Interspecific competitive interactions between *Rattus norvegicus* and *R. rattus*

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STACEY PATRICIA FOSTER

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ABSTRACT

Interspecific competition is observed when one species experiences reduced survivorship or fecundity, due to another controlling access to resources either through being superior at harvesting a shared resource (exploitation competition), or physically preventing the other species from accessing the resource, either through territory defence, or aggressive behaviour (interference competition).

The aim of this project was to investigate the idea that a balance of exploitation competition and interference competition working together contributes to governing the current distribution of ship rats and Norway rats in New Zealand.

The ship rat is the most abundant species, being widespread in native forest, while the Norway rat is largely restricted to farm buildings, rubbish tips, riparian sites and wharves.

Chapter Two aimed to test the null hypothesis that there are no differences in the ability of the two species to harvest resources above the ground in native forest. An artificial forest was created with stands of various heights, representing small trees; with inter connecting ropes of various widths to represent branches rats might encounter in the forest. Individual rats were placed in the artificial forest and their activity recorded during the night. As expected, ship rats were significantly faster climbing up and down all the stands, as well as being faster traversing the various ropes. They also utilised the artificial forest much more than Norway rats. This ability of the ship rat to utilise this habitat may give them advantages in exploitation competition.

Chapter Three aimed to test which species is superior at inference competition, when they meet on the ground. This was done using two methods: (1) inter- and intra- specific staged encounters in a small box, with a rat at each end, separated by a partition, with the rats behaviour remotely recorded, and (2) placement of the scent of the opposite species or the actual animal in a self contained cage somewhere within the artificial forest, which was used in the previous chapter. Ship rats appeared to be disturbed by the presence of Norway rats in the artificial forest, but they ignored displays of aggressive behaviour exhibited by the Norway rats during the staged encounters.

Chapter Four describes an attempt to validate the results found in Chapters Two and Three in the wild, under natural conditions. A 480 metre long trap line, with 17 trap stations, 30 metres apart was placed on Rahui Island, Lake Waikareiti. Each station consisted of two Victor snap traps with covers, one on the ground and one 2.0 metres above the ground on a platform, with seven trapping nights. Ship rats were trapped on the forest floor and 2.0 metres above the ground, while only one Norway rat was trapped, on the forest floor.

Chapter Five summarises the results from the previous chapters and also outlines possible avenues for future research in this area. The results described in this thesis are consistent with the prediction that the distribution of both species in New Zealand is governed by shifting advantages of exploitation competition and interference competition, mediated by habitat.

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RATTUS IN A WORLD SETTING

The order Rodentia is the largest among the mammals and is made up of 28 families, 431 genera and approximately 1999 species which are distributed all over the world. As a group, the rodents are successful in almost every type of habitat. Most rodent species eat vegetation or seeds and some live in close proximity with humans (King 2005; Gurnell and Hare 2008).

The four species of rodents that are found in New Zealand are all from the family Muridae. This family is comprised of 312 genera and 1477 species. These species are mainly found in tropical Africa, Australia and Asia. Most of the genus *Rattus* lives in Australasia and Asia. Three species of this genus are in New Zealand. They are the Pacific rat (Kiore) *Rattus exulans,* ship rat *R. rattus,* and Norway rat *R. norvegicus* (King 2005).

The Pacific rat or Kiore was the first to arrive with the early Polynesians in 1250-1300 AD, followed by the Norway rat, which arrived with the early European explorers between 1770 and 1820 and spread all over the country. The ship rat was the last to arrive with European settlers, between 1858 and 1865 (Moors 1985; Yom-Tov *et al.* 1999; Harper *et al.* 2005). As each new species arrived and became established in New Zealand, the existing species became limited in their distribution (Taylor 1984).

The Norway rat originated from north east China. It spread westwards, where it first invaded western European cities early in the eighteenth century. Following this, it became transported throughout the world on European and North American sailing ships, and became established in many countries (Amori and Clout 2002). In tropical regions, Norway rats colonise ports but tend not to move inland (Atkinson 1985).

The ship rat originated in India and spread to Britain by the third century AD. They are now distributed globally (apart from the polar regions), from Sweden to

Macquarie Island. The ship rat is divided into five different chromosomal groups which are of unknown taxonomic status. The most common are the European/Oceanic form and the Asian form. These two groups differ in the number of chromosomes they have, and some external features. They do not hybridise. The European/Oceanic form spread with humans with the early trading ships (Yosida *et al.* 1974).

