUEZ, R.A. 1996. Patch utilization by three species of Chilean rodents differing in body size and mode of locomotion. *Ecology* 77:2343-2351.

WATSON, J.S. 1961. Rats in New Zealand: a problem of interspecific competition. *Proc. 9th Pacific Science Congress* 19:15-16.

ZIV, Y., ABRAMSKY, Z., KOTLER, B.P., and SUBACH, A. 1993. Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos* 66:237-246.

# CHAPTER FOUR: BEHAVIOURAL AND REPRODUCTIVE RESPONSES OF MICE (*MUS MUSCULUS*) TO RATS (*RATTUS RATTUS, R. NORVEGICUS* AND *R. EXULANS*) IN LABORATORY TRIALS.

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**Abstract** – Ship rats (*Rattus rattus*) and house mice (*Mus musculus*) are the two most commonly occurring species of rodent on the North and South Islands of New Zealand. When ship rats are removed by poisoning, the detectability of mice in tracking tunnels and snap traps increases. This increase in detectability could be explained by an increase in activity of mice, or by an increase in the number of mice, when rats are removed. We attempted to distinguish between these hypotheses by measuring the behavioural and reproductive responses of house mice to the odour or presence of rats (ship rats, Norway rats, *R. norvegicus*, and Polynesian rats, *R. exulans*) in three separate experiments. We tested four hypotheses: (1) that mice could discriminate between their own odour and that of other rodents and avoid the odour of rats in a Y maze; (2) that mice are less active and more secretive in the presence of a caged ship rat; (3) that

mice reduce their reproductive rate when continuously exposed to the odour of ship rats in their home cages; and (4) that mice that had recently encountered a live ship rat would are more likely to avoid the odour of rats than mice who had not recently encountered a ship rat. Wood shavings that had been used as bedding by rats provided odours. Wild house mice did not avoid the odour of rats in a Y maze, even after recent experience with a ship rat, and spent significantly more time in the arm containing rat bedding. We used a two-sided arena to investigate the responses of wild mice to caged ship rats. Mice were introduced to the arena twice; once alone and once with a caged ship rat on one side of the arena. The ship rat's presence resulted in mice being less active and swapping sides of the arena less often than when they were alone. However, mice were not less secretive and spent similar amounts of time in each side of the arena regardless of whether a rat was present or not. We were unable to get wild mice to breed in captivity. Instead, we used Swiss-strain laboratory white mice to investigate the reproductive responses of mice to the odour of ship rats in their home cage and found that mice that received ship rat-tainted bedding had larger litters than control mice that had received clean bedding. The birth-weight of pups did not vary between treatments, but at weaning, pups that had been reared in rat-tainted environments may have weighed less than those reared in control environments. The birth-weight and weaning-weight of individuals are not independent. We tested the responses of Swiss-strain laboratory mice to ship rat odour in a Y maze. Swiss-strain mice showed the same behavioural responses to ship rat odour that wild mice did, and were probably a suitable substitute in this instance. Thus it appears that rats might influence the activity of mice, but this

influence is not odour mediated. Furthermore, mouse reproduction is unaffected by the mere presence of ship rats. It appears that the increase in detectability shown by house mice within days of rats removal may be due to a short-term increase in activity. We cannot rule out that long-term increases in mouse abundance are due to a reduction in rat predation.

**Keywords** - ship rats, *Rattus rattus*, house mouse, *Mus musculus*, rodents, interspecific communication, odours, rat-mouse interactions.

## INTRODUCTION

Ship rats (*Rattus rattus*) and mice (*Mus musculus*[1]) are the most commonly occurring rodents on the North and South Islands of New Zealand (Innes, 1990; Murphy and Pickard, 1990). Both species are found in a wide variety of habitats including forests, grasslands and as commensals with man; however they are not equally common in all habitats. At Pureora Forest Park, in the central North Island, mice were most common in "disturbed" habitats (i.e., grassland, road edges and young exotic plantation forest; King et al., 1996a), while ship rats were most common in older native broadleaf/podocarp forest. In the South Island, mice were common in southern beech (*Nothofagus*) forest where ship rats were much less abundant (King, 1982; King and Moller, 1997). It appears that when ship rats, cats and mustelid predators are common, mice survive only in areas with dense ground cover (Brown et al., 1996; King et al., 1996a).

In New Zealand, ship rats and mice are regularly monitored as part of the Department of Conservation's management operations to protect native species (Innes et al., 1995). The method used to detect the presence of rats and mice relies on tracking tunnels devised by King and Edgar (1977), in which the animal walks across a pad soaked in either dilute ferric nitrate or a dye located in the middle of a small tunnel. Animals leave footprints on either treated (with tannic acid, used in tunnels with ferric nitrate pads), or untreated (used in tunnels with dye pads) papers, located on either side of the dye as they leave the tunnel. Tunnels are usually baited with peanut butter and set for one or more nights. The papers are collected and scored daily for the presence of rodents or mustelids. Brown et al.(1996) were able to show a linear relationship between the density of ship rats and the number of tracking tunnels marked with rat footprints at one locality, so tracking tunnels have also been used for estimating rat abundance.

Brown et al. (1996) showed that ship rats and mice predominated in different habitats at Kaharoa (central North Island) with mice most common in scrubland and rats most common in forest. Both species, however, were recorded at both sites. Brown et al. (1996) removed ship rats and mice by kill-trapping to calibrate tracking tunnels as an index of abundance. As rats were removed, the rate at which mice used tracking tunnels significantly increased, despite the fact that mice were also being removed. This increase in the observability of mice has also been recorded by other authors after ship rat poisoning operations (Clout et al., 1995; Innes et al., 1995; Miller and Miller, 1995) and suggests that ship

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[1] Two separate species of mice are recognised: *Mus musculus* from Britain and Western Europe and *Mus domesticus* from Scandinavia and Eastern Europe. Mice in New Zealand share characteristics with both species, and await genetic determination (Murphy and Pickard, 1990).

rats might affect the demography and behaviour of mice in some habitats. From studies on other rodents, we see three, possibly interacting, ways that rats might affect the observability of mice in New Zealand forest: (1) rats might reduce the activity of mice at some times or places where they coexist (Ziv et al., 1993; Bouskila, 1995). This reduction may be observed because rats exclude mice from some areas; (2) rats may suppress the breeding of mice so that the productivity of mice in sympatric areas is lower (Ylonen and Ronkainen, 1994); or (3) rats might eat mice, and thereby reduce their numbers directly. Brown et al. (1996) seem to regard rats as predators of mice, and King et al. (1996b) recorded low recruitment in the presence of ship rats, but no study has demonstrated incidences of rat predation on mice.

The nature of the relationship between ship rats and mice is unknown, but it is plausible that rats eat mice, especially pups. King et al. (1996b) reported that fewer young mice were recruited in the interior of native forest than in the "disturbed" habitats they examined. Because there were no differences between habitats in breeding rates, this observation implies predation on young mice, perhaps by rats. Rats and mice may also compete for resources, since they eat similar foods (Innes, 1990; Murphy and Pickard, 1990). Competition between mammal species has usually been inferred from observations of territoriality and fighting between species, from microhabitat separation at high (but not low) density, or from rapid responses by one species to the removal of the other (Glass and Slade, 1980; Brown and Munger, 1986; Dickman,1991; Goodyear, 1992; Haering and Fox, 1995; Tomblin and Adler, 1998), but such observations have yet to be collected for rats and mice in New Zealand.

Dickman (1991) suggested that competing insectivores (species of *Sorex* and *Antechinus*) might detect each other's presence using olfactory or auditory cues. In addition, Krasnov and Khoklova (1996) found that mice avoided the odours of midday jirds (*Meriones meridianus*) in Y maze tests. Midday jirds are gerbils that compete with mice and are strongly avoided by mice in the semi-desert grasslands where they coexist. Mice use volatile compounds (some of which are listed in Goodrich et al., 1990) in conspecific urine and faeces to communicate with conspecifics (Goodrich et al., 1990; Hurst et al., 1994; Hurst and Barnard, 1995; Kavaliers and Colwell, 1993 and 1995). Mice are apparently able to discriminate heterospecific odour too, although this ability may not be innate (Dickman, 1992; Krasnov and Khoklova, 1996) and may depend on the test conditions (Garbe et al., 1993). In addition, laboratory mice have also shown an aversion to predator odours under some conditions (Garbe et al., 1993). Thus, it is possible that odours may be used, at least in part, to mediate interactions between mice and ship rats in New Zealand.

Rats and mice are difficult to study in the wild, because they are small and nocturnal. Different species and age classes are not equally trappable in the same traps (King et al., 1996a; King and Moller, 1997). Furthermore, it seems likely that the presence and trapping rate of one species would influence the presence and trapping rate of the other species, as it does in some other sympatric rodent populations (Krasnov and Khoklova, 1996). The hypotheses we wished to test were also difficult to approach in the wild because they required manipulations not easily achieved on a landscape scale. Instead, we used wild-caught mice held in a laboratory to test four hypotheses. Our hypotheses were: (1) that mice discriminate between their own odour and that of heterospecific rodents (ship rat, Norway rat, *Rattus norvegicus,* and kiore or Polynesian rat, *R. exulans*), and avoid heterospecific odour in a Y maze; (2) that mice are less active in the presence of a (caged) ship rat and use areas that provided more cover when a rat was present; (3) that mice reduce their reproductive rate when continuously exposed to the scent of ship rats in their bedding and cage; and (4) that experience of an encounter with a ship rat makes mice more likely to avoid the odour of rats in future trials. We conducted three experiments to test these hypotheses using wild-caught and laboratory bred mice.

## METHODS

*Experimental Animals.* We used a total of 18 wild-caught mice (divided into two groups of nine) in experiment 1 and an additional two (making 20) wild-caught mice in experiment 2. Mice used in experiments 1 and 2 were caught in houses in Hamilton City or farms in the Waikato region, where they presumably coexisted with ship rats and/or Norway rats (Innes, 1990; Moors, 1990). Mice were caught using Longworth small mammal traps (Penlon Ltd, Abingdon, England) baited with chocolate, bacon or grains of maize. Wild-caught mice had spent up to 6 months in captivity before the experiments commenced. We tried to get wild mice to breed in captivity on four occasions, but were unsuccessful each time. Mice used in experiment 3 were Swiss strain white laboratory mice, bred by AgResearch Ruakura (Hamilton, New Zealand), and were 6-13 weeks old when the experiments began. The laboratory mice had not come into direct contact with rats of any kind.

When not participating in breeding experiments, all mice were housed individually in opaque plastic tubs with wire tops (40 x 27 x 15 cm deep) or in glass aquaria measuring 60 x 30 x 30 cm deep. During the breeding experiments, all mice were held in plastic tubs. The plastic tubs had previously housed kiore, but had been cleaned twice with hot water and Vircon, a low foaming, low odour detergent, before mice inhabited them. Wood shavings covered the bottom of the cages and aquaria as bedding. All mice were provided with cardboard or plastic tubes and a tin can to act as retreats, along with shredded paper as further bedding material. Shavings and paper were changed fortnightly for wild mice (to minimise disturbance) and weekly for white mice. All mice had *ad libitum* access to water and food (Sharpes Diet 86 rat chow, Sharpes Grains and Seeds, Lower Hutt, New Zealand).

*Experiment 1*: *Donor Odours*. Sawdust bedding was collected from a total of 75 animals (30 kiore, 21 ship rats and 24 Norway rats) weekly for two weeks (Bramley, Chapter 3). This bedding was tainted with urine and faeces, and was used as a "donor" source of the species odour for the trials. The bedding of three randomly chosen, same sex, conspecific individuals was pooled into plastic bags, sealed, and stored frozen for periods of up to eighteen months in the same freezer before the mice were tested. Nine of the mice were tested on 23 and 24 June 1998; the remaining nine were tested on 16 and 17 July 1998. Mice tested in the second group of trials had encountered live ship rats 6-7 days previously (experiment 2).

*Experimental Tests*. The wild-caught mice were kept on a constant 14:10 light:dark schedule, with lights on at 2000 hrs, at temperatures between 15 and

24°C. We used a 10 cm diameter semi-round Y maze made of PVC as a test arena for mice (Figure 1). The maze was ducted at the beginning of each choice arm to draw any odour down the arms and out of the maze. The extractor fan that sucked air through the maze expelled it outside the trial room. Approximately 10 g of thawed bedding from donor rats was placed in one choice arm of the maze. Around 10 g of the animals' own (fresh) bedding was placed in the other choice arm as a control. The position of the donor bedding (left or right) was alternated. Each frozen odour had been allowed to thaw before use. Two identical mazes were used and after each test the maze was washed using Vircon soap powder and then towel-dried.

Animals were collected one at a time from the captive colony and transported in their cages, in darkness, to a separate trial room. They were then transferred into the experimental arena illuminated with red light. When the animals were in the maze, the red light was turned off and all observations were completed using infra-red light sources. Mice were free to explore immediately, but we did not begin to record behaviours until 1 minute after the observer had left the room. This allowed the mice time to settle down after we had left. Each test was 15 minutes long. Tests were recorded using a Videotronic Tri-Q CCD camera and Panasonic AG5260 video recorder. After each test, we returned each animal to its cage and then to the captive colony.

Each group of nine mice was tested in a trial using the same randomised incomplete block design. The design used two blocks, and tested each group against the bedding odours of all three types of rat: ship, Norway and kiore. Each of the nine mice was randomly allocated to a position in each block, with the proviso that it did not meet the same donor species twice. This meant that each mouse was tested twice, against two different donor species odours (hence the "incomplete" block design). Each donor species was used six times in each trial, three times for each sex, using different bedding each time. The position of each donor odour was randomised within each block for each trial. Thus there were two trials, each trial lasted two days and tested nine animals. All nine animals were tested once on both days.

Tests began one hour after the lights in the colony had gone off (1100 hrs) and continued sequentially until all animals had been tested. We recorded: (1) the time taken until the mouse visited each of the arms. A visit was defined as when the animal's body (not including the tail) was more than 5 cm down the arm; (2) the number of visits to the donor and control arms; (3) the time spent in each arm, and (4) a total activity score for each mouse, which was the number of visits to each arm summed together. Time measures were converted to a percentage of the total (15 minute) trial for analysis. The position of the donor bedding and the species of donor were recorded on the videotape after the trial, but were unknown to us when we scored the mouse's behaviour.

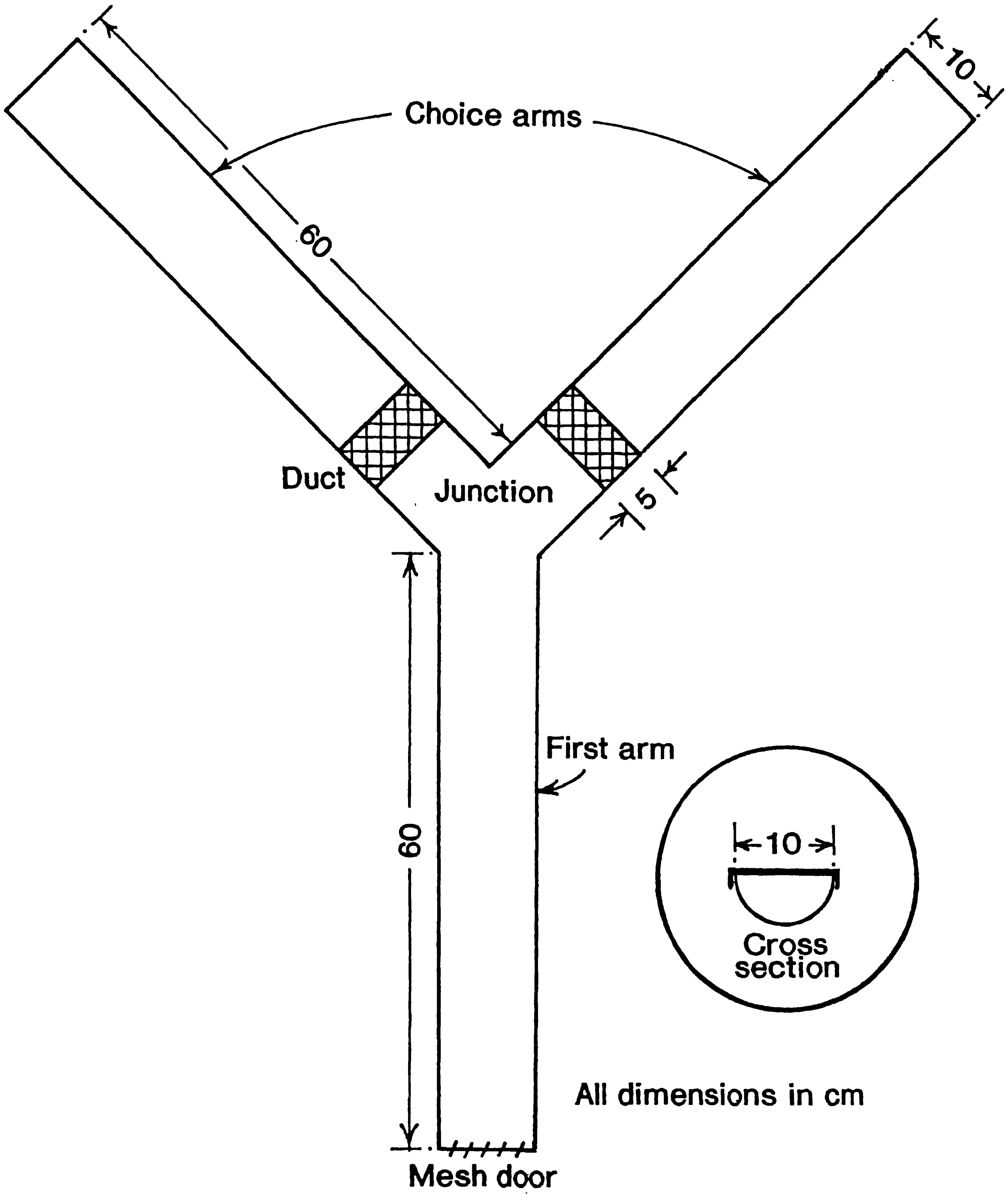

FIG. 1: The Y Maze apparatus used to test mouse responses to rat odours.

*Data Analysis*. We used the Generalised Linear Model (GLM) function of MINITAB (version 12.1) to perform an analysis of variance for each of the variables we measured, specifying odour (1-3) and trial number (1 or 2) as fixed effects and mouse (1-18) as a random effect. This allowed us to determine whether mice responded differently to different rat odours, and also if recent experience with a live ship rat affected mouse behaviour. To obtain response variables, we subtracted the number of visits to the control arm, the time spent in the control arm and the time taken to approach the control arm from the equivalent measures for the odour arms. We then used a Wilcoxon signed ranks test to investigate differences in response to control and rat odours.

*Experiment 2*. We carried out activity tests in a test arena made of two plastic bins measuring 710 x 490 x 295 mm deep with clear perspex lids (capacity of 70 L, Figure 2). The bins were connected to each other by two round cardboard tubes (diameter = 30 mm, length = 300 mm) so that mice could travel between them. Each bin was provided with shredded paper, two tin cans and two cardboard tubes to act as retreats. In one of the bins, a ship rat was restrained in a clear plastic cage (measuring 380 x 250 x 150 mm deep) with a wire top. A different ship rat (n=8) was used each day. The position of the rat (left or right bin) was alternated and the mouse was introduced to a randomly chosen side. All tests were recorded on video using the same equipment as described for experiment 1, but tests were recorded using dim red light and each test was 20 minutes long. Each mouse was introduced into the arena twice on consecutive days, once in the presence of a rat and once alone, with the empty rat cage. Ten randomly chosen mice received the rat treatment on their first introduction to the arena and ten on the second.

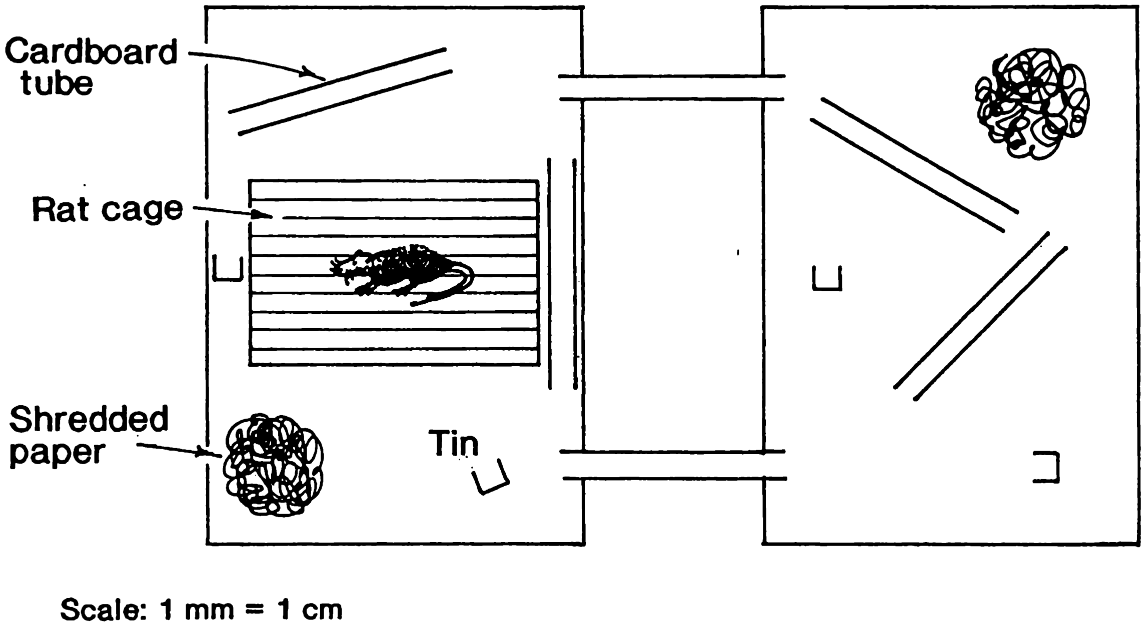

FIG. 2: The two-sided arena used to test responses by mice to the presence of a ship rat.