INTERSPECIFIC COMPETITION

The five main interactions between organisms are predation, parasitism, detritivory, mutualism and competition. These interactions can modify the environment and affect the survival and distribution of sympatric species (Begon *et al.* 1996). Competition among rats in New Zealand is the focus of this thesis.

Competition is defined as “the negative effects that one organism has upon another by consuming, or controlling access, to a resource that is limited in availability” (Keddy 1989 p. 2). Interspecific competition is observed when “individuals of one species suffer a reduction in fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of another species” (Begon *et al.* 1996 p. 265). Interspecific competition is important in the shaping of many animal and plant communities. The outcomes of these interactions determine the spatial and temporal organisation of the species present in the community, which have consequences for the species population size and habitat selection (Eccard and Ylonen 2003). The more ecologically similar two species are, the higher the intensity of competition is expected (Morse 1980) and the consequences for the two species in a competing situation can be different. One species may experience increased reproductive success, while the other may be excluded and forced to a less optimum habitat (Begon *et al.* 1996).

A mathematical model developed by Alfred Lotka and Vittora Volterra describes the interactions between two species using the same resource (Figure 1).

Species One: $\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$

Species Two: $\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right)$

Figure 1. Lotka-Volterra mathematical model for competition. Adapted from Smith & Smith (2001) p. 243.

N_1 and N_2 are the population sizes for species 1 and 2, r_1 and r_2 are the respective intrinsic rates of increase and K_1 and K_2 are the population carrying capacities. αN_2 is the coefficient that gives the competitive effect of species two, while βN_1 gives the competitive effect of species one. If no competition exists between the two species e.g. – α or N_2 (in the first equation) or β or N_1 (in the second equation) = 0, then the species would grow to its carrying capacity. This model has five assumptions which are: that there is no migration; the environment is stable; the effect of competition is instantaneous; coexistence will require a stable point and lastly that competition is the only important biological interaction. In the real world, these assumptions generally are not met.

Four different outcomes are predicted from this model and these depend on the values of K, α and β. (1) Species one will increase while inhibiting species two; after which species two will eventually disappear. (2) Species two will increase while inhibiting species one, and species one will eventually disappear. (3) Each species, when abundant, will inhibit the growth of the other species more than it inhibits it own growth. In this situation the winning competitor will become the most abundant. (4) The two species coexist but neither reaches numbers high enough to affect the other species (Smith & Smith 2001).

Numerous field studies have been conducted on interspecific competition, especially with rodents (reviewed by Grant 1972; Eccard and Ylonen 2003).The best way to test whether competition exists between two species, is a removal experiment. One species is either removed or decreased in population size and the reproduction rate or population size of the other species is monitored. If these increase, then competition exists between the species (Caughley and Sinclair 1994). For example, Redfield *et al.* (1977) studied voles *Microtus townsendii* and deermice *Peromyscus maniculatus*. Most species of deermice normally live in forests, but one group is found in grassland, where voles are also found. The authors removed voles from these areas and found that the numbers of deermice increased. Later when the control of voles was stopped, the deermouse numbers decreased. When the dominant species is removed, competitive release is observed, as the subordinate species increases its habitat range or diet (Sinclair *et al.* 2006). Interspecific competition commonly takes one of two forms, depending on how the common resource is distributed.

Interference competition

Interference competition may be inferred when members of one species physically prevent the other from obtaining a resource by aggressive encounters or territory defence (Keddy 1989; Smith and Smith 2001; Harris and Macdonald 2007). The dominant species in these interactions tends to be larger of the two (Morse 1980; Persson 1985). For this interaction, the more dominant species will be able to monopolise more resources, which will support greater growth for the dominant. This will increase resource acquisition and cause further damage to the subordinate species (Keddy 1989). Interference competition works best for the interfering species when the effects are high and the costs are low. For example, a species with horns, teeth or poisons used for predator defence or prey capture could easily use these for interspecific interactions at very low cost to the animal, but still have large effects (Case and Gilpin 1974). Eccard and Ylonen (2002) conducted an enclosure study to explain the interspecific competition between the bank vole *Clethrionomys glarcolus* and the field vole *Microtus agrestis*. Half of the enclosures used were the treatments, containing both bank and field voles, while the other enclosures contained only bank voles. The authors found that bank voles in the two-species enclosures had smaller territory sizes and lower survival compared with those in the non treatment enclosures. When food was experimentally reduced for both groups, space use was reduced, rather than increasing as expected. Individuals of opposite species actively avoided each other, which indicated direct interference competition acting on both species.

Exploitation competition

Exploitation competition may be inferred when one species is better than another at harvesting a given type of resource. This interaction is indirect and resources have to be in limited supply (Harris and Macdonald 2007). The ability of each species to utilise the resource at stake determines the outcome (Smith and Smith 2001). The dominant will lower the resource pool, but is also able to acquire resources more efficiently due to the newly captured energy being invested into resource acquisition; that in turn will further lower the resource pool for the subordinate species (Keddy 1989). A classic example of exploitation competition was discovered in two species of freshwater diatoms, *Asterionella formosa* and *Synedra ulna*, which require silicate for the construction of their cell walls. Tilman *et al.* (1981) grew both species alone in cultures, which had the resource silicate being continually added. Both species reached carrying capacities while maintaining the silicate at a low concentration; however, *Synedra* reduced the silicate concentration to lower levels than *Asterionella*. Subsequently, when both species were grown together in a mixed culture, *Synedra* reduced the silicate concentration so low that *Asterionella* was unable to survive. In this example *Synedra* was the superior competitor in harvesting the silicate resource.

Persson (1985) proposes that smaller species are more efficient at exploitation competition while the larger species are more efficient at interference competition. Both types of interspecific competition can be observed in many forms of interactions between the same species at the same time, though interference competition is the least common (Caughley and Sinclair 1994). However, interference competition is the easiest to detect as it is a direct interaction (Petren and Case 1995). Fellers (1987) documented both exploitation competition and interference competition between nine species of ants living in a woodlot in

Maryland, USA. The dominant ant species physically prevented the subordinate species from accessing the food whenever they met, but the subordinate species overcame this by being more efficient and quicker at gathering food. The author found that there was an inverse relationship between dominance and the relative speed with which the baits were accessed. The subordinate species was able to locate and use resources rapidly while the dominant species exhibited aggression, territoriality and used poisons. A balance between all forms of interference and exploitation competition allowed all nine species of ant to coexist.

Interspecific competition generally leads to coexistence of the species present either in sympatry (by resource partitioning) or in allopatry (by mutual habitat exclusion) (Harper *et al.* 2005). Coexistence can either be stable or unstable, and depends on the resources available in the environment. During periods of low resource availability, interspecific competition may be intense and only the best adapted species will survive, but then during years of high resource availability, all species may be able to utilise the environment.

Gause's Principle proposes that species can coexist if they each have adaptations enabling them to partition the resources in the habitat (Sinclair *et al.* 2006), and this is observed when species utilise different resources, in the same habitat. These resources may be separated spatially and temporally, while some species may be able to utilise the resource only in certain conditions (Begon *et al.* 1996). For example, resource partitioning was observed as a consequence of the foraging habits of three desert rodents *Dipodomys merriami, Perognathus formosus* and *P. longimembris*. *Perognathus* preferred to forage for dispersed seed resources, while the *Dipodomys* foraged for rich clumped seed resources (Bowers 1982).

Competitive exclusion is most evident when exotic species invade a new habitat and out-compete the native animals, eventually forcing the native species to move to a less optimum habitat or to extinction (Smith and Smith 2001). This is dependent on the ability of one species to utilise resources in a habitat relative to the abilities of another (Harper *et al.*2005). An example of this is found in two species of chipmunk. Brown (1971) looked at the interspecific interactions between two species of chipmunks *Eutamias dorsalis* and *E. umbrinus*. He found that *E. dorsalis* was dominant over *E. umbrinus* in habitat with few trees, because *E. dorsalis* could normally win aggressive encounters, but when the habitat was a complex forest, the primarily arboreal *E. umbrinus* was able to escape through the trees and *E. dorsalis* became the less dominant species in that environment. Brown (1971) noted that this relationship is similar to that of the Norway rat and the ship rat, in that the different abilities to take refuge in trees and buildings by the two species, and their differences in levels of aggression, are important in deciding the outcome of interactions between the two species.