Five mice were tested per day, and trials for 10 mice took place between 29 June and 2 July 1998. The remaining 10 were tested between 7 and 10 July 1998. In addition to recording the amount of time spent in each arena, we recorded the amount of time spent under cover in the arena and the amount of time spent in the open. Finally, when viewing the videos, we overlaid a 1 $cm^2$ grid onto the television screen and recorded the number of grid squares crossed by each mouse in each test.

*Data Analysis*. Data from each mouse in the absence of a rat were subtracted from the equivalent scores when a rat was present. This produced a single score for each mouse for the three values we measured (time under cover, number of grid squares crossed and time in the open). The score could be negative (implying the mouse was more active in the absence of the rat) or positive (implying the mouse was more active in the presence of the rat). The scores were then analysed using the nonparametric sign test (Sokal and Rohlf, 1995) in MINITAB, version 12.1.

*Experiment 3*. For our breeding experiments, 40 Swiss strain white mice were placed in opposite sex pairs within clean cages (40 x 27 x 15 cm deep plastic tubs with wire tops) on 21 July 1998 and provided with *ad libitum* water and food. These mice were matched for weight and maintained on a 12:12 light schedule with lights on at 0600 hours and temperatures of 16-22 °C. Ten of the pairs were provided with clean sawdust and shredded paper as bedding. The bedding was changed weekly. The remaining ten also received different bedding every week, but were given bedding that had been used by ship rats until that morning (n=10 ship rats). The ship rats were also changed weekly. These mice also received clean shredded paper weekly, and all mice were provided with a cardboard tube to act as a retreat. The mice were allowed to mate normally, and 16 days after pairing the males were removed. We recorded: (1) the weights of the males when they were separated from the females; (2) the weights of the females at parturition and at weaning; (3) the number of days between pairing and the birth of the litter; (4) the size of the litter, and (5) the weight of the litter at birth and at weaning (at 21 days old). We also recorded any incidences of infanticide.

In order to check that laboratory mice showed responses similar to those of wild mice when presented with an odour from a ship rat, 10 female Swiss mice were tested in the Y maze used for experiment 1. These females had served as controls (i.e., they did not received bedding tainted with ship rat odour) in experiment 3. The female mice being tested were given approximately 10 g of ship rat bedding in one arm of the maze (alternated) and 10 g of their own bedding in the other, as in the earlier experiment. The mice were tested on 11 September 1998, after their breeding experiments had concluded. Tests were recorded using the same equipment as in experiment 1, and we collected the same information. Each test consisted of a one minute acclimation period and a 15 minute test. The tests were conducted under natural light conditions during the day, since the laboratory mice had been handled in daylight during their breeding experiments and were normally diurnally active.

*Data Analysis.* We used two sample t-tests to compare the weight of the males at removal, the weight of the females and the weight of the litter at parturition. The litter size was not normally distributed for the two groups, so we transformed each value by taking its square root. We were then able to compare the two samples using a t-test. We were unable to normalise some data by transformation so we used Wilcoxon Mann-Whitney tests to compare the number of infants killed by each mother, the average weight of the pups per litter at weaning and the female weights at weaning.

We used the GLM procedure of MINITAB to check that Swiss strain mice did not differ from wild mice in their behavioural responses to ship rats. For each of the variables we measured, we created a model specifying odour and trial (1, 2 (wild mice) or 3 (Swiss mice)) as fixed effects, and mouse as a random effect. We used Tukey's tests to detect significant pairwise differences.

## RESULTS

*Experiment 1.* The wild mice in a Y maze did not vary the number of visits to a donor odour according to the odour ($F_{2,35}$=1.28, *P*=0.31), nor did they vary the time in the rat odour arm ($F_{2,35}$=0.11, *P*=0.893), or the time taken to approach the rat odour ($F_{2,35}$=0.08, *P*=0.925). None of the other variables we measured varied significantly with odour. When we compared the responses of mice to rat-tainted bedding and their own bedding, we found that the proportion of time spent in the rat odour arm (mean=26.87% of trial, s.e.=2.39%) was higher than the proportion of time spent in the control arm (mean=17.24% of trial, s.e=1.25%, Wilcoxon statistic=455.0, n=35, *P*=0.02). Mice also approached rat scented arms more quickly (mean=1.27 %, s.e.=0.33%) than control arms (mean=7.22%, s.e.=2.00%, Wilcoxon statistic =162.0, n=36, *P*=0.007). The number of visits to the odour was not significantly different from the number of visits to the control (Wilcoxon statistic=286.0, n=33, *P*=0.929).

*Experiment 2.* Mice were less active (i.e., moved over fewer grid squares) when there was a rat in the arena (mean=1377 ±213 (s.e.) squares) than when they were alone (mean=2461 ±242 (s.e.) squares; Sign Test, 19 below, 1 above,

$P<0.001$). Mice also swapped sides of the arena less often when there was a rat present (mean=20.8± 3.7 (s.e.) in presence of rat, mean=28.6±2.6 (s.e.) without rat; Sign Test, 15 below, 2 equal and 3 above, $P=0.008$). Mice did not differ in the proportion of time spent on the side with a rat cage, regardless of whether the cage contained a rat (mean=0.60, s.e.=0.06) or not (mean=0.54, s.e.=0.03; Sign Test, 8 below, 12 above $P=0.50$). They also spent similar amounts of time out in the open, regardless of whether or not a rat was present (mean=939 seconds, s.e.=113 s with a rat, mean=1170 s, s.e.=82.3 s without a rat; Sign Test, 14 below, 6 above, $P=0.11$).

*Experiment 3*. The weights of male mice at the time they were separated from the females did not vary according to whether the mice had been housed in rat-treated or control cages (mean=38.1 g for both samples, s.e.=0.8 g for treatment group and s.e.=0.99 g for control group). The length of time between pairing and giving birth was similar for both groups (median=21.5 days for treatment mice and 22 .0 days for control mice; W=88.0, $P=0.17$). Female mice in both groups were of similar weights at parturition (mean=31.9 g, s.e.=0.9 g for treatment females and mean=32.9, s.e.=0.6 for control females; T=-0.94, $P=0.36$). The litter size was larger for mice that received rat bedding (mean=11.5, s.e.=0.5) than it was for control mice (mean=10.3, s.e.=0.5; T=-23.01, $P<0.001$). There was a low overall level of infanticide: only four individual nestlings were eaten by three mothers in the treatment group and only one nestling was eaten in the control group. This difference between groups was not significant (W=115.5, $P=0.13$). The average weight of the pups at birth did not vary between the samples (T=-1.57, $P=0.14$), but may have differed at weaning (W=84.0, $P=0.06$), when treatment pups weighed an average of 9.97 g each (s.e.=0.46 g), and control pups weighed an average of 10.84 g each (s.e.=0.40 g). The weight of the mothers at weaning was not significantly different between our treatment and control groups (mean=31.1 g, s.e.=1.1 g, and mean=33.2, s.e.=1.0 g respectively; W=89.5, $P$=0.25). The GLM showed that Swiss strain mice spent longer (mean=26.05, s.e.=6.48) in the control arm than wild mice did (Trial 1 mean=16.22, s.e.=8.01; Trial 2 mean=14.14, s.e.=2.64, $F_{2,21}$=8.52, $P$=0.002, Tukey's T=3.71, $P$=0.004).

## DISCUSSION

It would be advantageous for mice to be able to discriminate and avoid the odour of predators and competitors only if those animals exerted a strong selection pressure on them. We could find no study that listed mice as a food item in ship rat diet, although young mice are without hair and predation on young animals might not leave traces in the faeces. Sturmer (1988 unpubl.) is the only author to have studied three species of sympatric rodents (ship, Norway rats and kiore on Stewart Island), and he makes no mention of the much smaller kiore appearing in the diet of the other two rat species. All four species have been introduced to New Zealand relatively recently, and they may not have had enough opportunities (in time or space) to influence each others' evolution. If it is true that ship rats are significant predators and/or competitors of mice in New Zealand habitats, one might expect mice to avoid rats or the odours deposited by them. On the contrary, we found no evidence that mice use cues derived from olfactory deposits to avoid rats, even when the mice had recently been exposed to a live rat. This raises two possibilities: either mice cannot discriminate the odour of heterospecifics, or they can, but do not avoid them. Since the mice spent longer in each rat odour arm than in the control arms, and investigated odour arms more quickly, it seems likely that mice could discriminate among the odours. Wild mice did not avoid the odour of any of the three rodents with which they could coexist in New Zealand. It is possible that the age of the frozen samples accounts for our results, since volatile components can presumably be lost or altered over time (Ferkin et al., 1995). It is not known how freezing would affect this decomposition process, but freezing is routinely used in preparation of conspecific odours for experiments (e.g., Mucignat-Caretta and Caretta, 1999). Furthermore, the Swiss mice in experiment 3 received bedding occupied by rats until the morning of testing and their responses were similar.

It therefore seems unlikely that New Zealand mice use heterospecific odours as cues to avoid areas of their habitat. The method we used was similar to that of another study that demonstrated that mice do use heterospecific olfactory cues (to avoid jirds; Krasnov and Khoklova, 1996) and we obtained a different result. Krasnov and Khoklova (1996) could have employed more suitable controls (Mappes et al., 1998). The mice used by Krasnov and Khoklova (1996) received a clean-odour choice arm and a jird-odour choice arm in the Y maze. The use of clean or odour-free treatments is not a suitable control because it is not an equal but innocuous stimulus. Using odour-free controls can lead to spurious results (e.g., Ylonen and Ronkainen, 1994; Mappes et al., 1998). However, when more than one smell is presented in a maze, as in our experiments, there is the possibility that smells will merge and/or interact, producing misleading results too. A better approach is that taken by Bramley et al. (Chapter 5), when we compared the response of rats to predator odours using herbivore odours as a control. Rats we tested experienced the treatment and control odours at different times against distilled water (no-odour) treatments in the other choice arm. Using the odour of other mice would have been an inappropriate control in this setting too, because mice use conspecific odours for communication (Goodrich et al., 1990; Hurst et al., 1994; Hurst and Barnard, 1995; Kavaliers and Colwell, 1993). Thus mice would be faced with two different potentially meaningful odours in each test rather than a meaningful odour and an innocuous one. In that scenario it would be impossible to determine what the mice were responding to. A better way to run the experiments would have been to use an innocuous odour such as rabbit or guinea pig-tainted bedding as a control and tested mice against it in a separate test. Nonetheless, some conclusions can be drawn from our experiment.

The mice we studied were less active in the presence of rats and swapped sides of the arena less, but their use of cover was unaffected. This may be because cover can reduce the detection and escape abilities of the prey species (Schooley et al., 1995). Our mice may have been stationary to avoid detection. If mice were introduced to the side of the arena where the rat was, they had little choice but to hide or freeze if they were to avoid detection. On the other hand, mice introduced to the rat-free side of the arena could escape detection by not venturing into the rat-containing side (i.e., by not swapping sides).

Swiss mice differed from wild mice only in the amount of time spent in the control arm. Since the amount of time spent in each of the arms is essentially independent (because mice could spend time in the first arm, which was not measured), this does not imply they spent less time in the rat-scented arm. Most measures were statistically insignificant, hence Swiss strain mice appear to be a suitable surrogate species for wild mice in this instance. We cannot explain the larger litter size of mice receiving rat-tainted bedding in our experiments, although the larger litter size may explain why treatment mice were smaller at weaning. The two variables are probably related since females could not devote infinite resources to the rearing of young, and the individuals in larger litters were likely to receive less food per individual than those in smaller litters.

Stapp and Van Horne (1996) checked whether odours mediated interactions between rodents living in prairie grasslands by conducting a live-trapping study using scented traps, and concluded they did not. Gurnell and Little (1992) reached a similar conclusion for woodland rodents in Britain. However, Wuensch (1992) reported an innate aversion shown by laboratory mice to the odour of laboratory rats. This aversion was reduced by cross-fostering mouse nestlings to rat mothers. Stapp and Van Horne (1996) suggested that stronger avoidance of odour cues might be observed in populations of rodents whose abundance cycles regularly. Many of the conclusions from the accumulated data on the responses of members of cyclic populations of voles are now in doubt (Wolffe and Davis-Born, 1997; Mappes et al., 1998).

Competition between existing rodents in New Zealand is poorly understood and has not been studied in an experimental way. Nonetheless, competition has been implicated in determining the abundance and distribution of the rodents found in New Zealand (Watson, 1961; Taylor, 1975 and 1984). Kiore were the first rodent introduced to New Zealand, possibly as long as 2 000 years ago (Holdaway, 1996). Since then, three more species have arrived with human voyagers, and different species assemblages are found on different islands and in different habitats (Atkinson and Moller, 1990; King et al., 1996a; King and Moller, 1997). Nowhere do all four species coexist in New Zealand, although they do elsewhere (e.g., Hawaii; Tomich, 1986). Mice and ship rats are both found more often on islands where Norway rats are absent (Taylor, 1984), but ship rats may have taken over from Norway rats as the most common rats on the main islands of New Zealand, at least in commensal habitats (Innes, 1990). Furthermore, the introduction of mice may account for the decline in kiore numbers and range (Taylor, 1975; Atkinson and Moller 1990). Competitive interactions will remain obscure until experiments are completed that place all four species in the same environment and observe and manipulate their interaction. Rebar and Conley (1983) used two-species experimental enclosures to define the microhabitat use between two species of heteromyid rodent, and were convincingly able to show a shift in habitat use when one species was removed. Brown and Munger (1986) and Dueser and Porter (1986) completed similar convincing experiments. This type of experiment is necessary to extend our understanding of the rodent pests that live in New Zealand and elsewhere. Experiments of this kind would also move our research forward from the straight descriptions of Taylor (1975 and 1984), Goodyear (1992), Haering and Fox (1995), King et al. (1996a), Tomblin and Adler (1998) and Bramley et al. (Chapter 2 in this thesis) towards an approach with more explanatory power.

Goodrich et al. (1990) recorded increases in the heart rate of mice exposed to volatile chemicals from conspecific faeces and urine. It is possible that changes which occur at a physiological level need not manifest themselves in behavioural changes such as the ones we recorded. It appears from our results in experiment 2 that mice can perceive the risk when presented with a live rat, and respond behaviourally, but a heightened level or responsiveness to odours would not necessarily be quantifiable by our experiments.

It seems most likely that the observed increase in mouse numbers when ship rats are removed (Clout et al., 1995; Innes et al., 1995; Miller and Miller, 1995; Brown et al., 1996) is due either to an increase in activity by mice already resident or a decrease in predation on young mice or both. So, the response is not odour mediated, and not a response affecting mouse reproduction. Opportunities for testing predation hypotheses directly will be limited because of ethical concerns (Huntingford, 1991). Nonetheless, properly designed and conducted experiments making use of large enclosures or experimental islands (as proposed by Veitch et al., 1992) would considerably enhance our understanding of the interactions determining rodent communities both in New Zealand and world-wide.

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# REFERENCES

ATKINSON, I.A.E., and MOLLER, H. 1990. Kiore, pp. 175-192, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland. New Zealand.

BOUSKILA, A. 1995. Interactions between predation risk and competition: A field study of kangaroo rats and snakes. *Ecology* 76:165-178.

BROWN, K.P., MOLLER, H., INNES, J.G., and ALTERIO, N. 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. *N.Z. J. Ecol.* 20:271-275.

BROWN, J.H., and MUNGER, J.C. 1986. Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology* 66:1545-1563.

CLOUT, M.N., DENYER, K., JAMES, R.E., and MCFADDEN, I.G. 1995. Breeding success of New Zealand pigeons (*Hemiphaga novaeseelandiae*) in relation to control of introduced mammals. *N.Z. J. Ecol.* 19:209-212.

DICKMAN, C.R. 1991. Mechanisms of competition among insectivorous mammals. *Oecologia* 85:464-471.

DICKMAN, C.R. 1992. Predation and habitat shifts in the house mouse, *Mus domesticus*. *Ecology* 73:313-322.

DUESER, R.D., and PORTER, J.H. 1986. Habitat use by insular small mammals: relative effects of competition and habitat structure. *Ecology* 67:195-201.

FERKIN, M.H., BURDA, J., O'CONNOR, M.P., and LEE, C.J. 1995. Persistence of the attractiveness of two sex specific scents in meadow voles (*Microtus pennsylvanicus*). *Ethology* 101:228-238.

GARBE, C.M., KEMBLE, E.D., and RAWLEIGH, J.M. 1993. Novel odours evoke risk assessment and suppress appetitive behaviours in mice. *Aggress. Behav.* 19:447-454.

GLASS, G.E., and SLADE, N.A. 1980. The effect of *Sigmodon hispidus* on spatial and temporal activity of *Microtus ochrogaster*: evidence for competition. *Ecology* 61:358-370.

GOODRICH, B.S., GAMBALE, S., PENNYCUIK, P.R., and REDHEAD, T.D. 1990. Volatiles from feces of wild male house mice: Chemistry and Effects on behavior and heart rate. *J. Chem. Ecol.* 16:2091-2106.

GOODYEAR, N.C. 1992. Spatial overlap and dietary selection of native rice rats and exotic black rats. *J. Mamm.* 73:186-200.

GURNELL, J., and LITTLE, J. 1992. The influence of trap residual odour on catching woodland rodents. *Anim. Behav.* 43:623-632.

HAERING, R., and FOX, B. 1995. Habitat utilization patterns of sympatric populations of *Pseudomys gracilicaudatus* and *Rattus lutreolus* in coastal heathland: A multivariate analysis. *Aust. J. Ecol.* 20:427-441.

HOLDAWAY, R.N. 1996. Arrival of rats in New Zealand. *Nature* 384:225-226.

HUNTINGFORD, F.A. 1991. Some ethical issues raised by studies of predation and aggression, pp. 39-45, *in* M. Stamp-Dawkins and M. Gosling (eds.). Ethics in research on animal behaviour: Readings from *Animal Behaviour.*

Published by Acadmic Press for the Association for the Study of Animal Behaviour and the Animal Behavior Society, London, England.

HURST, J.L., and BARNARD, C.J. 1995. Kinship and social tolerance among female and juvenile wild house mice: kin bias but not kin discrimination. *Behav. Ecol. Sociobiol.* 36:333-342.

HURST, J.L., FANG, J. and BARNARD, C. J. 1994. The role of substrate odours in maintaining social tolerance between male house mice (*Mus musculus domesticus*): relatedness, incidental kinship effects and the establishment of social status. *Anim. Behav.* 48:157-167.

INNES, J.G. 1990. Ship rat, pp. 206-225, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland. New Zealand.

INNES, J.G., WARBURTON, B., WILLIAMS, D., SPEED, H., and BRADFIELD, P. 1995. Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *N.Z. J. Ecol.* 19:5-17.

KAVALIERS, M., and COLWELL, D.D. 1993. Aversive responses of female mice to the odours of parasitized males: neuromodulatory mechanisms and the implications for mate choice. *Ethology* 95:202-212.

KAVALIERS, M., and COLWELL, D.D. 1995. Odours of parasitized males induce aversive responses in female mice. *Anim. Behav.* 50:1161-1169.

KING, C.M. 1982. Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*) in relation to seed fall of southern beech. *N.Z. J. Zool.* 9:467-480.

KING, C.M., and EDGAR, R.L. 1977. Techniques for trapping and tracking stoats (*Mustela erminea*); a review and a new system. *N.Z. J. Zool.* 4:193-212.

KING, C.M., INNES, J.G., FLUX, M., KIMBERLEY, M.O., LEATHWICK, J.R., and WILLIAMS, D.S. 1996a. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *N.Z. J. Ecol.* 20:215-240.

KING, C.M., INNES, J.G., FLUX, M., and KIMBERLEY, M.O. 1996b. Population biology of small mammals in Pureora Forest Park: 2. The feral house mouse (*Mus musculus*). *N.Z. J. Ecol.* 20:253-269.

KING, C.M., and MOLLER, H. 1997. Distribution and response of rats, *Rattus rattus* and *R. exulans*, to seedfall in New Zealand beech forests. *Pac. Cons. Biol.* 3:143-155.

KRASNOV, B., and KHOKLOVA, I. 1996. Discrimination of midday jird's odour by house mice. *Anim. Behav.* 52:659-665.

MAPPES, T., KOSKELA, E., and YLONEN, H. 1998. Breeding suppression in voles under predation risk of small mustelids: laboratory or methodological artifact? *Oikos* 82:365-369.

MILLER, C.J., and MILLER, T.K. 1995. Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poison operation. *N.Z. J. Ecol.* 19:19-27.

MOORS, P.J. 1990. Norway rat, pp. 192-206, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

MUCIGNAT-CARETTA, C., and CARETTA, A. 1999. Urinary chemical cues affect light avoidance behaviour in male laboratory mice, *Mus musculus*. *Anim. Behav.* 57:765-769.