An ecological effect of competition is that one species will be displaced from the habitat (Begon *et al.* 1996) and this is what happened when ship rats arrived in New Zealand. Harper (2006) suggested that the reason why the already established Norway rat has been excluded from the forest habitat is that the ship rat is more efficient at utilising the resources in the forest. Norway rats were excluded from the podocarp-broadleaf forest on Pearl Island, although the exact mechanism was not discovered. However Harper (2006) noted that the smaller ship rats and Pacific rats may have advantages in exploitation competition, as they are able to benefit from smaller items than can Norway rats.

SHIP AND NORWAY RATS IN NEW ZEALAND

The interspecific competitive interaction between the Norway rat *Rattus norvegicus* and the ship rat *Rattus rattus* are complex. In New Zealand the much larger Norway rat appears to have been displaced by the ship rat through interspecific competition (Innes *et al.* 2001).This is interesting as the Norway rat tends to be the dominant species in many other countries. Few studies have been conducted in New Zealand focussing on this pattern with these two species.

The Norway rat is the biggest of the rat species in New Zealand, and in Europe and America it dominates over the smaller ship rat (Taylor 1978a). Weights of the

Norway rat average between 200-300 grams though some can be up around 400 grams, while weights of the ship rat tend to be approximately 120-160 grams (Atkinson and Towns 2005). This size difference can be seen in Figure 3.

Throughout Britain and America, the ship rat is confined to urban areas, generally in the roofs of buildings (Taylor 1978a). In Britain, the ship rat is one of the rarest mammal species present (Innes 2001), however in New Zealand, the ship rat is the most common. They are found throughout New Zealand, inhabiting a wide range of forest types (Atkinson 1973; Taylor 1978b). They are most abundant in diverse, mature, lowland, podocarp-broadleaf forests, from the coast to the tree line, but rare in the alpine tussock. Other habitats include urban parks, hedgerows and in the ceilings of buildings (Innes 2005b). Non-commensal populations of the Norway rat are found at riparian sites in forest and along the coastline, while commensal populations can be found in almost any area containing a food source regularly added to by humans, which includes rubbish tips, wharves, farm buildings and sewers (Atkinson 1973; Taylor 1978b; Innes 2005a)

The physical differences between the Norway and ship rats, other than size, include the shorter, thicker tail and smaller eyes and ears on the Norway rat (Quy and MacDonald 2008) (Figure 2). They also tend to have different coloured fur. The ship rat most commonly has grey-brown or black fur on the back and white or grey on the belly, while the Norway rat has brown fur on its back and white tipped grey fur on the belly (Atkinson and Towns 2005).

Norway rats tend to be ground dwelling and are rarely seen climbing above 3 metres. They are also known for their burrowing and swimming abilities (Atkinson 1973; Brooks and Rowe 1979; Thorsen *et al.* 2000; Amori and Clout 2002), while ship rats are primarily arboreal and spend most of the time in the forest canopy, occasionally coming down to the forest floor to forage (Atkinson 1973; Hooker and Innes 1995; Lindsey *et al.* 1999; Amori and Clout 2002). Commensal Norway rats also tend to be especially wary of new objects (Atkinson, 1973), which is a condition known as neophobia (Macdonald *et al.* 1999), however non commensal populations tend to be naive and non neophobic, as populations from islands have been successfully eradicated. Taylor and Thomas (1993) reported no neophobia in the Norway rats on Breaksea and Hawea Islands as over 80% of the bait was taken the first night of poisoning, and almost 100% taken during the next three nights

Figure 2. A close up photo showing the heads of a female *Rattus norvegicus* (front) and a female *R. rattus* (back) (B Patty)

Figure 3. Dorsal view of a female *Rattus norvegicus* (bottom) and a female *R. rattus* (top), showing the body: tail proportions (B Patty)

These behavioural differences may contribute to their habitat preference. When the ship rat and the Norway rat are found together, the Norway rat is found on the ground or in basements while the ship rat is found up in the trees or in the upper storeys of a building (Innes 2005a).

RAT DAMAGE TO NEW ZEALAND FAUNA AND FLORA

New Zealand's native plants and animals evolved without the presence of four footed grazing mammals, so when mammals were introduced to New Zealand, it had devastating impacts on native flora and fauna. Currently, since humans arrived in New Zealand, at least 61 species of exotic mammals have been introduced to New Zealand, either accidently or intentionally, which 32 have established wild populations (Parkes and Murphy 2003). Rats have reduced or eliminated many populations of birds, reptiles and invertebrates in New Zealand (Moors 1985; Amori and Clout 2002), by predation, and maybe through competition for food (Innes *et al.* 1995; Dowding and Murphy 2001; Innes *et al.* 2010).

The Norway rat is a known predator of ground dwelling birds, while the ship rat is a known predator of ground-dwelling birds, and perching birds which live and breed in the canopy of trees (Amori and Clout 2002). The potential effect of the ship rat on native birds in New Zealand was clearly demonstrated when they reached Big South Cape and the Solomon Islands, 2.4 km south-west of Stewart Island, in about 1962. High numbers of ship rats irrupted on these islands, and immediately precipitated a marked decline in several bird species. These included the bellbird *Anthornis melanura*, the saddleback *Philesturnus carunculatus* and the robin *Petroica australis.* The Norway rat and Kiore have never reached these islands (Atkinson 1973).

Many sea birds are vulnerable to predation by Norway rats, which are large enough to take eggs and nestlings, and sometimes even kill adults. On offshore islands, the presence of the Norway rat is negatively correlated with seabird species richness (Russell and Clout 2004). The stomach contents of Norway rats trapped inland on Whale Island, (Moutohora), in the Bay of Plenty were dominated by the down and flesh of grey faced petrel *Pterodroma macroptera* chicks (Bettesworth and Anderson 1972).

Invertebrates also suffered with the arrival of rodents to New Zealand. On Rangitoto Island in the Hauraki Gulf, invertebrates made up the main component of the diet of the mice and ship rats whose stomach contents were analysed, with tree weta *Hemideina thoracica* being the most common food item (Miller and Miller 1995). Similar results were found when the stomach contents of Norway rats trapped along the shoreline were analysed on Whale Island, (Moutohora island), in the Bay of Plenty. Unlike the rats collected inland on the same island, which ate predominately chicks of the grey faced petrel *Pterodroma macroptera,* these rats had eaten predominantly insect remains with some invertebrates from the intertidal regions (Bettesworth and Anderson 1972).

New Zealand’s native flora has also suffered since the introduction of the two larger *Rattus* species. Both species eat fruits, seeds, foliage and other parts of the plant in native forest (Wilson *et al.* 2003). Allen *et al.* (1994) found that the regeneration of the indigenous forest on Breaksea Island increased considerably after Norway rats had been eradicated from the island.

NEW ZEALAND STUDIES

Most of the New Zealand rodent studies on competition have been done on offshore islands, and these generally concentrate on the species distributions. On Stewart Island where ship rats are present, Harper *et al.* (2005) and Harper (2006) trapped low numbers of Norway rats in podocarp-broadleaf forest, but more were found on the coastlines, in the subalpine shrub-land and sometimes in the manuka shrub-land. Ship rats were found in almost all vegetation types and were generally the only species found in the podocarp-broadleaf forest. The authors found that Norway rats had high affinities with plant species associated with damp sites, while ship rats were quite general in their habitat use. The Norway rat may have a physiological advantage over the ship rat in cold conditions, and this may be why they dominate in the subalpine shrubland. The absence of the Norway rat from the podocarp-broadleaf forest casts further doubt on the theory that predation by mustelids is the reason why they have disappeared from mainland forest, as there are no mustelids present on Stewart Island.

Norway rats tend to be found more often in the forest on islands where they are the only *Rattus* species present. On Mokoia Island in Lake Rotorua, Norway rats were trapped at low altitudes on the island, and in the forest more often during autumn (Beveridge and Daniel 1965). On the Noises and Motukawoa islands, Norway rats were trapped all over the islands in all habitats (Moors 1985). On other islands, Hawea Island in Fjordland (Taylor and Thomas 1989) and on Whale Island (Moutohora Island) (Bettesworth and Anderson 1972), Norway rats were trapped throughout the entire island but the authors noted that they were trapped more often on the coastline. On Raoul Island, where no ship rats were present, but Pacific rats were, the Norway rat was distributed evenly throughout the island, and was dominant in all optimal habitats present. The only habitat where the number of Pacific rats exceeded those of Norway rats was in the suboptimal beach fore-dune habitat. This suggests that the Pacific rat was avoiding areas of high Norway rat abundance (Harper and Veitch 2006).

The only study that has been conducted in a mainland forest where both the ship rat and the Norway rat were present was in Pureora Forest Park in the Central North Island. Only 43 Norway rats were caught compared to the 1793 ship rats in an array of traps equally good at catching both. The majority of Norway rats caught came from one trap next to a stream, while ship rats were caught throughout the podocarp forest (Innes *et al.* 2001). Morgan *et al.* (2009) trapped two Norway rats, and 19 ship rats, in a gully, in Hamilton city.