MURPHY, E.C., and PICKARD, C.R. 1990. House mouse, pp. 225-242, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland. New Zealand.

REBAR, C., and CONLEY, W. 1983. Interactions in microhabitat use between *Dipodomys ordii* and *Onychomys leucogaster*. *Ecology* 64:984-988.

SOKAL, R.R. and ROHLF, F.J. 1995. Biometry: The principles and practice of statistics in biological research. Third Edition. W.H. Freeman and Company, New York. USA.

SCHOOLEY, R.L., SHARPE, P.B., and VAN HORNE, B. 1995. Can shrub cover increase predation risk for a desert rodent? *Can. J. Zool.* 74:157-163.

STAPP, P., and VAN HORNE, B. 1996. Do olfactory cues mediate interactions between rodents on northern shortgrass prairie? *Can. J. Zool.* 74:26-232.

STURMER, A.T. 1988. Diet and coexistence of *Rattus rattus* (Linnaeus), *R. exulans* (Peale), and *R. norvegicus* (Berkenhout) on Stewart Island, New Zealand. Unpublished MSc. thesis. Department of Botany and Zoology, Massey University, Palmerston North. New Zealand.

TAYLOR, R.H. 1975. What limits kiore (*Rattus exulans*) distribution in New Zealand? *N.Z. J. Zool.* 2:473-477.

TAYLOR, R.H. 1984. Distribution and interactions of introduced rodents and carnivores in New Zealand. *Acta Zool. Fenn.* 172:103-105.

TOMBLIN, D.C., and ADLER, G.H. 1998. Differences in habitat use between two morphologically similar tropical forest rodents. *J. Mamm.* 79:953-961.

TOMICH, P.Q. 1986. Mammals in Hawaii: A synopsis and notational bibliography. Second edition. Bishop Museum Press, Honolulu. Hawaii.

VEITCH, C.R., FITZGERALD, B.M, INNES, J.G. and MURPHY, E.C. 1992. (eds.). Rodent working groups, pp. 39-42, *in* Proceedings of the National Predator Management Workshop. Threatened Species Occasional Publication No. 3. Department of Conservation, Wellington. New Zealand.

WATSON, J.S. 1961. Rats in New Zealand: a problem of interspecific competition. *Proc. 9th Pacific Science Congress* 19:15-17.

WOLFF, J.O., and DAVIS-BORN, R. 1997. Response of grey-tailed voles to odours of a mustelid predator: a field test. *Oikos* 79:543-548.

WUENSCH, K.L. 1992. Fostering house mice onto rats and deer mice: Effects on response to species odours. *Anim. Learn. Behav.* 20:253-258.

YLONEN, H., and RONKAINEN, H. 1994. Breeding suppression in the bank vole as an antipredatory adaptation in a predictable environment. *Evol. Ecol.* 8:1-9.

ZIV, Y., ABRAMSKY, Z., KOTLER, B., and SUBACH, A. 1993. Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos* 66:237-246.

# CHAPTER FIVE: THE RESPONSES TO PREDATOR ODOURS BY TWO POPULATIONS OF WILD NORWAY RATS (*RATTUS NORVEGICUS*).

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**Abstract** – If rats could be shown to reliably avoid the odours of predators, then conservation managers could manipulate this behaviour to exclude rats from important conservation sites. We evaluated the ability of six predator odours to elicit avoidance responses by wild-caught Norway rats (*Rattus norvegicus*) from two New Zealand populations (Kapiti Island and North Island). Kapiti Island is free of mammalian predators, while the North Island has established populations of felids, canids and mustelids. Three of the predator odours we used were real, and three were synthesised, volatile ingredients of real animal faeces or urine. We compared the rats responses to predator odours with their responses to three natural herbivore odours. We used a Y maze, and rats were offered the choice of an odour in one arm of the maze and distilled water in the other arm. Each choice arm was ducted near the maze junction to remove air and the odour. We recorded: (1) the time until the rat visited each arm, (2) the number of visits to each arm, (3) the amount of time spent in each arm, and (4) a total activity score for each rat. Kapiti rats showed an aversion to five of the six predator odours, despite never having encountered them before. Kapiti rats visited herbivore odours more often than carnivore odours and were less active in the presence of carnivore odours than they were when tested with herbivore odours. In addition, Kapiti rats may have approached some herbivore odours more quickly than they approached carnivore odours. North Island rats, despite being predator experienced, did not show an aversion to any of the carnivore odours tested. Both samples of rats, but particularly the North Island group, showed high individual variation and the two samples differed only in the amount of time spent in the odour arm when exposed to cat faeces: Kapiti rats spent less time in the proximity of the odour. We conclude that predator odours are unlikely to be an effective management tool for all populations of this species of rat.

**Key words** - Y maze, odour discrimination, predator odours, semiochemicals, avoidance behaviours, *Rattus norvegicus*, mustelids, red fox urine, *Vulpes vulpes*, *Felis catus*.

## INTRODUCTION

Rats (particularly *Rattus norvegicus*, Berkenhout, *Rattus exulans*, Peale, and *Rattus rattus* L.) are both economic and public health pests. Rats are widespread globally and can reach particularly high densities on islands (Gliwicz, 1980). In New Zealand, populations of introduced rats in forests and on island wildlife sanctuaries pose a threat to many native species of bird, lizard and invertebrates because they eat eggs, juveniles and adults as well as plants and seeds (Atkinson, 1985). To date, the control of rat populations has relied on extensive poisoning (Taylor and Thomas, 1989; Innes et al., 1995) or localised trapping around sites of significance. Poisoning and trapping are currently effective but can be labour intensive and costly (Taylor and Thomas, 1989 and 1993; Innes et al., 1995). Poisoning is also indiscriminate in its effects and may affect non-target species (Spurr, 1979 and 1991), while traps are not equally successful for all age classes, sexes or species of rat (King and Moller, 1997).

Rats have been eradicated from some offshore islands in New Zealand, but such islands are always susceptible to reinvasion. In addition, rat populations readily evolve resistance to poisons via behavioural, physiological or ecological mechanisms (Berdoy and Smith, 1993; Brunton et al., 1993). This means the development of new technology to repel or exterminate rats is always a high priority (Wace, 1986; Burwash et al., 1998).

Many rodents make foraging and reproductive decisions according to predation risk (Fenn and MacDonald, 1995; Randall et al., 1995; Ylonen and Ronkainen, 1994). For some species, the smell of a predator may be sufficient to trigger a response (Ylonen and Ronkainen, 1994, but see Mappes et al., 1998 for a critique and opposing data). Many herbivores (see Mason et al., 1992 for a review) also avoid odours derived from the urine or scent glands of carnivores. Nolte et al. (1994) suggested that this aversion could be due to the sulphurous odours associated with meat digestion, which are present in the urine of carnivores. Prey may identify sulphurous odours and use them to assess predator diet (Nolte et al., 1994). This assessment of the predator diet may provide an indirect measure of risk, to which a species can respond. Aversion to predator odours appears to be innate in some strains of laboratory rats and mice (Dell'Omo et al., 1994; Heale and Vanderwolf, 1994; Zangrossi and File, 1994). Although habituation may reduce the observed response in some animals, or to some odours (Sullivan et al., 1985), predator odours can be long lasting in their effects. For example, Boag and Mlotkiewicz (1994) were able to exclude rabbits (*Oryctolagus cuniculus*) from their warrens for up to five months after treatment with lion (*Panthera leo*) faeces.

Predator odours may act as repellents if: (1) the prey species is alerted to the odour and avoids the area on the expectation of encountering a predator; and/or (2) the smell itself is aversive (Englehart and Muller-Schwarze, 1995). The first case relies on occasional reinforcement by a predator. The second suggests a more lasting repellent effect and would be more useful in the New Zealand situation, where many island populations of rats are unfamiliar with mammalian predators. An effective repellent should result in immediate and long lasting avoidance of the source of the odour (Sullivan et al., 1985).

Our main aim was to determine whether odours derived from predators repelled wild-caught rats. We see at least two conservation applications for such a tool: (1) a general repellent may allow managers to keep rats from significant locations such as single trees or nests of rare species; and (2) repellents could be applied to possible invasion routes such as wharves on sanctuary islands. This might discourage rats landing from docked boats. To screen odours for potential use in field trials, we collected rats from two populations: Kapiti Island (40°51'S and 174°56'E), which is free of mammalian predators of rats, and various locations on the North Island, New Zealand, where mustelid, canid and felid carnivores are all present. We then tested their responses to both predator and non-predator odours in a Y maze with distilled water in the other (control) arm. By testing samples of predator-naïve and predator-experienced rats with the same smells, we hoped to be able to determine whether experience with predators influenced the responses of wild Norway rats. By including the smell of predators never found in New Zealand, and a herbivore odour unlikely to be encountered in the wild, we expected to discover how important neophobia might be in determining rat responses. We also included both real urine and faeces and synthetic volatile constituents of urines to evaluate the potential of more easily available synthetic products as potential rat deterrents.

## METHODS

*Animals.* All 25 animals used in the trials were adults, caught in live capture cage traps baited with peanut butter and apple, and had spent 1-33 weeks in captivity before the trials started. Fifteen of the animals were caught on Kapiti Island, on two traplines approximately 4.5 km apart. Ten of these animals were males and five were females. One male was blind in one eye when caught, but was still used in this study. One male died before the trials began, reducing our Kapiti sample to 14 rats. The other ten rats were collected from farms or houses on the North Island, eight around the Waikato region (at four sites within approximately 40 km of each other) and two in Northland (both at the same site). Six were males and four were females.

At the University of Waikato facilities, the animals were housed individually in plastic bottomed, wire cages (46 x 24 x 20 cm high). Rats had *ad libitum* access to water and food (Sharpes Diet 86 rat chow (Sharpes grains and seeds, Lower Hutt, New Zealand), occasional seed mixes and pieces of apple). Cages were provided with a can and a cardboard tube to act as retreats. Wood shavings covered the bottom of the cages as bedding material. The bedding was changed weekly. The rats were kept on a constant 12:12 light schedule, with lights on at 2200 hrs, and temperatures between 15 and 24°C during the trials. Rats from Kapiti Island were tested in December 1996, those from the North Island in March 1997. The two groups of rats were not housed or tested simultaneously.

*Odours*. The subjects responses to nine different odours were examined. Six of the odours were natural, from the faeces or urine of live animals, and three odours were commercially synthesised volatile ingredients of urine or faeces (provided by New Zealand Industrial Chemists, Gracefield, Lower Hutt, New Zealand). The natural odours were: cat (*Felis catus*) urine (provided by Five Cross Roads Veterinary Clinic, Hamilton, New Zealand), mongoose (*Herpestes auropunctatus*) faeces (collected in Hawaii, provided by New Zealand Industrial Chemists), guinea pig (*Cavia porcellus*) faeces, New Zealand white laboratory rabbit (*Oryctolagus cuniculus*) urine and red deer (*Cervus elaphus*) urine. Artificially synthesised chemicals were provided as 1% solutions in paraffin oil. Chemicals used were isopentyl methyl sulphide (IPMS, found in red fox, *Vulpes vulpes*, urine), n-propylthietane (PT, found in mustelid anal sac secretions, and hence probably also in their faeces), and S-methyl, methyl butanol (SMMBO, found in cat urine). Thus there were 3 synthesised predator smells, 3 natural herbivore smells and 3 natural predator smells. Of the natural odours, one of the herbivore and two of the predator smells were from faeces. The cat and rabbit urine was collected via catheterisation of animals held at the Veterinary Clinic or at Waikato Polytechnic (Hamilton, New Zealand). Guinea pig faeces were collected from guinea pig cages at the Polytechnic. The deer urine was collected from animals kept at the deer unit of AgResearch Ruakura (Hamilton, New Zealand). Urine and faeces always came from more than one donor animal, but only one donor was used at a time (i.e. samples were not pooled) except in the case of the deer urine. All natural odours were stored frozen.

Kapiti Island is a nature reserve that has no mammalian predators of rats or mammalian herbivores at present. However, earlier this century cats, dogs (*Canis familiaris*), sheep (*Ovis aries*), goats (*Capra hircus*), cattle (*Bos taurus*), deer (*Axis axis* and *Dama dama*) and possums (*Trichosurus vulpecula*) were all found on the island (Cowan, 1992). Mammalian predators on the North Island include stoats (*Mustela erminea*), ferrets (*Mustela furo),* weasels (*Mustela nivalis*), cats and dogs. There were also cows, sheep, goats and rabbits on many of the farms where rats were caught. There are no feral populations of Guinea pigs in New Zealand (King, 1990) and it is unlikely any of the rats we used had ever come into contact with Guinea pig odour.

*Tests.* Animals were collected one at a time from the captive colony and transported in their cages, in darkness, to a separate trial room. They were then transferred into an experimental arena illuminated with red light. While the animals were in the arena, we turned off the red light and completed all observations using infra-red light sources. Tests were videoed using a Videotronic Tri-Q CCD camera and Panasonic AG5260 video recorder. After each test, we returned the animal to its cage and then to the captive colony.

We used a 10 cm diameter, semi-round Y maze made of PVC to examine the responses of both groups of rats to odours (Figure 1). The odour and control stimuli were presented inside an opaque glass container as either 0.1 ml of solution pipetted onto a 1 cm$^2$ piece of Whatman filter paper or as 0.1 g of thawed faeces. Odours were presented in the maze with distilled water controls in the other choice arm. The position of the odour (left or right choice arm) was alternated. The position of the odour (left or right) and the type of odour (numbered 1-9) were recorded on the video tape after the trial but were unknown to us when we scored the rats behaviour.

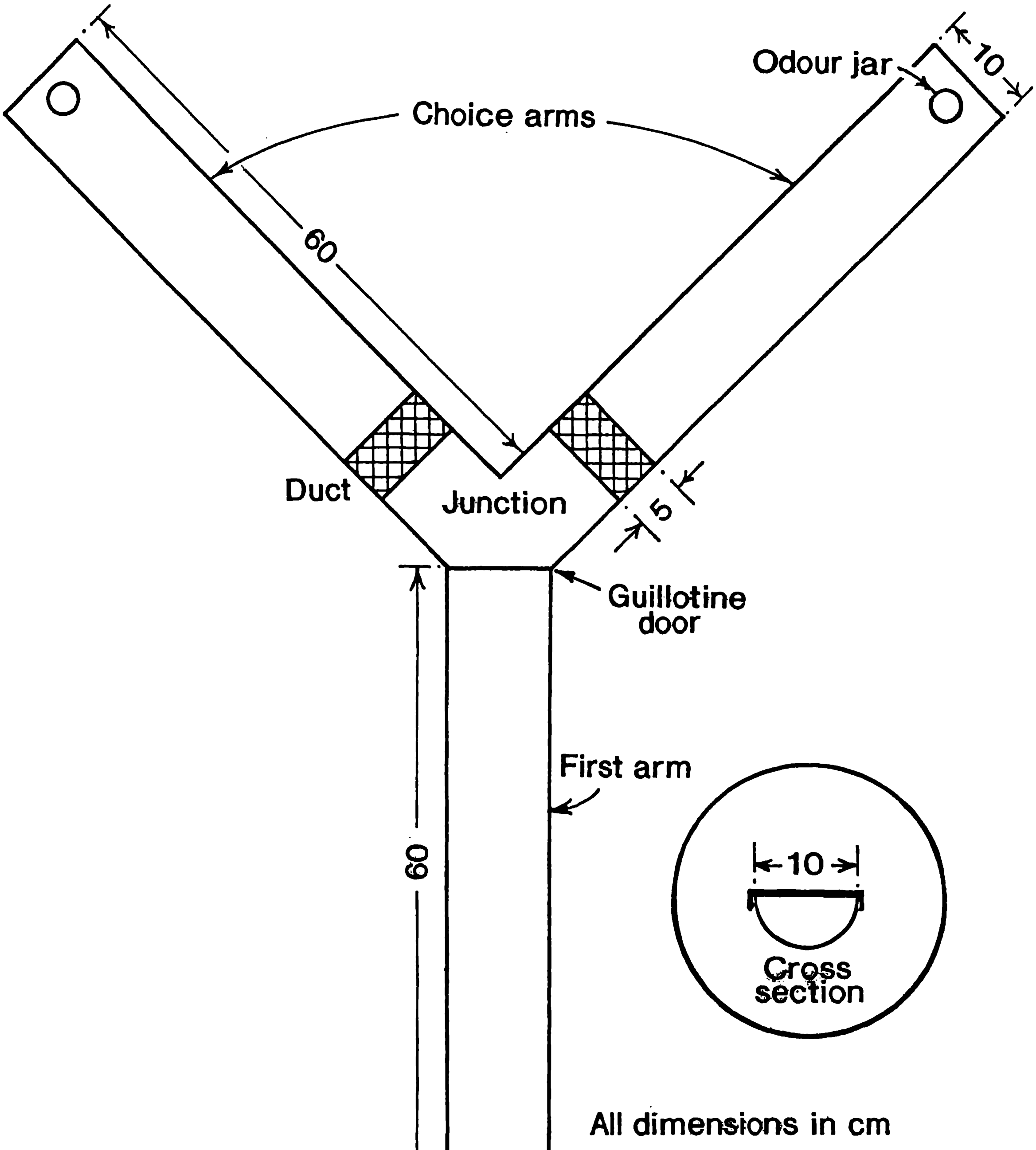

FIG. 1. The Y Maze apparatus used to test rats responses to herbivore and predator odours.

We used three identical mazes and after each test we washed the maze using hot water and Vircon soap powder and then dried it with a towel.

Rats from Kapiti Island were tested separately according to an incomplete block design using 18 blocks. North Island rats were tested according to a complete block design using 18 blocks. This means that as a group, Kapiti rats were tested against all nine odours, but each individual was tested with less than nine odours (hence an "incomplete" design), whilst each individual North Island rat was tested with all nine odours (hence a "complete" design). For both groups we tested, each block included five rats, and one block (of five rats and five odours) was tested per day. Each Kapiti rat was randomly allocated a position in six blocks (i.e., received each of six odours once over the 18 days of the trial). Each North Island rat was randomly allocated a position in nine blocks (i.e. received each of the nine odours once over the 18 days of the trial). Each odour was tested either 9 or 10 times in each trial. Tests began one hour after the lights in the colony had gone off (1100 hrs) and continued sequentially until five animals had been tested. Each test was usually conducted within 40 minutes of the previous one. Prior to the start of each test, the rat was placed in the first arm, with the door shut, the video recorder was then started and we left the room. Rats were confined to the first arm for a five-minute acclimation period. When the guillotine door (Figure 1) was opened (from outside the room), the rats were free to explore the maze for fifteen minutes. We recorded: (1) the time until the rat visited each of the arms (a rat was defined as making a visit when its head was more than 5 cm down the arm); (2) the number of visits to the odour and control arms; (3) the time spent in each arm; and (4) a total activity score for each rat, which was the number of visits to each arm summed together.

The day before being tested, each rat was introduced to the maze as outlined above, but in the absence of any odours. We recorded the same measures for each rat on videotape to detect any left or right bias and to establish that the rats would explore the maze. In the middle of the series of tests and at the end of the series, the rats were again introduced to clean mazes and their movements recorded. This was to check that each rat would still explore the maze in the absence of smells and that the rats had not developed a left or right preference during the trials. Recordings of rats in a clean maze were done after the day's tests (on other rats) had concluded.

*Data Analysis.* Data for the two groups of rats were analysed independently and then combined to look for population differences. We considered that the most important variable from a management perspective was the number of visits to each arm. We analysed the number of visits to each arm for each sample (i.e., Kapiti and North Island) using the Residual Maximum Likelihood procedure (REML) in the GENSTAT statistical package, and a square root transformation to stabilise the variance. We considered the odour to be a fixed effect and examined the differences between individual rats and blocks as random effects. The data were backtransformed to produce predicted means, which, along with the standard errors of the difference between these means (SEDs), are presented here.

Since the number of visits to the odour and control arms were very similar, we considered that the predator odours might have affected visits to the control arm also. Because of this, and because rats could apparently discriminate herbivore odours from predator odours, we treated their behaviour in the presence of herbivore odours as a control and compared them it with their responses to predator odours in subsequent analyses. We also conducted a REML on the rats activity in each test with the different odours to account for the fact that some rats "froze" immediately at the start of the test (i.e., they became motionless when first exposed to some of the odours) and as a result never left the first arm.

All subsequent analyses were done using MINITAB (Version 12.1). For the Kapiti rats, we used a Generalised Linear Model (GLM, a form of ANOVA), specifying rat as a random effect (factor) and using odour and block as fixed effects (predictors). Our data violated some of the assumptions of ANOVA (the data were not normal and the variances differed), but ANOVAs are robust and can still provide interpretable results under such conditions (Underwood, 1981). We used Tukey's tests to detect significant differences between smells. For North Island rats, each of the measures was compared across different odours using a Friedman two-way analysis of variance by ranks test to determine whether rats responded to any of the smells differently to any of the others. This was possible because each of the North Island rats received all of the smells, whereas the individual Kapiti rats received only six of the nine odours (different individuals received different combinations of all nine odours). Whilst the GLM will give interpretable results, the Friedman two-way ANOVA by ranks is not constrained by the same assumptions, so is the more appropriate test to use. Each of the measures was compared using odour as the predictor, blocked by rat. When the Friedman test indicated significant differences among the samples, we used Wilcoxon Mann-Whitney tests to compare the measures for each pair of smells.