OVERSEAS STUDIES

Both the Norway rat and the ship rat are found in the Seychelles archipelago. One study looked at the distribution and morphology of the introduced rats on these islands. They found only one species on most islands. The only islands where both species were trapped were the two largest islands of the archipelago, Mahe and Praslin and also on Long Island. The authors suggested three possible explanations: (1) relatively few colonisation events; (2) the Norway rat has been present in this archipelago for only a short time, and (3) competitive exclusion of new arrivals by the original colonisers (Hill *et al.* 2003). Russell and Clout (2004) also concluded that all three species of rat in New Zealand can exist together only on larger islands, and distribution on smaller islands depended on colonisation events.

Kartman and Lonergan (1955) found in the Hamakua district of Hawaii that both ship rats and Norway rats were trapped in sugarcane fields and in small cultivated areas, but fewer Norway rats. By contrast, another study conducted in Hawaii by Tobin and Sugihara (1992), trapped 526 Norway rats and 139 ships rats in various sugarcane plantations, over the 11,200 trap nights. The authors noted that Norway rats were most often trapped in the middle of the sugarcane fields while ship rats were most often trapped on the edges.

Populations of both species were found to be living at Bradley's Head in Australia but in quite different habitats. The Norway rats were more often trapped in the zoo grounds, near a refuse tip, while the ship rats were more often trapped in the bush land reserve surrounding the zoo. After Norway rats were experimentally removed from the zoo grounds, ship rats did not move into the vacant habitat (Williams *et al.* 2003).

In the territory of Riga, in Latvia, both the Norway rat and the ship rat are present (Zorenko and Leontyeva 2003). The aim of their study was to determine mammalian species diversity throughout this area in various zones classified by the authors. Norway rats were more common in buildings, yards of fruit and vegetable storehouses and the edges of highways. Fewer ship rats were detected, and these were only found at the sea port.

Cavia *et al.* (2009) looked at rodent diversity in the city of Buenos Aires. Both the Norway rat and the ship rat were among the rodents which were trapped throughout the city. The Norway rat was trapped in all three shantytowns sampled, in two out of the three parklands sampled and in a natural reserve, while the ship rat was found in one of the shantytowns, in all industrial-residential areas sampled and in one parkland. The authors noted that the ship rat was more prevalent in the industrial-residential areas, as their climbing ability allowed them to utilise the large buildings, while the Norway rat showed an affinity for areas with more natural vegetation cover such as parks, and areas with water bodies nearby.

In the Galapagos Islands habitat use by the two species was investigated by Key and Woods (1996) using the spool-and-line method. Both species were present at three of the sites where animals were tracked, while the fourth site only had ship rats. Significantly less line was collected for Norway rats than ship rats. Ship rats spent significantly more time in the trees than the Norway rats, while the Norway rats spent more time running along underground cracks and crevices in the rocks. Ship rats at the site with no Norway rats spent more time on the ground than those at the sites where Norway rats were present.

In California, Stroud (1982) found a population of Norway rats and ship rats living along a riparian habitat. This study used a mark recapture technique to look at the population dynamics of both species. Stroud (1982) found that the population of Norway rats exceeded that of the ship rats throughout the entire study period.

PROJECT AIMS AND STRUCTURE

Because both rat species are pests, any information relating to their behaviour and ecology may be useful. I aim to facilitate control of these species in areas of varying habitats, particularly when a mixed assemblage of rat species is coexisting. It would be useful to be able to predict the behaviour of one species when the other is removed, and to estimate habitat-specific trapping success. Knowledge of the ability of both species to gain access to food (e.g. bird’s nests) will be useful for conservationists deciding on safe havens for translocation of endangered birds.

Project hypothesis: I predict that in the forest habitat of New Zealand, the Norway rat *Rattus norvegicus* will be the superior competitor in situations of interference competition, and the ship rat *R. rattus* will be the superior competitor in exploitation competition. A balance of these two competitive processes working together could explain the current distribution of these two species in New Zealand.

Objective 1: To test the agility and climbing ability of both the rat species by presenting obstacles with food rewards above the ground, simulating conditions encountered in the New Zealand forest.

Prediction: The ship rat will show greater agility and ability to overcome the obstacles presented to gain food.

Objective 2: To determine which species is the superior competitor in situations of interference competition, when they meet on the ground. This will be tested in two ways:

a) Odours of the opposite species will be placed throughout a known path on the obstacles and the reaction of an animal familiar with that path will be measured. Alternatively, actual animals may be placed among the obstacles, isolated in a cage to prevent contact.

b) An individual of both species will be placed in a small cage with a partition between them, and their behaviour will be recorded for a set amount of time.

   Predictions: If interference affects the behaviour of the two species, the ship rat will be less willing to get close to the Norway rat than the Norway rat will be to the ship rat. In the staged encounters, the ship rat will exhibit more submissive behaviour and position itself far away from the Norway rat, whereas the Norway rat will behave aggressively towards the ship rat.

Objective 3: To determine the ratio of ship rat and Norway rats trapped on the ground versus 2 metres in the trees, in native forest supporting both species.

Prediction: The majority of ship rats will be trapped in the trees, while the majority of Norway rats will be trapped on the ground.

The structure of the thesis is as follows:

Chapters Two, Three and Four are formatted as a collection of scientific papers written for submission to the relevant scientific journals. Chapters One and Five are not intended for separate publication but link the document together as a thesis, so some repetition between chapters is inevitable.

Chapter one reviews the literature, focussing on Norway rats and ship rats throughout the world and in New Zealand. The theory of interspecific competition and examples from other systems, as well as studies focussing on these two species are summarised.

Chapter two and three describes the work done in captivity. Chapter two describes experiments testing the climbing ability of both species as this may be important in exploitation competition in native forest. Chapter three describes two different methods that were used to document interference competition between the Norway rat and the ship rat, testing to determine which species is socially dominant, in face to face encounters.

Chapter four describes field work undertaken on Rahui Island on Lake Waikareiti, looking at the arboreality of wild individuals of both these species in native forest.

Chapter five summarises all of the results discovered in the project, outlines implications of these results and suggests future avenues of research in this topic.

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CHAPTER TWO

The climbing ability of *Rattus norvegicus* and *R. rattus*

ABSTRACT

Exploitation competition is a possible explanatory mechanism governing the current distributions of Norway and ship rats in New Zealand. Ship rats are now found throughout the country, most abundantly in native forest, while Norway rats are largely confined to riparian habitats, wharves, rubbish tips and farm buildings. However before ship rats arrived in New Zealand, Norway rats were found throughout the country. The greater climbing ability of ship rats may improve their success at exploitation competition.

The aim of this chapter was to test the agility and climbing ability of both rat species by presenting obstacles with food rewards above the ground, comparable to what is encountered in the New Zealand forest. Rats were placed individually in aviary-style pens, with stands supporting food reward at various heights, and

ropes of various widths linking the stands. The rats’ activities were recorded by video cameras for 12 hours each night.

Ship rats were significantly faster than Norway rats at climbing up and down the various stand heights, as well as traversing the different widths of rope. Ship rats also utilised the stands more often than Norway rats, and spent significantly more time on the stands. However, the Norway rats did not avoid climbing: all individuals used in this experiment climbed most of the heights. This illustrates that Norway rats can climb.

The results from this work provide some evidence that ship rats are better than Norway rats at utilising above-ground resources in the forest environment, which may give them an advantage in exploitation competition in this habitat. However, this would not necessarily exclude Norway rats from this habitat at times of abundant food supplies.

INTRODUCTION

Interspecific competition is observed when “individuals of one species suffer a reduction in fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of another species” (Begon *et al.* 1996, p. 265). Interspecific competition commonly takes one of two forms: interference and exploitation competition.

Interference competition is observed when one species is physically preventing another from accessing a resource, whether or not it is abundant, either through territory defence or aggressive encounters (Keddy 1989; Smith and Smith 2001; Harris and Macdonald 2007). Exploitation competition is observed when one species is better than another at harvesting a given type of resource. This is an indirect interaction, and arises only if the resource is in limited supply (Harris and Macdonald 2007). Animals are responding to the resource level, which in turn is being affected by the other competitors in that habitat (Begon *et al.* 1996).