To determine whether rats had a left or right bias we counted the number of visits to each arm of a clean maze and compared the two using the Chi-square procedure. Finally, Wilcoxon Mann-Whitney tests were used to compare North Island rats responses to those of Kapiti rats for each of the variables we thought might be significant, judged from the mean and variance of the samples. A *P*-value of 0.05 was taken to be significant in all cases.

## RESULTS

*Kapiti Rats. REML Analysis of Visits to the Odour.* Rats avoided some of the predator odours when compared to the herbivore odours, but the number of visits to the control (distilled water) and the odour arm were similar for each smell (Table 1). Table 2 presents the backtransformed average number of visits to each arm and the mean activity score when the odours are grouped into herbivore, real predator and synthesised predator odours. Rats did not appear to discriminate between real predator odours and synthesised predator odours, but they did react differently to herbivore odours.

*Generalised Linear Model.* Initial exploratory data analysis of the mean and standard error values of males and females, and of choices based on the position of the smell (left or right choice arm) revealed considerable overlap. Sex and position were not significant in the REML model either; hence data were pooled for further analysis. In our REML and GLM analysis, we specified rat as a predictor, and thereby ensured that sex was considered implicitly in our models as an attribute of the rat. The only measure that may have varied significantly with odour was the time taken to approach the odour (F=2.06, df =8, *P*=0.06). Pairwise comparisons showed that the only odours that were different were deer urine (mean=49.93% of the trial elapsed before the odour was approached, s.e.=15.1%) and cat urine (mean=81.6% of the trial elapsed before the odour was approached, s.e.=12.4%, T=3.25, *P*=0.051).

TABLE 1: RESPONSES OF THE KAPITI RATS TO THE NINE ODOURS TESTED.[*]

| Odour | Mean number of visits to the control adjusted for rat and block | Mean number of visits to the odour adjusted for rat and block. | Mean activity adjusted for rat and block |
|---|---|---|---|
| **Predator odours** | | | |
| Cat faeces | $1.9^{a}$ | $1.4^{bc}$ | $3.2^{ac}$ |
| Mongoose | $1.5^{ab}$ | $2.1^{ac}$ | $3.5^{ac}$ |
| Cat urine | $0.5^{b}$ | $0.4^{b}$ | $0.8^{bc}$ |
| **Synthesised odours** | | | |
| SMMBO | $0.8^{ab}$ | $1.2^{bc}$ | $2.0^{bc}$ |
| IPMS | $1.8^{ab}$ | $0.7^{bc}$ | $2.5^{bc}$ |
| PT | $1.2^{ab}$ | $0.5^{b}$ | $1.8^{bc}$ |
| **Herbivore odours** | | | |
| Guinea pig | $2.2^{a}$ | $1.7^{bc}$ | $3.9^{a}$ |
| Deer urine | $2.1^{a}$ | $3.2^{a}$ | $5.3^{a}$ |
| Rabbit urine | $1.4^{ab}$ | $1.7^{bc}$ | $3.1^{ac}$ |
| **Maximum SED** | 0.67 | 0.73 | 1.22 |

[*] Numbers presented are backtransformed values from a REML analysis. Means in the same column (of nine odours) marked with different letters are significantly different at the 0.05 level.

TABLE 2: RESPONSES OF THE KAPITI RATS TO THE NINE ODOURS TESTED GROUPED BY SOURCE.*

| Odour | Mean number of visits to the control adjusted for rat and block | Mean number of visits to the odour adjusted for rat and block | Mean activity adjusted for rat and block |
|---|---|---|---|
| Real Predator | 1.3$^b$ | 1.3$^a$ | 2.5$^b$ |
| Synthesised Predator | 0.8$^b$ | 1.3$^a$ | 2.1$^b$ |
| Herbivore | 2.2$^a$ | 1.9$^a$ | 4.1$^a$ |
| **Maximum SED** | 0.42 | 0.38 | 0.7 |

*Numbers presented are backtransformed values from a REML analysis. Means in the same column marked by different letters are significantly different at the 0.05 level.

*Rats Use of a Clean Maze.* Each rat explored an empty maze on three occasions. Kapiti rats made a mean number of 2.4 visits to the left arm (s.e.=0.3) and 2.4 visits to the right arm (s.e.=0.4). They made a total of 99 visits to the left choice arm and 100 to the right choice arm ($\chi^2$=0.005, df=1, ns). Five of the rats remained in the first arm (ie. froze) on one of the three occasions. Thus rats did not appear to have a bias towards the left or right sides, and readily explored the maze in the absence of smells.

*North Island Rats. REML Analysis of Visits to the Odour.* North Island rats differed in response to the odours presented when judged by the number of visits they made to the odour arm (Table 3). Rats often froze when exposed to any of the odours, and no one odour caused predictable freezing behaviour with activity levels similar for all smells (Table 3). Rat responses varied according to sex, but not odour (Table 4).

TABLE 3: RESPONSES OF THE NORTH ISLAND RATS TO THE NINE ODOURS TESTED.*

| Odour | Mean number of visits to the control adjusted for rat and block | Mean number of visits to the odour adjusted for rat and block | Mean activity adjusted for rat and block |
|---|---|---|---|
| **Predator Odours** | | | |
| Cat faeces | 2.7 $^{a}$ | 2.7$^{a}$ | 5.4$^{a}$ |
| Mongoose | 1.2 $^{a}$ | 1.2 $^{ab}$ | 2.4 $^{ab}$ |
| Cat urine | 1.1 $^{a}$ | 1.0$^{b}$ | 2.1$^{b}$ |
| **Synthesised Odours** | | | |
| SMMBO | 1.6 $^{a}$ | 2.0 $^{ab}$ | 3.6 $^{ab}$ |
| IPMS | 1.0 $^{a}$ | 0.9$^{b}$ | 1.9$^{b}$ |
| PT | 1.2 $^{a}$ | 0.9$^{b}$ | 2.1$^{b}$ |
| **Herbivore odours** | | | |
| Guinea pig | 2.6 $^{a}$ | 1.9 $^{ab}$ | 4.4 $^{ab}$ |
| Deer urine | 1.2 $^{a}$ | 1.0$^{b}$ | 4.5$^{b}$ |
| Rabbit urine | 2.0 $^{a}$ | 2.5 $^{ab}$ | 2.2 $^{ab}$ |
| **Maximum SED** | 0.85 | 0.81 | 1.57 |

[*] Numbers presented are backtransformed values from a REML analysis. Means in the same column (of nine odours) marked with different letters are significantly different at the 0.05 level.

### Table 4. Responses of The North Island Rats to the Nine Odours Tested Grouped by Source and by Sex.[*]

| Odour | Mean number of visits to the control adjusted for rat and block | Mean number of visits to the odour adjusted for rat and block | Mean activity adjusted for rat and block |
|---|---|---|---|
| Real Predator | 1.6 | 1.7 | 3.3 |
| Synthesised Predator | 1.2 | 1.3 | 2.5 |
| Herbivore | 1.9 | 1.8 | 3.7 |
| **Maximum SED** | 0.49 | 0.47 | 0.91 |
| Male (n=6) | $0.8^{b}$ | $0.9^{b}$ | $1.7^{b}$ |
| Female (n=4) | $2.4^{a}$ | $2.3^{a}$ | $4.7^{a}$ |
| **Maximum SED** | 0.61 | 0.42 | 0.99 |

[*] Numbers presented are backtransformed values from a REML analysis. Male and female means are significantly different from each other at the 0.05 level (indicated by letters), but the means according to source are statistically indistinguishable from each other.

*Friedman Two-way ANOVA by Ranks.* Rats spent a larger amount of time in the control arm than in the odour arm when exposed to rabbit odour (mean in control arm=29.4%, s.e.=11.1%, mean in odour arm=13.2, s.e.=7.6, S=15.10, df=8, *P*=0.057). None of the other variables measured was affected by odour.

*Rats use of a clean maze.* North Island rats made 1.7 visits to the left arm and 1.6 visits to the right arm on average (s.e.=0.4 and 0.3, respectively). North Island rats made a total of 52 visits to the left choice arm and 49 to the right choice arm ($\chi^2$=0.089, df=1, ns). Eight of the rats stayed in the first arm during one trial and two rats remained in the first arm on two of three occasions. Thus North Island rats did not show a preference for the left or right arm, but all of them chose not to explore the maze at all on at least one occasion.

*Comparison of the Two Populations.* Both samples of rats showed a high degree of individual variation in all the variables we measured (Tables 1 and 3). On the basis of the means and standard errors, the two populations do not differ significantly in most of the variables we measured. North Island rats may have spent more time in the control arm (mean=29.4%, s.e.=11.1%) during tests with rabbit urine than Kapiti rats (mean=5.0%, s.e.=2.5%), but this result was not significant at the 0.05 level (Mann-Whitney W=127.0, *P*=0.097). The amount of time spent in the odour arm when exposed to cat faeces differed between samples (Mann-Whitney W=126.0, *P*=0.037), because Kapiti rats spent less time in the presence of the odour than North Island rats (mean=2.3%, s.e.=0.7% and mean=18.4%, s.e.=6.6%, respectively). For all the other variables we measured, the two samples were statistically indistinguishable.

## DISCUSSION

It appears extremely unlikely that predator odours would be an effective large-scale management tool to protect rare species from rats in New Zealand or elsewhere. However, at least some populations of wild rats avoid some odours. Our results indicate that Norway rats might be able to differentiate the odours of carnivores from those of herbivores. Because Kapiti rats show more evidence of discrimination than North Island rats, it may be that this innate ability is weak or was not fully expressed in the context of this experiment. Several authors have shown that laboratory Norway rats are innately averse to predator odours (Heale and Vanderwolf, 1994; Zangrossi and File, 1994; Perrot-Sinal and Petersen, 1997), but none has shown an innate aversion in a wild population that has never been exposed to predators.

It is not obvious why a predator-naïve population (Kapiti) should show more evidence of aversion than the predator-experienced one we sampled (North Island). We have considered several possible explanations: (1) perhaps the length of time spent in captivity influenced the results. If that was the case, then one would predict that rats that had been housed longer would show less response (e.g., Ward et al., 1996). However, the Kapiti rats had been confined longer than their North Island counterparts; (2) we cannot exclude a seasonal effect since the rats were tested at different times of the year. However this seems unlikely, as both groups had at least one week to acclimate to the standard light and temperature regime. This should have been long enough to phase-shift the rats and entrain them to the new light cycle (Palmer, 1976), and the rats had no other exogenous cues as to the actual season that we could detect; (3) the age of the rats may be important. On the basis of size, all except one of the rats was a mature adult when captured, and at the time of testing all were mature. The rats were not aged, but given that the length of time in captivity must correlate with age, Kapiti rats were probably, on average, older; (4) perhaps Norway rats are innately averse to predators, as evidenced by the predator naïve Kapiti rats, but this aversion is modified by experience. Wuensch (1992) found that newborn mice (*Mus musculus*) fostered onto laboratory rats were more active in subsequent tests using wood chips scented with rat odour than those reared by conspecifics or deer mice (*Peromyscus maniculatus*). Rats raised in a farm setting would probably be exposed to a wide variety of predator odours from an early age, without necessarily encountering them directly. For example, all the farms where we trapped rats had resident cats and dogs housed near where the rats were caught. Thus the odour of cats and dogs may have pervaded rat colonies without any risk of predation. If this were true then rats would habituate to odours while still young. If they subsequently failed to encounter a serious predation threat, then they may continue to ignore odours as they grow older. Such rats might be more likely to respond if they have been at risk of predation since leaving their nest (Tobin et al., 1995) or if the threat of predation is real and imminent (e.g., Fenn and MacDonald, 1995). This would explain our results, since there was no real threat of predation in our trials. If rats and mice learn about risk from encounters with predators, then one would expect white laboratory mice and rats to habituate to predator odours in laboratory trials where there is no chance of death or injury, but they apparently do not (Zangrossi and File, 1994; Kemble and Bolwahnn, 1997). The effect of age and learning on rats responses to predator odours remains to be tested.

Burwash et al. (1998) evaluated eight synthetic and one real odour for eliciting avoidance responses in wild-caught ship rats (*R. rattus*) using 100 subjects, testing each one once. They did not report any statistically significant changes in behaviour depending on odour, but concluded that Hawaiian ship rats did avoid predator odours (i.e., predator odours were biologically significant to rats) based on trends in their data. Tobin et al. (1995) had already shown in field trials that ship rats avoided mongoose-scented traps. Burwash et al. (1998) suggested that their lack of statistically significant results reflected the high individual variability shown by the rats, and that this individual variation had contributed to the global success of that species. High individual variability was also evident in our experiments, and as indicated by Burwash et al. (1998), it may not have been reduced by a larger sample size.

Kapiti rats appeared to generalise their aversive reactions to all predator odours, except mongoose faeces. This may be because urines are more effective than faeces at deterring herbivores (Sullivan et al., 1985, Nolte et al., 1994). Cat urine was more effective at decreasing activity than cat faeces in our experiments with Kapiti rats. Also, Kapiti rats showed an aversion to all the predator odours we tested (except mongoose faeces), despite the fact that all the odours they met were novel. Neophobia can explain some aversions in mice, particularly if the smell is pungent (Kemble and Bolwahnn, 1997), but can not explain the differing responses of Kapiti rats to herbivore and carnivore odours. We can not rule out the idea that neophobia was the reason that North Island rats chose to spend less time in the arm containing rabbit odour than the control arm, since we do not know the experience of each individual rat. However, no similar result was obtained for novel Guinea pig odour.

Ward et al. (1996) found that recently caught wild hedgehogs (*Erinaceous europaeus*) showed a larger increase in oxygen consumption in response to badger (*Meles meles*) odour than individuals who had spent a longer time in captivity. Long-term captive hedgehogs were variable and inconsistent in their responses. However, they also reported that observable activity was not significantly correlated with oxygen consumption. Similarly, Cocke and Thiessen (1986) reported physiological changes in gerbils (*Meriones unguiculatus*) to cat odour that were not reflected in changes to locomotor activity. It is possible that the rats we studied were showing physiological responses that we did not measure that were not reflected in their behaviour.

The pungency of the odours presented may have contributed to our results (Kemble and Bolwahnn, 1997). The synthesised odours smelt much stronger to a human nose than the natural odours, and we attempted to partially control for this by using both natural cat urine and SMMBO, a synthesised component of cat urine. All of the natural odours were equally strong to our noses, but the strong avoidance of SMMBO, IPMS and PT shown by the Kapiti rats may have been because they were more pungent. However, real cat urine was as efficient at deterring rats as SMMBO. Also, the pungent odours were no more effective in deterring North Island rats than the less pungent natural odours.

Garbe et al. (1993) found that the type of arena that mice were tested in affected their risk assessment behaviours (e.g., orientation to odour, time to approach, immobility, defensive burying etc) in response to odours. In their first experiments, in a purpose built arena, Garbe et al. (1993) reported no increase in risk assessment behaviours when laboratory mice were exposed to cat fur as one of four novel odours. In the second trial in the subjects' home cages, cat fur did cause an increase in risk assessment behaviours over the control odours. Y mazes or their variants are regularly used for odour discrimination tests (e.g. Krasnov and Khoklova, 1996) and represent an advantage over home cage trials because the subjects, at least potentially, have a "neutral" or no-choice area they can utilise, making time in each choice arm independent. The ducts removing air at the beginning of each choice arm in our apparatus should have created such a situation, where the rat had to reach the junction before encountering the odour, whereupon it would choose an arm. However, it is possible that the extractor fan was not removing all of the odour, and rats in the first arm may have been able to detect it. This would mean that they would have been effectively moving up wind towards the odour, which may be why some rats froze in the first arm. Thus the distilled water control may not have served its intended purpose of an odour free choice. This problem is likely to affect many studies that make use of a Y maze or four-arm (plus) maze apparatus.

Tests of an animal's ability to discriminate carnivore and herbivore odours have been widely published, but results are often contradictory. For example, some authors have claimed that responses to odours by mice are innate (e.g., Zangrossi and File, 1994) and others, using wild or wild-caught subjects, have claimed that they are not (e.g., Dickman, 1992; Krasnov and Khoklova, 1996). The issue has been further clouded because authors have used different measures to gauge avoidance, different experimental arenas, and at times the same behaviour has been interpreted differently by different authors (Burwash et al., 1998 and references therein). Many authors have also chosen to apply odours to food sources (e.g., Sullivan et al., 1985), while others have not. By testing our samples of rats in a Y maze, according to the same protocol, using the same odours, the same measures and by not including the complicating factor of food, we have avoided many of these difficulties in interpretation. The differences shown by our samples appear to be real ones.

Sympatric, congeneric Kangaroo rats (*Dipodomys*) differ in their ability to discriminate snake odour (Randall et al., 1995). Strains of laboratory mice differ in their responses to odours (Dell'Omo, 1994) and it appears from our study that different results can also be obtained from different populations of the same species using the same measures and the same experimental protocol. Future studies should be directed at how individual experience affects rats responses, with the aim of contributing to an understanding of predator avoidance in mammals and clarifying what biological phenomenon leads different populations, strains and congeneric species to exhibit such different responses.

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## REFERENCES

ATKINSON, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, pp 35-81, *in* P.J. Moors (ed.). Conservation of island birds: Case studies for the management of threatened island species. International Council for Bird Preservation Technical . Publications No. 3.

BERDOY, M., and SMITH, P. 1993. Arms race and rat race: Adaptations against poisoning in the brown rat. *Rev. Ecol. (Terre Vie)* 48:215-228.

BOAG, B., and MLOTKIEWICZ, J.A. 1994. Effect of odor derived from lion faeces on behavior of wild rabbits. *J. Chem. Ecol.* 20:631-637.

BRUNTON, C.F.A., MACDONALD, D.W., and BUCKLE, A.P. 1993. Behavioural resistance towards poison baits in brown rats (*Rattus norvegicus*). *Appl. Anim. Behav. Sci.* 38:159-174.

BURWASH, M.D., TOBIN, M.E., WOOLHOUSE, A.D., and SULLIVAN, T.P. 1998. Laboratory evaluation of predator odours for eliciting an avoidance response in roof rats (*Rattus rattus*). *J. Chem. Ecol.* 24:49-66.

COCKE, R., and THIESSEN, D.D. 1986. Chemocommunication among prey and predator species. *Anim. Learn. Behav.* 14:90-92.

COWAN, P.E. 1992. The eradication of introduced Australian brushtail possums, *Trichosurus vulpecula*, from Kapiti Island, a New Zealand nature reserve. *Biol. Conserv.* 61:217-226.

DELL'OMO, G., FIORE, M., and ALLEVA, E. 1994. Strain differences in mouse response to odours and predators. *Behav. Proc.* 32(2):105-116.

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

ENGELHART, A., and MULLER-SCHWARZE, D. 1995. Responses of beaver (*Castor canadensis* Kuhl) to predator chemicals. *J.Chem. Ecol.* 21:1349-1364.

FENN, M.G.P., and MACDONALD, D.W. 1995. Use of middens by red foxes: risk reverses rhythms of rats. *J. Mamm.* 76:130-136.

GARBE, C.M., KEMBLE, E.D., and RAWLEIGH, J.M. 1993. Novel odours evoke risk assessment and suppress appetitive behaviors in mice. *Aggress. Behav.* 19:447-454.

GLIWICZ, J. 1980. Island populations of rodents: Their organisation and functioning. *Biol. Rev.* 55:109-138.

HEALE, V.R., and VANDERWOLF, C.H. 1994. Toluene and Weasel (2-Propylthietane) odors suppress feeding in the rat. *J. Chem. Ecol.* 20:2953-2958.

INNES, J.G., WARBURTON, B., WILLIAMS, D.S., SPEED, H., and BRADFIELD, P. 1995. Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *N.Z. J. Ecol.* 19:5-17.

KEMBLE, E.D., and BOLWAHNN, B.L. 1997. Immediate and long-term effects of novel odors on risk assessment in mice. *Physiol. Behav.* 61:543-549.

KING, C.M. 1990. (Editor) *The Handbook of New Zealand Mammals*. Oxford University Press, Auckland, New Zealand.

KING C.M., and MOLLER, H. 1997. Distribution and response of rats, *Rattus rattus* and *R. exulans*, to seedfall in New Zealand beech forests. *Pac. Conserv. Biol.* 3:143-155.

KRASNOV, B., and KHOKLOVA, I. 1996. Discrimination of midday jird's odour by house mice. *Anim. Behav.* 52:659-665.

MAPPES, T., KOSKELA, E., and YLONEN, H. 1998. Breeding suppression in voles under predation risk of small mustelids: laboratory or methodological artifact? *Oikos* 82:365-369.

MASON, J.R., EPPLE, G., and NOLTE, D.L. 1992. Semiochemicals and improvements in rodent control, pp. 327-346, *in,* B.G. Galef, M. Mainardi and P. Valsecchi (eds.). Behavioral Aspects of Feeding: Basic and applied research in Mammals: 6th Workshop of the International School of Ethology, Ettore Majorana Centre for Scientific Culture, Erice, Sicily, Italy, 8-14 June 1992. Harwood Academic Publishers, Chur, Switzerland.

NOLTE, D.L., MASON, J.R., EPPLE, G., ARONOV, E., and CAMPBELL, D.L. 1994. Why are predator urines aversive to prey? *J. Chem. Ecol.* 20:1505-1516.

PALMER, J.D. 1976. An introduction to Biological Rhythms. Academic Press Inc. New York, USA.

PERROT-SINAL, T., and PETERSEN, K. 1997. Exposure to predator odor reduces locomotor activity levels in adult male rats: Lack of effect of hippocampal lesion. *J. Chem. Ecol.* 23:2175-2186.

RANDALL, J.A., HATCH, S.M., and HEKKALA, E.R. 1995. Inter-specific variation in antipredator behavior in sympatric species of kangaroo rat. *Behav. Ecol. Sociobiol.* 36:243-250.

SPURR, E.B. 1979. A theoretical assessment of the ability of bird species to recover from an imposed reduction in numbers, with particular reference to 1080 poisoning. *N.Z. J. Ecol.* 12:23-32.

SPURR, E.B. 1991. Effects of brushtail possum control operations on non-target bird populations. *Acta XX IOC*:2534-2545.

SULLIVAN, T.P., NORDSTROM, L.O., and SULLIVAN, D.S. 1985. Use of predator odors as repellents to reduce feeding damage by herbivores I. Snowshoe Hares (*Lepus americanus*). *J. Chem. Ecol.* 11:903-919.

TAYLOR, R.H., and THOMAS, B.W. 1989. Eradication of Norway rats (*Rattus norvegicus*) from Hawea Island, Fiordland, using Brodifacoum. *N.Z. J. Ecol.* 12:23-32.

TAYLOR, R.H. and THOMAS, B.W. 1993. Rats eradicated from rugged Breaksea Island (170 ha), Fiordland, New Zealand. *Biol. Conserv.* 65:191-198.

TOBIN, M.E., ENGEMANN, R.M., and SUGIHARA, R.T. 1995. Effects of mongoose odors on rat capture success. *J. Chem. Ecol.* 21:635-639.

UNDERWOOD, A.J. 1981. Techniques of Analysis of Variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.* 19:513-605.

WACE, N.M. 1986. The rat problem on oceanic islands – research is needed. *Oryx* 20:79-86.

WARD, J.F., MACDONALD, D.W., DONCASTER, C.P., and MAUGET, C. 1996. Physiological response of the European Hedgehog to predator and nonpredator odour. *Physiol. Behav.* 60:1469-1472.

WUENSCH, K.L. 1992. Fostering house mice onto rats and deer mice: Effects on response to species odours. *Anim. Learn. Behav.* 20:253-258.

YLONEN, H., and RONKAINEN, H. 1994. Breeding suppression in the bank vole as an antipredatory adaptation in a predictable environment. *Evol. Ecol.* 8:658-666.

ZANGROSSI, H. and FILE, S.E. 1994. Habituation and generalisation of phobic responses to cat odor. *Brain Res. Bull.* 33:189-194.

# CHAPTER SIX: LABORATORY AND FIELD EVALUATION OF PREDATOR ODOURS AS REPELLENTS FOR KIORE (*RATTUS EXULANS*) AND SHIP RATS (*R. RATTUS*).

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**Abstract** – Predator odours may serve to stop rats entering conservation areas in New Zealand or to decrease predation, food consumption and other damage by rats in areas tainted with predator odour. We compared the efficacy of real predator odours and synthetic odours (derived from the urine and faeces of carnivores) as rat repellents with real herbivore odours as controls in a Y maze. Ship rats (*Rattus rattus*) and kiore or Polynesian rats (*R. exulans*) showed no aversion to any of the six odours we tested (real cat (*Felis catus*) urine and faeces, mongoose (*Herpestes auropunctatus*) faeces, n-propylthietane, S-methyl, methyl butanol and isopentyl-methyl sulphide)) when compared with herbivore odours. The herbivore odours we used were: red deer (*Cervus elaphus*) urine, guinea pig (*Cavia porcellus*) faeces and white rabbit (*Oryctolagus cuniculus*) urine. However, ship rats may have avoided synthesised odours more than real ones. We applied two odours (S-methyl, methyl butanol and n-propylthietane) to purpose-built feeders in native forest but recorded no change in either visitation rate or duration of visits for rodents (rats and mice (*Mus musculus*)) or possums (*Trichosurus vulpecula*). The consumption of maize at feeders was strongly correlated with the number and duration of possum visits, but only weakly with visits by rodents, and was unaffected by the odour associated with the feeder. It is unlikely that the odours we tested will be useful in deterring rodents or possums from areas where they have been removed for economic, public health or conservation reasons.

**Keywords** – *Rattus rattus,* ship rat, semiochemicals, odour avoidance, predator odours, Polynesian rat, *R. exulans*, rat repellents, pest management.

## INTRODUCTION

Predator-based repellents have been used experimentally to reduce damage to crops caused by wildlife (Sullivan et al., 1985a and 1985b; Boag and Mlotkiewicz, 1994) and food consumption by domestic herbivores (Arnould et al., 1993). The behavioural and physiological responses of prey species to repellents include the avoidance of treated food and traps, freezing, hiding, analgesia and physiological arousal (reviewed by Kats and Dill, 1998). Burwash et al. (1998) tested eight artificially synthesised semiochemicals (and one real one) and, despite no statistically significant results, concluded from trends in their data that ship rats (*Rattus rattus*) avoid odours derived from carnivores. They went on to suggest that the application of such chemicals might reduce rat damage to the economically important macadamia nut (*Macadamia integrifolia*) crop in Hawaii, by causing rats to reduce their consumption.

Mason et al. (1994) believed that volatile sulphurous compounds in the faeces and urine of carnivores derived from the digestion of meat mediated the responses of prey animals, and this is supported by data (e.g., Nolte et al., 1994). Mason et al. (1994) used the term semiochemical to describe these sulphurous chemicals that provide biologically important information to other animals. They hypothesised that omnivores such as rats (genus *Rattus*) should be attracted to semiochemicals because they may provide them with reliable information on sources of food, whilst herbivores should be repelled from areas contaminated with semiochemicals to avoid encountering a predator. However, many authors have reported that rats avoid predator odours or show reduced activity in their presence (reviewed by Kats and Dill, 1998).

Published accounts of mammals' ability to discriminate and avoid predator odours have been contradictory, in part because different authors have interpreted the same behaviour in different ways (Burwash et al., 1998 and references therein). Interpretations may have been further clouded because the efficacy of predator-based repellents varies with cover (Merkens et al., 1991) and different test arenas can produce different results (Garbe et al., 1993) and both these factors have varied in different trials. Rodent responses to semiochemicals might also vary with experience (e.g., Wuensch, 1992), although this remains untested. Furthermore, responses to semiochemicals appear to differ in different congeneric species, subspecies, strains and populations. For example, Bramley et al. (Chapter 5) showed that rats from a predator naïve population of Norway rat (*Rattus norvegicus*) avoided semiochemicals, but rats from another (predator experienced) population did not. Differences in laboratory mouse strains in response to predator odours have also been recorded (Dell'Omo et al., 1994). Furthermore, different strains of mouse have shown different responses to intraspecific odours too. For example, *Mus musculus musculus* spent longer investigating semiochemicals deposited by other *M. m. musculus* individuals, whilst *M. m. domesticus* showed no such preference. The difference in response may be a precopulatory isolating mechanism that accounts for asymmmetric hybridisation between the two subspecies (Christophe and Baudoin, 1998).

In addition to the variability found in different populations, subspecies and strains of rodent, some authors have used "no odour" treatments as a control for predator odours and in so doing have failed to provide adequate experimental controls. This may have produced erroneous results in some cases (see Wolff and Davis-Born, 1997, and Mappes et al., 1998, for a critique).

In New Zealand, there are four species of rodent (roof or ship rat, Norway rat, Polynesian rat or kiore *R. exulans* and the house mouse[1]). All four species were introduced with human voyagers (Atkinson and Moller, 1990; Holdaway, 1996). Although the four species do not coexist in the same places (Atkinson and Moller, 1990) or habitats (King et al., 1996; King and Moller, 1997), all are regarded as pests because of their adverse effects on native wildlife and vegetation (Atkinson, 1985; Towns, 1991). Ship rats are most common on the two main islands of New Zealand (Innes, 1990) whilst kiore are limited to smaller offshore islands, having been replaced, firstly by Norway rats and then ship rats in most habitats on the two main islands (Atkinson and Moller, 1990; King and Moller, 1997).

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[1] There are two species of house mouse recognised *M. musculus* and *M. domesticus*. Mice in New Zealand share morphometric characteristics with both species and await genetic determination (Murphy and Pickard, 1990).

Control of rodent populations has relied on extensive poisoning using second-generation anticoagulants (MacDonald, 1984). In New Zealand, rat populations have been eradicated from offshore islands and greatly reduced in large areas of forest on the main islands using these poisons (Taylor and Thomas, 1993; Innes et al., 1995). Reinvasion to mainland management areas is rapid (Innes et al., 1995) and the threat of reinvasion to often-visited island reserves is always present (Wace, 1986). Thus if rats could be shown to reliably avoid predator odours then this response could be exploited by conservation managers as part of an arsenal of techniques to protect native species from rats in New Zealand. It could also be economically useful since ship and Norway rats are two of the most serious worldwide pests of crops and stored foods and they harbour diseases like bubonic plague and typhoid (MacDonald, 1984). Repelling rats from areas such as zoological gardens and wildlife parks or sanctuaries may also prove beneficial to the animals living there.

We determined whether two species of rat (kiore and ship rat) would discriminate and avoid odours derived from the urine and faeces of predators in a Y-shaped maze. Garbe et al. (1993) showed that mouse responses to odour varied with the kind of arena used. Also, when animals are housed in captivity there is always the possibility that their behaviour will change as a result of being held captive (Ward et al., 1996). Because of these important considerations, we also examined the responses of ship rats to two of the odours we used in our laboratory trials in the wild. The two semiochemicals we tested in our field trials (S-methyl, methyl butanol and n-propylthietane) had both proved effective in deterring Norway rats from Kapiti Island in laboratory trials (Bramley et al., Chapter 5). Both the artificial semiochemicals we used are components of predator urine or faeces (cats, *Felis catus*, and mustelids respectively). Both these predators are found on the North Island of New Zealand. Thus it is likely that free-living rats on the North Island had encountered them or their odours before. All visits to feeders were recorded on videotape and thus we were also able to collect incidental observations on the avoidance behaviour of brush-tailed possums (*Trichosurus vulpecula*).

## METHODS

*Animals.* Thirty animals were used in the laboratory trials: 15 kiore and 15 ship rats. All animals were adults, and 10 of the ship rats and nine kiore were females. The ship rats were caught in cage traps baited with apple and peanut butter along the banks of the Waikato River at Tamahere, south of Hamilton City, North Island, New Zealand. Kiore were captured using traditional Maori pitfall traps on islands in the Hen and Chickens group near Whangarei, northern North Island, New Zealand, and supplied to us by the Ngati Wai tribal resource management group. Both groups of rats were collected between January and April 1997.

At the University of Waikato facilities, the ship rats were housed individually in plastic bottomed, wire cages (46 x 24 x 20 cm high) and kiore were housed individually in plastic tubs with wire tops (40 x 27 x 15 cm deep). All animals had *ad libitum* access to water and Sharpes Diet 86 rat chow (Sharpes Grains and Seeds, Lower Hutt, New Zealand), occasional seed mixes and pieces of apple; kiore were also given fresh grass seed heads. Cages were provided with a tin and a cardboard tube to act as retreats. We used wood shavings as bedding and changed it weekly. The rats were housed in two separate rooms and maintained on a constant 12:12 light schedule, with lights on at 2200 hours. Temperatures in the rooms were between 16 and 24°C. Ship rats were tested in May 1997 and kiore in June 1997.

*Odours*. We examined the subjects responses to nine different odours. Six of the odours were natural, from the faeces or urine of live animals, and three odours were the commercially synthesised volatile ingredients of urine or faeces (provided by New Zealand Industrial Chemists, Gracefield, Lower Hutt, New Zealand). The natural odours were: cat urine (supplied by Five Cross Roads Veterinary Clinic, Hamilton, New Zealand), mongoose (*Herpestes auropunctatus*) faeces (collected in Hawaii by A. Woolhouse of New Zealand Industrial Chemists), guinea pig faeces, New Zealand white laboratory rabbit (*Oryctolagus cuniculus*) urine and red deer (*Cervus elaphus*) urine. The cat and rabbit urine was collected via catheterisation of laboratory animals held at the Veterinary Clinic or Waikato Polytechnic (Hamilton, New Zealand). Guinea pig faeces were collected from the guinea pig cages at the Polytechnic. The deer urine was collected from animals kept at the deer unit of AgResearch Ruakura (Hamilton, New Zealand). Artificially synthesised chemicals were provided as 1% solutions in paraffin oil. Chemicals used were isopentyl methyl sulphide (IPMS, found in red fox, *Vulpes vulpes*, urine), n-propylthietane (PT, found in stoat and ferret anal sac secretions, and hence probably also in their faeces), and S-methyl, methyl butanol (SMMBO, found in cat urine). Thus there were three synthesised predator smells, three natural herbivore smells and three natural predator smells. Of the natural odours, one of the herbivore and two of the predator smells were from faeces. Urine and faeces was always collected from more than one donor animal, but only one donor was used at a time (i.e., samples were not pooled) except in the case of the deer urine. All natural odours were stored frozen.

Islands in the Hen and Chickens group are free of mammalian predators of kiore. Kiore are the only rat known to live there (Atkinson and Moller, 1990), so kiore collected there should be naïve to all the smells we tested. Ship rats collected on the North Island should be familiar with felids, canids and mustelids, which have long-established populations on the North Island of New Zealand. There were also cows, sheep, deer, goats and rabbits on farms near where the ship rats were caught. There are no feral populations of guinea pigs (*Cavia porcellus*) in New Zealand (King, 1990) and it is unlikely any of the rats we used had ever come into contact with guinea pig odour.

In the field trials, odours were supplied as 5% W/V impregnated in casein squares measuring approximately 30 x 30 x 5 mm high and weighing 4.8-5.2 g (New Zealand Industrial Chemists, Wellington, New Zealand). Only two odours were used in the field trials (SMMBO and PT). We chose to use 5% W/V concentrations because we wanted the odours to be detectable at some distance in forest, and for them to persist for the whole length of the trial. The chemistry of herbivore urine and faeces has not been well studied (A. Woolhouse, New Zealand Industrial Chemists, Wellington, New Zealand, pers. comm.) and it was not possible to use synthetic herbivore derived odours as a control. Instead we used two other controls: odour-free casein squares applied to the feeder and no casein squares. The casein squares had a slight odour of their own, and thus these controls represent an odour (casein) and a no odour (no square) treatment.

*Maze Experiments*. Animals were collected one at a time from the captive colony and transported in their cages, in darkness, to a separate trial room. They were then transferred into an experimental arena lit with red light. When the animals were in the arena, the red light was turned off and all observations were completed using a 20 cm diameter spotlight with an infra-red filter. The spotlight was powered by a Hitachi 12 V, 7 Ah, sealed lead-acid battery. Tests were videoed using a Videotronic Tri-Q CCD camera and a Panasonic AG5260 video recorder. After being tested animals were returned to their cage and then to the captive colony.

We used a Y maze made of PVC piping (10 cm in diameter) to examine the responses of both groups of rats to odours (Figure 1). The odour stimulus was presented inside an opaque glass container as either 0.1 ml of solution pipetted onto a 1 $cm^2$ piece of Whatman filter paper or as 0.1 g of thawed faeces. Odours were presented in the maze with distilled water controls, presented in the same way, in the other choice arm. The position of the odour (left or right) and the type of odour (numbered 1-9) were recorded on the video tape after the trial, but were unknown to us when we scored the rats behaviour. Three identical mazes were used and after each test the maze was washed using hot water and Vircon soap powder and then towel dried.

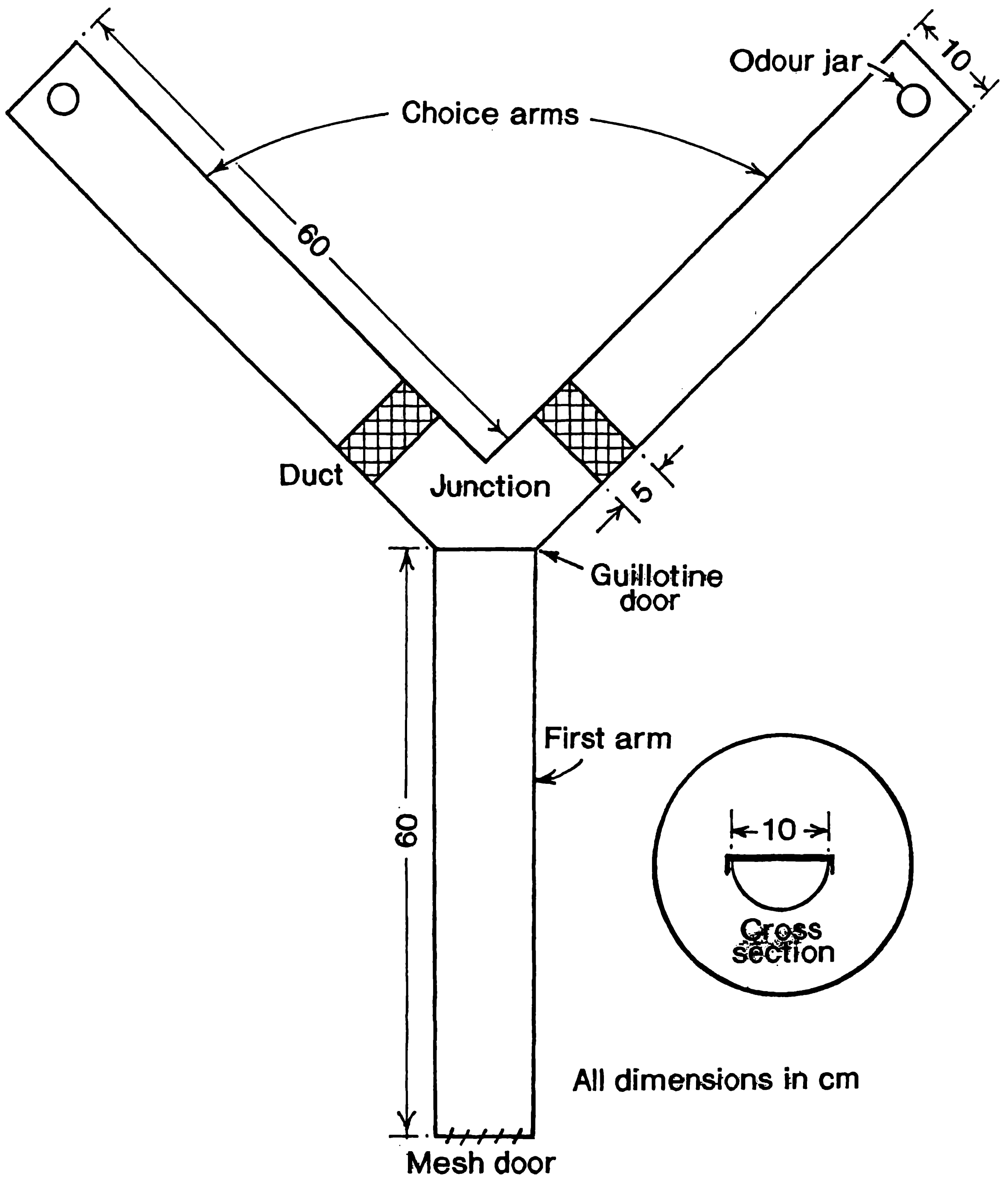


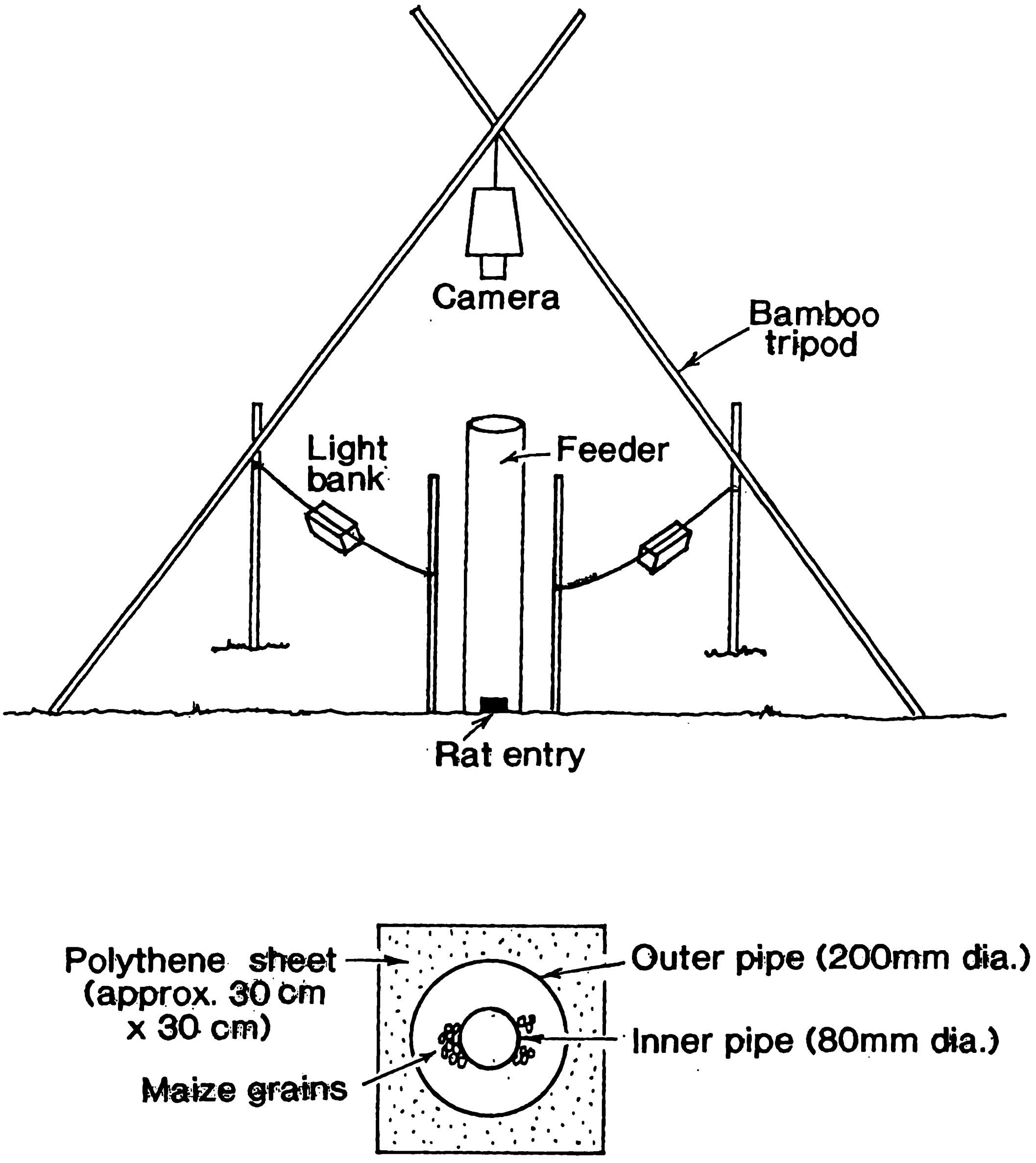
FIG. 1: The Y maze apparatus used to test the responses of rats to the odour of predators and herbivores.

Ship rats and kiore were tested separately according to an incomplete block design using eighteen blocks. Each block consisted of five rats. One block (of five rats and five odours) was tested per day. Each rat was randomly allocated a position in six blocks (i.e., received each of the six odours once over the 18 days of the trial). Tests began one hour after the lights in the colony had gone off and continued sequentially until five animals were tested. Each test was usually conducted within 40 minutes of the previous one. Prior to the start of each test, rats were placed in the first arm of the maze, with the guillotine door shut (Figure 1). The video recorder was then started and the observer left the room. After five minutes the guillotine door was opened (from outside the room) and the rats were free to explore the maze for fifteen minutes. We recorded: (1) the time until the rat first visited each of the arms. A visit was defined as occurring when the rat's head was more than 5 cm down the arm; (2) the number of visits to the odour and control arm; (3) the time spent in each arm; and (4) a total activity score for each rat, which was the number of visits to each arm summed together.

The day before being tested, each rat was introduced to the maze as outlined above, but in the absence of any odours. We recorded the same measures for each rat on videotape to detect any left or right bias and to establish that the rats would explore the maze. In the middle of the series of tests and at the end of the series, the rats were again introduced to clean mazes and their movements recorded. This was to check that each rat would still explore the maze in the absence of smells and that the rats had not developed a left or right preference during the trials. Recordings of rats in a clean maze were done after the days tests (on other rats) had concluded.

*Field Experiments*. Four feeding stations (Figure 2) were set up in each of seven different forests or forest remnants on the North Island. The feeding stations were positioned approximately 20 m from a central point, one each in a north, south, east and west direction. The seven forest sites were: Tahae Block (Pureora Forest Park), Pouakani Scenic Reserve (near Pureora), Yarndley's Bush (north of Te Awamutu), Walter Scott Reserve (29 km west of Te Awamutu), Whewell's Bush (Matangi), Te Kauri Scenic Reserve (Kawhia) and Te Tapui Scenic Reserve (13 km east of Matamata). The seven study areas were widely separated geographically. They also differed in topography, climate, altitude, aspect, geology, history, dominant vegetation and probably in rodent density and species composition too. We expected that each site would have ship rats and mice, but the relative densities of each species were unknown and we did not know whether or not Norway rats were present at any site.

Each feeding station consisted of a feeder (made up of an inner PVC pipe (diameter=8 cm, 1 m tall) and an outer PVC pipe (diameter=20 cm, 1 m tall)). The inner pipe was filled with approximately 550 g of maize grains, and had two small holes cut at the bottom to allow the corn to flow out. The larger pipe had three squares (10 x 10 cm) removed from the bottom to allow rodents access to the inner pipe (Figure 2). Each feeder was positioned on top of a 30 x 30 cm piece of black polythene to protect the corn from the ground's moisture and was held in place by guy ropes attached to surrounding vegetation or support poles. Each feeder was monitored by a Videotronic Tri-Q CCD camera positioned approximately 1.65 m above the ground, suspended on a tripod of three bamboo poles tied together at the top.



PLAN VIEW OF RAT FEEDER

FIG. 2: A rat feeding station and camera used to record visits by rodents (rats and mice) and possums (*Trichosurus vulpecula*). Each feeder consisted of two PVC pipes, and odours were attached to the outside of the larger pipe, near the rat entrance. Four stations were positioned in each of seven forested areas. All four cameras were connected to a central time-lapse video recorder (see text).

The feeder and camera units were numbered according to their position with feeder and camera 1 being the northernmost one. Each camera was secured inside an inverted plastic bucket to protect it from the elements. On either side of the feeder (approximately 55 cm above the ground) a bank of 16 infrared light emitting diodes provided illumination for the cameras. These two light banks lit up an area of approximately 50 x 50 cm around the base of the feeder. The four cameras were connected via approximately 20 m of cable to a Panasonic WJ-420 four-input screen splitter. The splitter was connected to a GYYR VHS timelapse recorder (Model TLC 1800X) set to record 48 hours on a 3-hour tape. The splitter, video recorder and camera control boxes were protected inside plastic boxes and covered with polythene to exclude water. The splitter and video recorder were connected to a Motormate PS-200-2 DC-AC power inverter. The power inverter, lights and cameras were connected to three 63 Ah Sonnenschein 12 V lead acid batteries connected in parallel via a Grasslin 12 V electronic timer.

Three casein squares impregnated with the odours were attached to the outer pipe of each feeder using plastic electrical insulation tape. A latin square design was used to assign odours to feeders. Study areas at each locality were located on the flattest ground we could find. On day 1 of a test, cameras and feeders were assembled and feeders were filled with a known amount of maize. The timer and video recorder were set to begin recording after dark and to stop recording before dawn. The exact length of recordings varied slightly with season. Once the system was in place, activity at each feeder was automatically recorded on videotape for the next three nights. After three nights we returned, weighed the remaining corn, added fresh corn if required, removed the videotape and left the area for 10 nights. After 10 nights, we returned and removed the casein squares impregnated with odour and weighed any remaining corn. We then wiped the outside of each plastic feeder with methyl alcohol to remove any remaining smell and allowed it to air dry. We refilled the feeders, re-set the video recorder and placed new casein squares impregnated with different odours on each feeding station. We video taped activity for a further three nights, and then returned and weighed the corn again (replenishing it if necessary). We allowed the feeders to remain *in situ* for 10 more days. After this we reweighed any remaining corn, then moved the feeders to the next site. Thus from each site we had six nights of recording from two sessions separated by 10 days. Each of the feeders had a different smell associated with it (according to our latin square design) in each test. We began these experiments on 20 December 1997 and concluded them on 21 June 1998. We watched each video four times (focussing on one feeder during each viewing). We recorded the number of visits made by rodents (rats or mice) and brush-tailed possums (*Trichosurus vulpecula*) to each feeder and the duration of the visits. We then summed the number and duration of visits for: (1) the first night and (2) the three nights of each session. We separated our data in this way because subjects might habituate to the odours over the three days of a test. We also recorded consumption of maize on nights 1-3 and nights 4-10 of each session for each odour.

*Data Analysis. Maze Experiments.* We used the Generalised Linear Model (GLM) function of MINITAB (version 12.1) to investigate the responses of each species of rat in a Y maze. For each species and each variable, we created a model that included the rat (numbered 1-15) and the block (numbered 1-18) as random effects and the odour as a fixed effect. We then grouped the odours into herbivore, real carnivore and synthesised carnivore and created models for each measure using odour type as a fixed predictor and rat and block as random predictors. We also created a model investigating the effect of sex on activity for each species. We used Tukey's tests to discriminate pairwise differences where GLM results were significant.

*Field Experiments.* To determine whether rats visited feeders differentially according to the treatments attached to them, we again used the GLM procedure. We created different models for each measure and specified the smell as a fixed predictor and location, test (1 or 2) and feeder (1-4) as random effects. To check that most maize consumption was by the rodent and possum visitors we recorded (and not by, for example, diurnal birds), we correlated the consumption on nights 1-3 with the number of visits by rats and possums for those three nights in both sessions.

## RESULTS

*Maze Experiments.* Exploratory data analysis showed that the number of visits to the arm containing the distilled water control were similar to the number of visits to the odour arm for both groups of rats. Thus we chose not to use the distilled water arm as a control because it was likely that the odour arm affected the subject's behaviour throughout the whole maze. Instead we used the data collected when rats were exposed to herbivore odours as the control.

In our experiments with kiore neither the odour, nor the odour type, significantly affected the variables we measured (Table 1).

TABLE 1: F-VALUES RESULTING FROM GENERALISED LINEAR MODELS DESIGNED TO DETERMINE THE EFFECT OF SEMIOCHEMICALS ON KIORE BEHAVIOUR.*

| Factor | Activity | Visits to odour | Visits to control | Time in odour | Time in control | Time to approach odour | Time to approach control |
|---|---|---|---|---|---|---|---|
| **Fixed effects** | | | | | | | |
| Odour | 0.72 | 0.75 | 0.54 | 0.69 | 1.23 | 0.95 | 0.65 |
| Odour type | 0.17 | 0.25 | 0.16 | 0.53 | 0.22 | 1.44 | 0.51 |
| **Random effects** | | | | | | | |
| Rat | 2.29* | 2.21* | 2.15* | 1.01 | 1.22 | 2.37* | 2.55** |
| Block | 1.20 | 1.01 | 1.21 | 1.09 | 1.08 | 1.11 | 1.03 |

*F-values marked with one asterix are significant at $P$=0.05, those marked with two asterixes are significant at $P$=0.01. Nine odours were tested in all: three real predator odours, three synthesised predator odours and three herbivore odours. The odours were each tested individually in one model as "odour" and then assigned into groups (real predator, synthesised predator and herbivore) for "odour type" in a second model to see if ship rats differed in responses according to odour source.

In no case was the block significant either, which indicates that rat behaviour did not vary significantly on different days. There was a high level of individual variation in the sample and the individual rat was a significant predictor for all of our measures except time in the odour arm (Table 1). Male kiore were more active (mean=9.89 visits, s.e.=1.56) than female kiore (mean=5.00 visits, s.e.=0.87; $F_{1,89}$=8.66, *P*=0.004). The effect of sex is implicit in the designation "rat" in our model, and thus is already partially accounted for.

One of the female ship rats escaped during her first test and could not be recaptured alive. Another female rat showed an abnormally high level of activity (approximately 230 visits to the left arm in a 15 minute trial) so was excluded from the analysis. This reduced our sample size to 13 animals. Of the variables we measured, only the number of visits to the odour may have been affected by the odour type ($F_{2,77}$=3.1, *P*=0.054) with herbivore and real predator odours being visited more often (mean=14.32 visits, s.e=2.38 and mean=13.96, s.e.=1.78 respectively) than artificially synthesised predator odours (mean=10.33, s.e.=1.89; T=2.26, *P*=0.07). All other variables were unaffected by odour or odour type (Table 2) but some behaviours (activity, number of visits to the control, time to approach the control; Table 2) were affected by the block number, indicating that rats behaved differently on different days. There was no trend in the behavioural changes through the period of the trial, for example rats did not become predictably more or less active as the trial progressed, rather they were more active on some days than they were on others. All measures, except the time spent in the odour and control arms, and the time to approach the smell, were significantly affected by the subject, indicating high individual variability. Ship rat activity was also affected by sex ($F_{1,77}$=8.58, *P*=0.005). Female ship rats were more active than males (mean for males=17.4 visits, s.e.=3.06, mean for females=30.5 visits, s.e.=3.00). The effect of the sex of the rat is again accounted for in our models.

TABLE 2: F-VALUES RESULTING FROM GENERALISED LINEAR MODELS DESIGNED TO DETERMINE THE EFFECT OF SEMIOCHEMICALS ON SHIP RAT BEHAVIOUR.*

| Factor | Activity | Visits to odour | Visits to control | Time in odour | Time in control | Time to approach odour | Time to approach control |
|---|---|---|---|---|---|---|---|
| **Fixed effects** | | | | | | | |
| Odour | 1.14 | 1.78 | 1.05 | 0.73 | 1.23 | 1.44 | 1.13 |
| Odour type | 1.92 | 3.1 | 0.3 | 0.24 | 0.43 | 1.67 | 0.12 |
| **Random effects** | | | | | | | |
| Rat | 9.06** | 6.80** | 5.67** | 1.96 | 1.77 | 1.6 | 3.44** |
| Block | 1.89* | 1.44 | 1.91* | 0.84 | 0.71 | 1.42 | 2.05* |

* F-values marked with one asterix are significant at $P$=0.05, those marked with two asterixes are significant at $P$=0.01. Nine odours were tested in all: three real predator odours, three synthesised predator odours and three herbivore odours. The odours were each tested individually in one model as "odour" and then assigned into groups (real predator, synthesised predator and herbivore) for "odour type" in a second model to see if ship rats differed in responses according to odour source.

*Rats Use of a Clean Maze.* Each rat explored an empty maze on three occasions. Kiore made a total of 104 visits to the left choice arm and 109 visits to the right choice arm ($\chi^2$=0.12, df=1, ns). Seven of the rats remained in the first arm during their first experience in the maze. A further three rats remained in the first arm on two occasions, thus ten of the kiore (66%) chose not to explore the maze on at least one occasion.

Ship rats made a total of 339 visits to the left choice arm and 361 to the right choice arm ($\chi^2$=0.69, df=1, ns). Only two of the ship rats remained in the first arm on one occasion, and one of those two remained in the first arm on a second occasion. We concluded that both species of rat readily explored the maze in the absence of odours, although kiore were more reluctant to explore the maze when they first experienced it and were less active overall. Neither species of rat showed a preference for one side of the maze.

*Field Experiments.* On some occasions, either one of the cameras or the time-lapse video recorder failed to work. Two of the cameras stopped recording after one night at Yarndley's Bush. During the second test at Yarndley's Bush, the video recorder stopped working after one night, thus reducing the number of feeding stations for which we had data for all three nights from 56 to 46. On some occasions maize weights were not recorded because the remaining maize became wet and heavy due to rain. These losses reduced our sample size for maize consumption on nights 1-3 from 56 to 50, and on nights 4-13 from 56 to 52.

Average maize consumption on days 1-3 varied between 120 g (at feeders with SMMBO) and 159 g (at feeders with odour free casein squares on them). The amount of maize consumed on days 1-3 of a test did not vary according to odour ($F_{3,49}$=0.31, $P$=0.82), but more than five times as much corn was eaten during the second test (mean=219 g, s.e.=30 g) as there was during the first test (mean=48 g, s.e.=10 g, $F_{1,49}$=22.38, $P$=0.0001). Maize consumption for days 4-13 of each test did not vary with smell either ($F_{3,51}$=0.36, $P$=0.78), but did vary with the test (again more maize was eaten in the second test, $F_{3,51}$=7.48, $P$=0.009) and with the location ($F_{6,51}$=9.78, $P$=0.0001). The amount of maize consumed on days 4-13 varied from an average of 120 g at Pouakani Scenic Reserve to 519 g at Walter Scott Scenic Reserve.

The number of rodents visiting feeders on night 1 of a test did not vary according to the semiochemical that was attached to the feeder (means ranged from 4.0-7.1 visits per feeder, $F_{3,55}=0.81$, $P=0.49$), but at some locations rat activity was generally higher (means ranged from 0.6-19.3 visits per location, $F_{6,55}=7.64$, $P=0.0001$). The number of brush-tailed possums visiting on the first night of a test did not vary according to odour either (range of means 0.6-2.1 visits per feeder, $F_{3,55}=1.72$, $P=0.18$) but there was also more possum activity at some locations (means ranged from 0.1-2.4 visits per location, $F_{6,55}=2.49$, $P=0.03$). More possum visits were recorded during the first night of the second test (mean = 2.0 visits) than on the first night of the first test (mean =0.6 visits, $F_{1,55}=7.35$, $P=0.01$).

The number of rat and mouse visits over the three day test did not vary according to odour (range of mean values = 20.1-25.0, $F_{3,45}=0.21$, $P=0.89$), but did vary according to location (range of mean values = 1.0-60.9 visits, $F_{6,45}=9.64$, $P=0.0001$). The same was true for possums (range of means 4.1-5.8, $F_{3,45}=0.32$, $P=0.81$ for odour, and range of means 0.4-12.3 visits, $F_{6,45}=7.49$, $P=0.0001$ for location). The amount of time spent at each feeder by rats and mice on night one was not dependent on the odour attached to the feeder (means ranged between 948s and 1578s, $F_{3,55}=0.17$, $P=0.92$), although it did vary with location (range of means = 146-4030s, $F_{6,55}=3.46$, $P=0.007$). Possums spent more time at feeders on the first night of the second test than they did on the first night of the first test (mean = 110s for night one, mean = 1130s for night two, $F_{1,55}=10.61$, $P=0.002$). The amount of time spent at feeders by possums on the first night of the second test did not vary according to smell ($F_{3,55}=2.12$, $P=0.11$).

When we considered the total amount of time spent at a feeder during the three nights of video recording, location was the only significant predictor for rodents (means between 69s and 10279s, $F_{6,45}=3.72$, $P=0.006$) and for possums (means between 77s and 8468s, $F_{6,45}=3.59$, $P=0.008$).

The total maize consumption at each feeder was strongly correlated with the number of possums that we recorded visiting the feeders ($r=0.57$, $P=0.0001$) but only weakly correlated with the number of rodents ($r=0.20$, $P=0.17$). The maize consumption on days 1-3 was weakly correlated with the amount of time rats and mice spent at a feeder ($r=0.27$, $P=0.08$), but strongly correlated with the amount of time possums spent there ($r=0.57$, $P=0.0001$). The number of rodent visits and possum visits was unrelated ($r=0.03$, $P=0.83$), but the length of time spent at feeders by rodents was correlated with the length of time spent there by possums ($r=0.332$, $P=0.02$).

## DISCUSSION

It might be expected that rats would be more likely to avoid the odours of predators that they encounter most frequently (Dickman, 1992) or those that pose the most significant threat (Jedrzejewski et al., 1993). We included both familiar and unfamiliar predators of ship rats in our laboratory experiment, yet neither species showed avoidance of any of the odours at the concentrations we used. It is obvious from both the field and laboratory experiments that semiochemicals would not be effective rat repellents in the sense that we envisaged. Not only do ship rats and kiore visit areas tainted with carnivore odours as often as they visit control areas (tainted with herbivore odours) in laboratory trials, they also spent similar amounts of time and consumed similar amounts of food in treatment and control areas in field trials.

Interestingly, the two species of rat we studied did not appear to be attracted to the predator odours, as predicted by Mason et al. (1994), either. This may be because they cannot tell the odours apart. However, ship rats may be able to discriminate at least some of the odours since they spent more time in arms containing odours from real predators or herbivores than they did in arms containing synthesised semiochemicals. Since the synthesised chemicals smelt stronger to the human nose than the real ones, it may be that this difference in behaviour is due to strength or pungency of the odour stimulus rather than the odour itself. Kemble and Bolwahnn (1997) reported that pungency alone could explain mouse aversion of novel chemicals, although this has not been tested for the species of rat we studied. The laboratory tests conducted by Burwash et al. (1998) used only one (familiar) real odour; the other eight were artificially synthesised. Burwash et al. (1998) do not report any dilution of their chemicals, and although they used small amounts (0.01 ml), the avoidance behaviour they report may be a response to strong novel odours, rather than avoidance of predator odours per se. The odours we used in our field trials were stronger than those we used in the laboratory trial, although they were familiar, and there was no effect on rat behaviour. Thus pungency alone cannot explain the different results reported by Burwash et al. (1998) and this study. Kiore showed no differences in their responses to odours and it remains unknown whether they can discriminate between the odours we tested or not.

Discrimination tests for both species of rat would be useful because they could help to interpret their lack of avoidance behaviour. It seems likely that ship rats and kiore can distinguish the odours apart, because rats are generally well endowed with olfactory neurons (Nef, 1998). Furthermore, olfaction is considered to be one of the most important means of communication (Brown, 1985) and orientation (Lavenex and Schenk, 1998) for rats. Olfaction has been well documented as a way of detecting predators for rodents (Kats and Dill, 1998). In order to observe odour discrimination in the absence of an avoidance response, it may be necessary to determine whether rats can be trained to recognise the odour as significant by operant conditioning (e.g., Terry and Johanson, 1996). If the rats are able to discriminate predator odours from others, then it remains to be explained (1) why, in the context of our experiments, they ignore the information these semiochemicals can potentially convey, and (2) what methods they employ to detect and avoid predators in the wild.

Cocke and Thiessen (1986) and Ward et al. (1996) both reported changes in the level of physiological arousal of animals (gerbils, *Meriones unguiculatus,* and hedgehogs, *Erinaceous europaeus*, respectively) in laboratory trials that were not manifested in behavioural changes. It is possible that the rats we studied were showing changes to their metabolism that we could not measure and future studies should consider this.

Both the ship rats and the kiore we tested in laboratory trials showed a high degree of individual variation. Burwash et al. (1998) suggested that it is the high level of individual variability that has allowed ship rats to become such a globally successful species. Bramley et al. (Chapter 5) found that, despite high individual variation, individuals from a predator-naïve population avoided predator odours, whilst individuals that had presumably come in contact with predators showed no such aversion. They suggest that avoidance might be an innate behaviour for Norway rats, but that it might be modified by experience, with experienced rats being more accurate at assessing risk. This may also be true for ship rats, since the ship rats we studied had presumably encountered predators or their odours in the past.

The kiore that we studied were from predator-free islands. They showed no innate aversion to odours. In order to make sense of these observations and understand the development of odour-mediated avoidance, experiments are necessary that manipulate the individual experience of the rats being tested. Only by knowing the experience of each individual being tested will experimenters be able to draw sensible conclusions about how responses to predator odours might vary with age or experience. The role individual experience plays in discriminating odours and responding to them has usually been studied by changing the background odour in the weaning period (e.g., Terry and Johanson, 1996) or by cross-fostering (e.g.,Wuensch, 1992). Neither approach is suitable for studying predator avoidance. In order to mimic the experience of encountering a predator in the wild, and to allow meaningful ecological interpretations, it will be necessary to pair the presentation of a semiochemical with a negative stimulus. Measuring the number of presentations necessary to engender avoidance and the length of time individuals maintain avoidance responses post-experience would be useful in helping workers determine whether chemicals provide meaningful ecological information or not.

Laboratory studies have shown, usually with laboratory strains of Norway rat or house mouse, that odours are important for individual recognition (Gheusi et al., 1997), social interactions (Hurst et al., 1994; Hurst and Barnard, 1995), orientation in the home range (Lavenex and Schenk, 1998), feeding (Galef, 1993) and mate selection (Kavaliers and Colwell, 1995). Laboratory studies have also shown that laboratory rats and mice recognise and avoid predator odours (see Kats and Dill, 1998, for a review). This reductionist laboratory approach has allowed significant progress in our understanding of rodent social systems. However, little is known about how wild populations of rat respond to either conspecific or heterospecific odours, and whether odours are used by wild rats and mice when exploring their home range. The few studies that have been conducted in the wild (Dickman, 1992; Gurnell and Little, 1992; Stapp and Van Horne, 1996) have produced contradictory results. Large enclosures represent a kind of middle ground between these two approaches, and have allowed successful manipulation of the presence, density and encounters of wild animals (e.g., Drickamer, 1997). In order to understand odour-mediated communication in small mammals, more field-based or enclosure experiments are necessary to determine the conditions under which semiochemicals are important (e.g., Merkens, 1991).

We detected no preference for either side of the maze by ship rats or kiore, but the behaviour of ship rats appeared to change according to the experimental block they were assigned to. This change was unexpected but should have had only a minimal effect on our results since smells were positioned in blocks throughout the trial and rats were randomly assigned to blocks. Thus five randomly chosen rats received one randomly chosen smell each on any given day, and any smell tested on a day when the rats were inactive would also have been presented to other rats on other days.

In the field trials we conducted, the one consistently significant predictor of maize consumption and visitation rate was the location of the test. This is probably because rodent and possum density varied at the different sites, and feeders in areas with more animals received more visits. It appears from our field trials that possums were unaffected by predator odours. This result contrasts with data reported by Woolhouse and Morgan (1995) who applied semiochemicals (one of which was PT) to pine (*Pinus radiata*) seedlings, and recorded a decrease in consumption by possums. It may be that propylthietane has an aversive taste.

The strong correlation between maize consumption and possum visits implies that possums were eating most of our maize. Nonetheless, rodents also visited the feeders often, and since rodent and possum visits were not correlated (either positively or negatively) it appears possums did not exclude rats and mice from visiting. The observed positive correlation between the amount of time spent at feeders for rats and possums is further support that neither species adversely affects the behaviour of the other.

Rats and possums consumed more maize during the second test in an area than they had in the first test. This result is to be expected since resident animals have had longer to locate feeders and assess food palatability by the time the second trial began.

It is apparent from this study and that of Bramley et al. (Chapter 5) that all rodents, even congeneric species, do not respond to predator odours in the same way. Studies of the type outlined above looking at the development of aversion and manipulating experimental conditions such as cover and risk are needed to help clarify how heterospecific odours are used by different species, and under what conditions avoidance evolves and is maintained by a population. Future research should also focus on the effect of age on avoidance responses and what other antipredator strategies might operate under different conditions.

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## REFERENCES

ARNOULD, C., ORGEUR, P., SEMPERE, A., SIGNORET, J.P., and VERDIER, M. 1993. Repulsion alimentaire chez trois especes d'ongules en situation de paturage: effet des excrements de chien. *Rev. Ecol. (Terre Vie)* 48:121-131.

ATKINSON, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, pp. 35-81, *in* P.J. Moors (ed.). Conservation of island birds: Case studies for the management of threatened island species. International Council for Bird Preservation Technical Publication No. 3.

ATKINSON, I.A.E., and MOLLER, H. 1990. Kiore, pp. 175-192, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

BOAG, B., and MLOTKIEWICZ, J.A. 1994. Effect of odor derived from lion faeces on behaviour of wild rabbits. *J. Chem. Ecol.* 20:631-637.

BROWN, R.E. 1985. The Rodents II: Suborder Myomorpha, pp. 345-457, *in* R.E. Brown and D.W. MacDonald (eds.). Social Odours in Mammals, Volume 1. Oxford University Press, Oxford. United Kingdom.

BURWASH, M.D., TOBIN, M.E., WOOLHOUSE, A.D., and SULLIVAN, T.P. 1998. Laboratory evaluation of predator odours for eliciting an avoidance response in roof rats (*Rattus rattus*). *J. Chem. Ecol.* 24:49-66.

CHRISTOPHE, N., and BAUDOIN, C. 1998. Olfactory preferences in two strains of wild mice, *Mus musculus musculus* and *Mus musculus domesticus*, and their hybrids. *Anim. Behav.* 56:365-369.

COCKE, R., and THIESSEN, D.D. 1986. Chemocommunication among prey and predator species. *Anim. Learn. Behav.* 14:90-92.

DELL'OMO, G., FIORE, M., and ALLEVA, A. 1994. Strain differences in mouse response to odours and predators. *Behav. Proc.* 32:105-116.

DICKMAN, C.R. 1992. Predation and habitat shifts in the house mouse, *Mus domesticus. Ecology* 73:313-322.

DRICKAMER, L.C. 1997. Responses to odors of dominant and subordinate house mice (*Mus domesticus*) in live traps and responses to odors in live traps by dominant and subordinate males. *J. Chem. Ecol.* 23:2493-2506.

GALEF, B.G. 1993. Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission. *Anim. Behav.* 46:257-265.

GARBE, C.M., KEMBLE, E.D., and RAWLEIGH, J.M. 1993. Novel odors evoke risk assessment and suppress appetitive behaviors in mice. *Aggress. Behav.* 19:447-454.

GHEUSI, G., GOODALL, G., and DANTZER, R. 1997. Individually distinctive odours represent individual conspecfics in rats. *Anim. Behav.* 53:935-944.

HOLDAWAY, R.N. 1996. Arrival of rats in New Zealand. *Nature* 384:225-226.

HURST, J.L., FANG, J., and BARNARD, C.J. 1994. The role of substrate odours in maintaining social tolerance between male house mice (*Mus musculus domesticus*): relatedness, incidental kinship and the establishment of social status. *Anim. Behav.* 48:157-167.

HURST, J.L., and BARNARD, C.J. 1995. Kinship and social tolerance among female and juvenile wild house mice: kin bias but not kin discrimination. *Behav. Ecol. Sociobiol.* 36:333-342.

INNES, J.G. 1990. Ship rat, pp. 206-225, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

INNES, J.G., WARBURTON, B., WILLIAMS, D., SPEED, H., and BRADFIELD, P. 1995. Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *N.Z. J. Ecol.* 19:5-17.

JEDRZEJEWSKI, W., RYCHLIK, L., and JEDRZEJEWSKA, B. 1993. Responses of bank voles to odours of seven species of predators: Experimental data and their relevance to natural predator-vole relationships. *Oikos* 68:251-257.

KATS, L.B., and DILL, L.M. 1998. The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361-394.

KAVALIERS, M., and COLWELL, D.D. 1995. Odours of parasitized males induce aversive responses in female mice. *Anim. Behav.* 50:1161-1169.

KEMBLE, E.D., and BOLWAHNN, B.L. 1997. Immediate and long-term effects of novel odors on risk assessment in mice. *Physiol. Behav.* 61:543-549.

KING, C.M. 1990. (Editor). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand. 600pp.

KING, C.M., INNES, J.G., FLUX, M., KIMBERLEY, M.O., LEATHWICK, J.R., and WILLIAMS, D.S. 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *N.Z. J. Ecol.* 20:215-240.

KING, C.M., and MOLLER, H. 1997. Distribution and response of rats, *Rattus rattus* and *R. exulans,* to seedfall in New Zealand beech forests. *Pac. Conserv. Biol.* 3:143-155.

LAVENEX, P., and F. SCHENK. 1998. Olfactory traces and spatial learning in rats. *Anim. Behav.* 56:1129-1136.

MACDONALD, D.W. 1984. (Ed.). The Encyclopedia of Mammals (2). George Allen and Unwin. London, United Kingdom.

MAPPES, T., KOSKELA, E., and YLONEN, H. 1998. Breeding suppression in voles under predation risk of small mustelids: laboratory or methodological artifact? *Oikos* 82:365-369.

MASON, J.R., EPPLE, G., and NOLTE, D.L. 1994. Semiochemicals and improvements in rodent control, pp. 327-346, *in* B.G. Galef, M. Mainardi and P. Valsecchi (eds.). Behavioral Aspects of Feeding: Basic and Applied Research in Mammals. Harwood Academic Publishers, Chur, Switzerland.

MERKENS, M., HARESTAD, A.S., and SULLIVAN, T.P. 1991. Cover and efficacy of predator-based repellents for Townsend's vole (*Microtus townsendii*). *J. Chem. Ecol.* 17: 401-412.

MURPHY, E.C., and PICKARD, C.R. 1990. House mouse, pp. 225-242, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

NEF, P. 1998. How we smell: The molecular and cellular bases of olfaction. *News Physiol. Sci.* 13:1-5.

NOLTE, D.L., MASON, J.R., EPPLE, G., ARANOV, E., and CAMPBELL, D.L. 1994. Why are predator urines aversive to prey? *J. Chem. Ecol.* 20:1505-1516.

STAPP, P., and VAN HORNE, B. 1996. Do olfactory cues mediate interactions between rodents on northern shortgrass prairie? *Can. J. Zool.* 74:226-232.

SULLIVAN, T.P., NORDSTROM, L.O., and SULLIVAN, D.S. 1985a. Use of predator odors as repellents to reduce feeding damage by herbivores I. Snowshoe hares (*Lepus americanus*). *J. Chem. Ecol.* 11:903-919.

SULLIVAN, T.P., NORDSTROM, L.O., and SULLIVAN, D.S. 1985b. Use of predator odors as repellents to reduce feeding damage by herbivores II. Black-tailed deer (*Odocoileus hemionus columbianus*). *J. Chem. Ecol.* 11:921-935.

TAYLOR, R.H., and THOMAS, B.W. 1993. Rats eradicated from rugged Breaksea Island (170 ha), Fiordland, New Zealand. *Biol. Conserv.* 65:191-198.

TERRY, L.M., and JOHANSON, I.B. 1996. Effects of altered olfactory experiences on the development of infant rats' responses to odors. *Develop. Psychobiol.* 29:353-377.

TOWNS, D.R. 1991. Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: the kiore (*Rattus exulans*). *J. Roy. Soc. N.Z.* 21:119-136.

WACE, N.M. 1986. The rat problem on oceanic islands - research is needed. *Oryx* 20:79-86.

WARD, J.F., MACDONALD, D.W., DONCASTER, C.P. and MAUGET, C. 1996. Physiological response of the European Hedgehog to predator and nonpredator odour. *Physiol. Behav.* 60:1469-1472.

WOLFF, J.O., and DAVIS-BORN, R. 1997. Response of grey-tailed voles to odours of a mustelid predator: a field test. *Oikos* 79:543-548.

WOOLHOUSE, A.D., and MORGAN, D.R. 1995. An evaluation of repellents to suppress browsing by possums. *J. Chem. Ecol.* 21:1571-1583.

WUENSCH, K.L. 1992. Fostering house mice onto rats and deer mice: Effects on response to species odours. *Anim. Learn. Behav.* 20:253-258.

# CHAPTER SEVEN: CONCLUSIONS

*Summary of Thesis Research.* In this thesis, I have presented data on the coexistence of rats on Kapiti Island (Chapter 2) which showed that kiore and Norway rats were associated with different habitats over a five-year period (1992-1996). Norway rats were associated with tall, open vegetation, in areas that were poorly drained and possibly steep. Kiore, on the other hand, were associated with dense, low vegetation on flat or slightly sloping, well drained land.

Kiore produced more young per female (as evidenced by uterine scars and embryos) in kanuka and kohekohe forest and fewest in five-finger forest. Kiore were also larger in kohekohe forest and kanuka forest. Norway rats produced a similar number of young and reached similar sizes in all habitats I sampled. Kiore were least abundant in the areas where they were larger and most productive and I believe this indicates competition, with kiore excluded from the best habitat by the larger Norway rat. The resource the rats might be competing for is unknown, but is likely to be food or cover.

Radio-tracking in an area of grass and shrubland, where both kiore and Norway rats lived, showed that kiore had much smaller home ranges than Norway rats, and that their home ranges overlapped with other kiore and with Norway rats. The home ranges of Norway rats also overlapped, both with other Norway rats and with kiore. Kiore were associated with sites that excluded more light than Norway rats, which implies that they used sites that afforded them more cover than the sites chosen by Norway rats. I found only weak evidence that radio-carrying Norway rats and kiore avoided each other in my study area.

All radio-tracked rats died within 10 days of poison (20 ppm brodifacoum) being distributed on Kapiti Island. The home ranges of rats did not appear to change post-poisoning. However rats eventually moved smaller distances between fixes then remained in one place for many hours before death.

In laboratory trials (Chapter 3), kiore may have avoided the odour of other rats. It appears that kiore might be influenced by the odour of other rats when moving about their habitat. The other species of rat may not be deterred from exploring parts of their range by odour cues deposited by other species of rat. However, it should be noted that sample sizes were too small to produce definitive results. The sex of the test animal was an important predictor of most measures I used (but not for kiore), and it is possible that one sex relies on odours as cues more than the other sex. It is not obvious from my results which sex might be the most responsive, although female ship and Norway rats were more active in my trials. The use of odour cues by kiore might help explain the weak avoidance I recorded on Kapiti and the statistically significant negative correlation between kiore and Norway captures recorded earlier by Dick (1985, unpubl.).

Odours do not appear to be mediating the interaction between ship rats and mice (Chapter 4). Mice apparently could not (or chose not to) distinguish the odour of ship rats from their own odour in activity tests, even when they had recently been exposed to a live rat. However, mice were less active when presented with a live ship rat in an experimental arena. Mice did not spend more time under cover or more time on the side of the arena away from the rat, therefore they may have been relying on crypticity rather than cover for protection. Pairs of laboratory mice that were exposed to ship rat odour gave birth to larger litters than control (no odour) pairs. Pups from treatment pairs also weighed less (on average) at weaning than control pairs.

Norway rats from Kapiti Island appeared to distinguish the odour of predators from that of herbivores and avoided predator-tainted areas, despite never having encountered any of the predators before (Chapter 5). However, Norway rats from the North Island did not avoid predator odours. Both samples showed a high level of individual variability and were statistically indistinguishable, despite the different results obtained for each group. Ship rats and kiore also showed no evidence of avoidance in either field or laboratory trials (Chapter 6), but there were differences between the two sexes for ship rats. It appears unlikely that free-ranging rats use predator odours as cues when exploring their habitat. It remains unknown how important predation is as a selective force for New Zealand rodents.

*Competition Between Rodents in New Zealand.* The species of rodent I studied show a patchy distribution throughout New Zealand and the Pacific (Marshall, 1962; Taylor, 1984; Tomich, 1986; Atkinson and Moller, 1990). Communities of rodents on islands could simply be a sample of species drawn from those available (i.e., synanthropic species and others with good dispersal ability), weighted by island size, habitat complexity and species colonising ability according to biogeographic theory (Dueser and Porter, 1986). Taylor (1984) partially tested this assertion (he did not consider habitat) for the New Zealand islands by relating the distribution of rodents and their predators to the isolation and size of islands, the dispersal ability of each species, competition and predation. He concluded the New Zealand data did not support the theoretical model depending only on isolation, rather that interspecific competition and predation had shaped rodent communities here.

Dueser and Porter (1986) were able to quantify competition between rodents from a live trapping study. They found evidence of competition between many of the pairs of species they studied, but they considered it to be only weak. Dueser and Porter (1986) conducted an analysis similar to that of Taylor (1984), but also considered habitat. They believed that habitat was more important than competition in structuring rodent communities on Assateague Island (Virginia Barrier islands group, North America).

Competition remains to be demonstrated between rodents in New Zealand. If it ever is, the role of habitat will become clearer, since at present it is not possible to say whether or not competition limits some species to habitats they do not prefer. The study by King et al. (1996a) and the work done by myself and others on Kapiti Island (Chapter 2 of this thesis) have provided the strongest evidence to date that competition between rodents is real. Both studies have shown that microhabitat use differs between sympatric species of rodent, and that different species are not equally common, nor do they recruit the same number of young, in all habitats. This does suggest competition between rodents for some limiting resource, but on the other hand, these instances could equally well be explained by larger species preying upon smaller species, or by different habitat preferences. Competitive interactions between species of rats must be studied both in the wild and in captivity (e.g., in large enclosures). These studies should manipulate the species composition and density to identify any changes in habitat preference brought about when other species are present. Close investigation should also show whether rats kill other species of rats or mice, and at what stage individuals are most vulnerable. The ethical considerations of such experiments are beyond the scope of this discussion.

The most obvious resources over which rodents could compete are food, living space and cover (Glass and Slade, 1980; Brown and Munger, 1985; Roberts and Craig, 1990). It will be necessary to identify resources over which rats compete; this will require quantifying resource availability.

In terms of food as a potential resource, previous authors (summarised by Innes, 1990; Atkinson and Moller, 1990; Moors, 1990; and Murphy and Pickard , 1990) have provided a considerable volume of information on rat and mouse diet. Studies are needed that set out to measure the availability of important diet items (such as lepidoptera larvae and grass seed) and then measure their use by each species, where possible, in both single-species and multi-species communities. Understanding the availability and use of resources by different species, and how use changes in the presence of other species, will allow workers to discriminate between the competing hypotheses of competition, predation and habitat preference suggested by my work.

It remains unknown whether the mechanism of any competitive interaction is interference or exploitation. Rats and mice do not appear to avoid the odour of heterospecifics (Chapters 3 and 4). If interference competition is important in structuring rodent communities in New Zealand, then it is mediated by some more direct method (such as physical encounters or fighting) than odours alone.

Alternatively, exploitation competition could be involved, or some combination of the two dependent on the competing species concerned.

It appears from trends shown by kiore when presented with heterospecific odour (Chapter 3), that kiore might be more responsive to heterospecific odours than other species of rat. The trends I have presented indicate that kiore (*Rattus exulans*) may avoid the odours of other rat species more than either ship rats (*R. rattus*) or Norway rats (*R. norvegicus*). If this were true, then one might predict that weaker competitors would be those most likely to respond to odours, since they are the most likely to lose any competitive encounter, and might reduce costs by avoiding better competitors all together. However, mice do not show an avoidance of ship rat odours consistent with this assertion (Chapter 4). The exact nature of the rat-mouse relationship remains unknown and it is also unclear whether mice are more efficient foragers than rats. Since kiore have been all but extirpated on the main islands (Atkinson and Moller, 1990), it would seem likely that they are weaker competitors than the other two rat species under New Zealand conditions. Mice have also spread over both main islands as kiore have declined (Atkinson and Moller, 1990). The study of rat responses to odours of other rats (reported in Chapter 3) needs to be replicated using larger samples and different populations, preferably using equipment and/or measures similar to my study so that the data are comparable. A suitable control for such experiments would be an innocuous odour such as rabbit faeces. Gurnell and Little (1992) and Stapp and Van Horne (1996) have concluded that odours are unimportant in regulating interactions between small mammals in woodland and prairie habitats respectively. A live trapping study using traps scented with the odour of other rodents similar to that conducted by Gurnell and Little (1992), on Stewart Island or the smaller Pearl Island (where all three species of rat coexist), might help illuminate the role of odours in determining habitat use there. Radio-tracking of rats and the recording of microhabitat use to detect differences between species on Stewart Island might aid our understanding by discovering habitat preferences. Careful manipulations of density or species composition in an area will be required to separate the effects of habitat preference from the effects of competition and predation.

Placing individuals of different species in an enclosure, or on a small island (Veitch et al., 1992), and manipulating density (Glass and Slade, 1980; Dickman, 1992), food supply (Brown and Munger, 1985), cover, and predation risk (perhaps indirectly by influencing light levels; Plesner-Jensen and Honess, 1995) would provide potentially interpretable results on the relative competitive abilities and interactions between species when they coexist.

More studies of island rodents using radio-telemetry and measuring microhabitat use may demonstrate interactions and preferences, but future workers would most usefully contribute by moving beyond a descriptive approach and actively manipulating variables to test hypotheses. Better knowledge of the mechanisms that allow or facilitate coexistence (for example, niche separation or avoidance of other species) is necessary from both a theoretical and a management point of view. Questions concerning the competitive abilities (which species is most competitive?), habitat use (how do species use habitat when alone and when coexisting with other species?), diet (does diet change in the presence of other species?), behaviour (which species is the most efficient forager?) and physiology (which species is the most energetically efficient?) of all four species of rodent require answering in order to understand rodent coexistence. Acquiring this knowledge will require some method of close monitoring of live individuals (probably radio-tracking or similar), and could perhaps most easily be achieved using large enclosures containing a known number of marked individuals. Any enclosure studies will require verification in the wild somewhere where more than one species lives.

*Rat Habitat Use.* It appears from the work completed by myself and others on Kapiti Island (Chapter 2), that kiore and Norway rats use different habitats when they are sympatric, with kiore being more common in dense habitat, including grassland. Kiore were not most productive in grassland, however, which suggests a situation similar to that observed by King et al. (1996b) for mice (*Mus musculus*) sympatric with ship rats. In the populations King and her colleagues studied at Pureora Forest Park, mice were virtually limited to disturbed habitats with dense ground cover, especially a young pine plantation. Kiore have often been compared with mice. Kiore only coexist with mice on four islands in New Zealand (three of them > 7 000 ha in size), which suggests they may have very similar ecological requirements, at least in the presence of other rats (Atkinson and Moller, 1990). At Pureora, mouse reproduction rates (as evidenced by uterine scars), were no different between the pine plantations and the native forest, although age-class structure was. King et al. (1996b) interpreted this to mean there was a failure to recruit young mice in native forest where ship rats were common. This failure to recruit young may also explain some of our observations on Kapiti Island: kiore were more productive (shown by uterine scars) in kohekohe and kanuka forest, but most common in grassland. This suggests either a failure to recruit young kiore in kohekohe and kanuka forest where Norway rats were common (Chapter 2), or movement from kohekohe and kanuka forest into grassland as rats age. I found no evidence of movement between habitats by rats on Kapiti, but can not rule it out, since no age data were collected (Chapter 2). Roberts and Craig (1990) also found differences in the annual production of young of kiore in different habitats on Tiritiri Matangi Island. In their study, kiore were most productive near human habitation (the lighthouse) followed by grassland and then forest. Females trapped in forested areas of Tiritiri Matangi were more likely to have survived winter and bred more often, compared with females trapped in grassland. These observations suggest that the productivity of kiore varies with habitat. Kiore are apparently more productive in areas that provide abundant food and cover. Norway rats might also be important in influencing kiore productivity, but whether this influence is due to competition, predation or both is unknown.

I cannot rule out that ship rats eat mice in the wild, but mouse behaviour and reproduction in laboratory trials was unaffected by ship rat odours (Chapter 4). This indicates a more direct mode of interaction between ship rats and mice, i.e., mouse activity could be affected by the physical presence of ship rats, but not by their odour alone. This suggests that in areas of low ship rat density, mouse-tracking indices are likely to be reliable (because there are few rats to exclude mice from tracking tunnels). The sudden (<5 days) increase in the tracking rate of mice when rats are removed recorded by Brown et al. (1996), is likely to be due to an increase in activity of mice when dense ship rat populations are removed. The more prolonged increase in mouse detectability (up to 5 months) recorded by Clout et al. (1995), Innes et al. (1995) and Miller and Miller (1995), may be due to a more prolonged breeding response (King et al., 1996b). This assertion could be verified by comparing mouse population parameters in areas with different densities of ship rats. This will require translocation of mice to areas where rats have been removed, or studies in large enclosures. Both methods would ensure that the presence and density of mice is known, and that any differences in detectability are due to differences in activity rather than numbers.

*The Effect of Predator Odours on Rat Habitat Use.* Some populations of Norway rats are likely to show an innate avoidance to predator odours (Chapter 5), but the response is not universal and there is great individual variability. This limits the utility of predator odours as rat repellents, because the avoidance will need to be demonstrated in every population before use. Furthermore, it is unlikely that all rats reaching island sanctuaries would avoid predator odours. Ship rats and kiore also show a high degree of individual variability (Chapter 6), but kiore do not appear to have the same innate aversion to predator odours shown by Norway rats.

The odours I used in my experiments (Chapters 5 and 6) smelt stronger to me than the urine and faeces of real animals. It is possible, but it seems unlikely, that more effective repellency might be achieved using even stronger smells to provide a supernormal stimulus (e.g., Boag and Mlotkiewicz (1994) used lion (*Panthera leo*) faeces to repel rabbits (*Oryctolagus cuniculus*) from their warrens for up to five months). However, strong, offensive odours would make conditions for human workers or visitors unpleasant.

From a theoretical point of view, more research is needed to determine how odour aversions develop, how they are either maintained or lost by individuals and populations, and whether responses to odours change with age. Experiments that expose young rats to the odour of predators paired with negative stimuli are required to simulate an escape from a predator. Varying the number of presentations and the time until rats are to be tested with the odours might indicate how many encounters are required to engender avoidance and how long the avoidance response persists. Varying the time between responses might also suggest how age affects responses. Varying the strength of the paired negative stimuli might indicate the level of risk necessary for the animal to show avoidance in the future. Occasional reinforcement for some animals prior to testing would indicate whether repeated exposure to the odour was necessary to maintain the avoidance response.

Results from Chapters 3, 5 and 6 indicate that there is a difference in activity between sexes. My sample sizes were too small to detect whether both sexes respond in the same way, with their responses being different in magnitude, or whether the two sexes actually differ in response, with, for example, one sex avoiding predator odours and the other ignoring them. The difference between sexes in response to odours might prove a fruitful area for further research in order to understand development of odour aversion, since more active animals are more likely to be preyed upon (Norrdahl and Korpimaki, 1998). Thus the naturally more active sex might be more sensitive to odour cues than the less active sex. Experiments similar to mine, but using larger samples of only one sex may be enough to illustrate differences.

*Research Methods.* A Y maze was used in several of the experiments reported in this thesis because it appeared from the literature that Y mazes or four-arm mazes produced reliable results in odour discrimination tests (e.g.,Wuensch, 1992; Krasnov and Khoklova, 1996). From my own results (particularly Chapters 5 and 6), I consider it important that future tests of odour discrimination test subjects against an innocuous odour in a separate test (i.e., at another time, not paired with treatment odours) as a control. An innocuous odour is necessary to provide animals with a similar stimulus (c.f. distilled water for example, which provides no stimulus; Mappes et al., 1998). It is necessary to separate the tests in time to avoid the mingling of odours (and responses) in each individual test. By using an incomplete (or in one case a complete) randomised block design, I was able to reduce the sample size needed to detect significant differences substantially, because each individual was tested more than once. This allowed comparison of between-individual variation and saved time and effort in housing the animals and in data collection. Few authors have chosen to do this (e.g., Burwash et al., 1998, used 100 rats, but tested each one only once), but it is an easy and practicable way to reduce the number of animals subjected to experimental treatments. This is important for animal welfare (Still, 1991; McConway, 1991), but is particularly important for the workers involved when the animals are wild-caught and difficult to capture and handle. There are more statistical tests designed to cope with complete block designs, hence they are easier to analyse. Sample sizes for wild animals may still need to be larger than the sample sizes I used.

*Rodent Management.* The most pressing research need from a management perspective is to determine what effect feral mice have on native ecosystems (other than beech (*Nothofagus*) forests, where their effects have been well studied; Fitzgerald et al., 1996 and the references therein). Studies on mice are needed because the impact of high mouse populations is unknown and mice living independently of humans are difficult to control. To understand the effects of mice on native wildlife, population studies of key native species that appear in mouse diets are required. So too is knowledge of resource availability and use by mice. Close monitoring (such as radio-tracking) of mice in native habitats to learn more about patterns of habitat use and ranging are required. Such studies will identify what native species are likely to be affected. Further studies should focus on key species thus identified to determine what effect mice have on populations of native flora and fauna.

In order to manage rodent populations effectively in the long term, it is imperative that we understand natural population regulation. At present it is unknown whether rodent populations are regulated in a "top-down" or "bottom-up" way (sensu Wratten, 1992). Kiore are not the most common wildlife pest in New Zealand, nor are mice. Surprisingly then, more is known about the population regulation of kiore and house mice in New Zealand than the other two species. It appears that kiore might be regulated in both ways - from the bottom by food supplies and shelter (Bunn and Craig, 1989; Roberts and Craig, 1990) and from the top by competition and perhaps predation by other species (Taylor, 1984; Chapter 2). Mice appear to be regulated from the bottom most of the time in some habitats (e.g., South Island beech forests; King, 1982; Fitzgerald et al., 1996) and by predators or competitors in other habitats (broadleaf-podocarp forest at Pureora; King et al., 1996a, b). The method of population regulation has important implications for management, because the assumption by managers has been that regulation is bottom-up. Furthermore, because many operations aim to control more than one pest species in New Zealand, traps and poisoned foods are often distributed in winter or spring, when food could be expected to be limiting. If a species is limited in a top-down fashion in some habitats (as implicated for mice by King et al., 1996b), then it is likely that different control methods are necessary in different areas. The level of predation on rodent populations remains unknown. More basic population studies that examine causes of mortality, productivity and identify critical life history stages, are necessary to understand population regulation in a range of environments. Such studies will require the monitoring of live animals going about their normal lives rather than descriptive kill trapping studies, which allow inference of reproductive, but not mortality events. If predation is a relatively infrequent cause of mortality in New Zealand rodent populations, then that might explain why predator odours are not effective repellents for rats in forest (Chapter 6).

*Eradication of Rats on Kapiti Island.* The data I presented in Chapter 2 showed that, despite the presence of more than one species, all radio-carrying animals were killed by the aerial poison operation. Subsequent monitoring (R. Empson, pers. comm.) has shown that eradication is possible on large islands where Norway rats and kiore live if aerial distribution of bait is used. Rats were eradicated from Kapiti despite the different habitat use I reported for the two species and the removal of baits for caching by Norway rats I recorded. The LD 50 (amount of poison (or lethal dose) required to kill 50% of animals) for Norway rats ingesting brodifacoum is 0.27 mg/kg (the LD50 for kiore is unknown; R.Empson, pers.comm.). Nearly 32 tonnes of bait was dropped to kill the estimated 40 000 (maximum estimate, R. Empson, pers. comm.) rats on Kapiti. Less than 10% of this was necessary to kill 40 000 rats if it had all been ingested by rats. The large amount of bait used may have contributed to the success of the eradication. Because of the small home range size of kiore, and differences in microhabitat use exhibited by the two species, it appears that bait stations would have been prohibitively labour-intensive and unlikely to achieve success on Kapiti.

*Recommendations.* Rat control is being achieved using current technology, and it is likely that this technology will be sufficient to eradicate rats from more offshore islands around New Zealand and elsewhere in the future. We should not expect that current technology will always be suitable. On the main islands of New Zealand it seems unlikely that current technology will continue to be effective in the long term, because populations that have frequently been subject to poison operations will develop resistance (Berdoy and Smith, 1993). Furthermore, toxins may persist and/or accumulate in the environment rendering their future use inappropriate. Management on the main islands is likely to rely on continuing production and application of new poisons, but research must also be directed in other areas, since the public regards poison application as increasingly unacceptable. More research of the kind identified in this chapter is required to understand population control and behaviour to suggest alternative management strategies. The priorities for enhancing management are not necessarily the priorities for theoretical research, but regardless of the aim, more basic research is required to achieve long-term rodent control. What follows is my opinion of one useful direction for future research on live animals.

1. The most urgent need is to identify the effect of mice on native invertebrate and plant communities (other than beech forest) in the wild when rats are removed. House mice are likely to be present, but undetectable, before rats are removed, but then appear to increase in number. Hence, it is important to determine the consequences of this increase for native plants and animals. Concurrent with this, the use of habitat by mice in relation to habitat availability could be quantified. It will probably be necessary to conduct this research in the absence of rats if sufficient numbers of mice are to be obtained.
2. It is necessary to calculate the availability of habitats (food, dens, space) for rat species (particularly free-living ship rats) and quantify habitat use. Habitat preferences of different species can then be derived and compared. The extent and availability of habitat has previously been ignored in studies of habitat use and diet. This might allow more efficient targeting of bait and is likely to lead to insights into likely competitive interactions when species coexist. After quantifying individual species' habitat use, an investigation of the habitat use of species in enclosures or in the wild, comparing habitat use when alone and when in the presence of other species, is necessary.

3. More information is needed on the causes of rat and mouse mortality. This is likely to be collected incidentally in a study of habitat use.
4. It is important to determine, as soon as possible, whether rats eat other rats and mice. If they do, it will be necessary to quantify the frequency of predation events. A sound knowledge of predation and competition events and their outcomes will allow workers to distinguish the relative importance of predation (by rats and other predators) and competition in shaping rodent communities in New Zealand. This knowledge can then be integrated with a knowledge of habitat use to provide a more satisfying explanation of rodent distribution than that given by Watson (1961) or Taylor (1984).
5. Predator odours as deterrents do not appear to be a suitable management tool and further investigation may not contribute to rat management. However, almost nothing is known about the use of odours by rats in the wild and the conditions under which odours are important. The development and maintenance of odour aversion has not been studied. Testing animals of known age and experience with predator odours under different experimental conditions (mentioned above) is required. Training animals to recognise odours and then measuring how their responses change over time (with and without reinforcement) may help explain the contradictory accounts already published and allow a deeper understanding of odours as a mechanism for communication amongst rodents.

# REFERENCES

ATKINSON, I.A.E., and MOLLER, H. 1990. Kiore, pp. 175-192, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

BOAG, B., and MLOTKIEWICZ, J.A. 1994. Effect of odor derived from lion faeces on behaviour of wild rabbits. *J. Chem. Ecol.* 20:631-637.

BERDOY, M., and SMITH, P. 1993. Arms race and rat race: Adaptations against poisoning in the brown rat. *Rev. Ecol. (Terre Vie)* 48:215-228.

BROWN, K.P., MOLLER, H., INNES, J.G., and ALTERIO, N. 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. *N.Z. J. Ecol.* 20:271-275.

BROWN, J.H., and MUNGER, J.C. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology* 66: 1545-1563.

BUNN, T.J., and CRAIG, J.C. 1989. Population cycles of *Rattus exulans*: population changes, diet and food availability. *N.Z. J. Zool.* 16:409-418.

BURWASH, M.D., TOBIN, M.E., WOOLHOUSE, A.D., and SULLIVAN, T.P. 1998. Laboratory evaluation of predator odours for eliciting an avoidance response in roof rats (*Rattus rattus*). *J. Chem. Ecol.* 24:49-66.

CLOUT, M.N., DENYER, K., JAMES, R.E., and MCFADDEN, I.G. 1995. Breeding success of New Zealand pigeons (*Hemiphaga novaeseelandiae*) in relation to control of introduced mammals. *N.Z. J. Ecol.* 19:209-212.

DICK, A.M.P. 1985. Rats on Kapiti Island. Coexistence and diet of *R. norvegicus* (Berkenhout) and *R. exulans* (Peale). Unpublished MSc. thesis, Department of Botany and Zoology, Massey University, Palmerston North, New Zealand.

DICKMAN, C.R. 1992. Predation and habitat shifts in the house mouse, *Mus domesticus*. *Ecology* 73:313-322.

DUESER, R.D., and PORTER, J.H. 1986. Habitat use by insular small mammals: relative effects of competition and habitat structure. *Ecology* 67:195-201.

FITZGERALD, B.M., DANIEL, M.J., FITZGERALD, A.E., KARL, B.J., MEADS, M.J., and NOTMAN, P.R. 1996. Factors contributing to fluctuations in house mouse (*Mus musculus*) populations in hard beech (*Nothofagus truncata*) forest. *J. Roy. Soc. N.Z.* 26:237-249.

GLASS, G.E., and SLADE, N.A. 1980. The effect of *Sigmodon hispidus* on spatial and temporal activity of *Microtus ochrogaster*: evidence for competition. *Ecology* 61:358-370.

GURNELL, J., and LITTLE, J. 1992. The influence of trap residual odour on catching woodland rodents. *Anim. Behav.* 43:623-632.

INNES, J.G. 1990. Ship rat, pp. 206-225, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

INNES, J.G., WARBURTON, B., WILLIAMS, D., SPEED, H. and BRADFIELD, P. 1995. Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *N.Z. J. Ecol.* 19:5-17.

KING, C.M. 1982. Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*) in relation to seed fall of southern beech. *N.Z. J. Zool.* 9:467-480.

KING, C.M., INNES, J.G., FLUX, M., KIMBERLEY, M.O., LEATHWICK, J.R., and WILLIAMS, D.S. 1996a. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *N.Z. J. Ecol.* 20:215-240.

KING, C.M., INNES, J.G., FLUX, M., and KIMBERLEY, M.O. 1996b. Population Biology of small mammals in Pureora Forest Park: 2. The feral house mouse (*Mus musculus*). *N.Z. J. Ecol.* 20:253-269.

KRASNOV, B., and KHOKLOVA, I. 1996. Discrimination of midday jird's odour by house mice. *Anim. Behav.* 52:659-665.

MAPPES, T., KOSKELA, E., and YLONEN, H. 1998. Breeding suppression in voles under predation risk of small mustelids: laboratory or methodological artifact? *Oikos* 82:365-369.

MARSHALL, J.T. 1962. Geographic distribution and color phases of Micronesian rodents, pp. 39-44, *in* T.I. Storer (ed.). Pacific Island rat ecology: Report of a study made on Ponape and adjacent islands 1955-1958. Bernice P. Bishop Museum Bulletin No. 225. Honolulu, Hawaii.

MCCONWAY, K. 1991. The number of subjects in animal behaviour experiments: is Still still right?, pp. 35-38, *in* M. Stamp-Dawkins and M. Gosling (eds.). Ethics in Research on Animal Behaviour: Readings from *Animal Behaviour*. Published by Academic Press for the Association for the Study of Animal Behaviour and the Animal Behavior Society, London, England.

MILLER, C.J., and MILLER, T.K. 1995. Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poison operation. *N.Z. J. Ecol.* 19:19-27.

MOORS, P.J. 1990. Norway rat, pp. 192-206, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

MURPHY, E.C., and PICKARD, C.R. 1990. House mouse, pp. 225-242, *in* C.M. King (ed.). The Handbook of New Zealand Mammals. Oxford University Press, Auckland, New Zealand.

NORRDAHL, K., and KORPIMAKI, E. 1998. Does mobility of sex of voles affect risk of predation by mammalian predators? *Ecology* 79:226-232.

PLESNER-JENSEN, S., and HONESS, P. 1995. The influence of moonlight on vegetation height preferences and trappability of small mammals. *Mammalia* 59:35-42.

ROBERTS, M., and CRAIG, J.C. 1990. The demography of kiore, *Rattus exulans*, in three habitats. *N.Z. J. Zool.* 17:43-53.

STAPP, P., and VAN HORNE, B. 1996. Do olfactory cues mediate interactions between rodents on northern shortgrass prairie? *Can. J. Zool.* 74:26-232.

STILL, A.W. 1991. On the number of subjects used in animal behaviour experiments, pp. 27-34, *in* M. Stamp-Dawkins and M. Gosling (eds.). Ethics in Research on Animal Behaviour: Readings from *Animal Behaviour*. Published by Academic Press for the Association for the Study of Animal Behaviour and the Animal Behavior Society, London, England.

TAYLOR, R.H. 1984. Distribution and interactions of introduced rodents and carnivores in New Zealand. *Acta Zool. Fenn.* 172:103-105.

TOMICH, Q.P. 1986. Mammals in Hawaii: A synopsis and notational bibliography. Second Edition. Bishop Museum Press, Honolulu, Hawaii.

VEITCH, C.R., FITZGERALD, B.M., INNES, J.G., and MURPHY, E.C. 1992. (eds.). Proceedings of the National Predator Management Workshop. Threatened Species Occasional Publication No. 3. Department of Conservation, Wellington, New Zealand.

WATSON, J.S. 1961. Rats in New Zealand: a problem of interspecific competition. *Proc. 9th Pacific Science Congress* 19: 15-16.

WRATTEN, S. 1992. Population regulation in insect herbivores - top-down or bottom-up?. *N.Z. J. Ecol.* 16:145-147.

WUENSCH, K.L. 1992. Fostering house mice onto rats and deer mice: Effects on response to species odours. *Anim. Learn. Behav.* 20:253-258.