An example of exploitation competition was found in two species of gecko in Hawaii, the native asexual gecko *Lepidodactylus lugubris* and the sexual gecko *Hemidactylus frenatus* during enclosure studies. Petren & Case (1996) found that the reason why populations of L. *lugubris* decline in the presence of *H. frenatus* is because of differences in the ability of both species to exploit food resources. *H. frenatus* depletes insect resources to a very low level which reduces resource acquisition by *L. lugubris.* This causes a reduction in the body condition, survivorship and fecundity of the *L. lugubris.*

The Norway rat *R. norvegicus* was transported to New Zealand, from 1770, with the early European explorers, traders and early settlers, up to about 1865. After about 1865, the ship rat, *R. rattus* arrived with the later European settlers, and soon spread right throughout the country. During this time the previously widespread Norway rat became restricted in distribution (Moors 1985; Yom-Tov *et al.* 1999; Harper *et al.* 2005; Innes 2005a; Innes 2005b).

The Norway rat is the largest of the three rats in New Zealand, with weights averaging 200-300 grams, while ship rat weights average 120-160 grams. The Kiore (*R. exulans)* is the smallest, weighing on average between 60-80 grams (Atkinson and Towns 2005). Kiore were the first species to arrive in New Zealand and appeared to become displaced when the two European rats spread through the country (Atkinson 1973).

Currently, ship rats are found throughout New Zealand, inhabiting a wide range of forest types (Atkinson 1973; Taylor 1978). They are most abundant in diverse, mature lowland podocarp-broadleaf forests, from the coast to the tree line, but not in the alpine tussock (Innes 2005b). This is in contrast to Norway rats, which are largely confined to farm buildings, riparian sites, coastlines, rubbish tips, and wharves (Atkinson 1973; Taylor 1978; Innes 2005a).

Norway rats tends to be ground dwelling and are rarely seen climbing above 3 metres. They are also known for their burrowing and swimming abilities (Atkinson 1973; Thorsen *et al.* 2000), while ship rats are primarily arboreal and spend most of their time in the forest canopy, occasionally coming down to the forest floor to forage (Atkinson 1973; Hooker and Innes 1995; Lindsey *et al.* 1999). Norway rats are known predators of ground dwelling birds, while ship rats prey upon both ground-dwelling and perching birds (Atkinson 1973; Thorsen *et al.* 2000).

A prediction of competition theory is that one species will be displaced from a given habitat when an ecologically similar species arrives (Begon *et al.* 1996), and this seems to have happened to Norway rats, when ship rats arrived in New Zealand. My hypothesis is that there is a shifting balance of exploitation competition and interference competition, which could explain the current distribution of ship rats and Norway rats in New Zealand. In this balance, ship rats are expected to be superior in exploitation competition, especially in native forest, while Norway rats will be expected to be superior in interference competition, when they encounter each other on the ground.

Harper (2006) suggested that the reason why Norway rats have been excluded from the forest habitat on Stewart Island is that ship rats are more efficient at harvesting the resources in the forest. Norway rats were excluded from the podocarp-broadleaf forest on Pearl Island by an unknown mechanism, but Harper (2006) noted that smaller species, such as the ship rat and the kiore may have advantages with food extraction, as they are able to efficiently utilise a wider range of food sizes. Further evidence to support this was found when only ship rat and kiore abundances increased during the rimu seed mast event on Stewart Island (Harper *et al.* 2005), though this is not conclusive evidence because Norway rats may not eat rimu seeds.

The ability to access and harvest resources in the forest canopy may give ship rats a competitive advantage over Norway rats. The climbing ability of both these species may be an important factor determining which species is the superior competitor in exploitation competition in native forest. Only one study by Creel (1913) has tested the climbing ability of both species, but because of the methods used, the results cannot be treated as conclusive.

Other studies have looked at the climbing ability of rodents to help explain interspecific competition between sympatric species. Layne (1970) examined the climbing behaviour of the Florida mouse *Peromyscus floridanus* and the cotton mouse *P. gossypinus* to help understand the distribution of these two species in Southeastern United States. Layne (1970) concluded that the greater arboreality of the cotton mouse allowed them to occupy a wider range of habitats than the Florida mouse.

The aim of this phase of work was to test the agility and climbing ability of both rat species by presenting obstacles with food rewards above the ground comparable to what the rats might encounter in the New Zealand forest. The null hypothesis was that there would be no significant difference between the species in their ability to overcome obstacles simulating a forest environment, and gain food resources above the ground.

METHODS

Trapping

Representatives of both species were trapped in the wild. The ship rats were trapped in the Waikato district in a large garden on the outskirts of Hamilton and at the Waterworks Reserve in the Te Miro district. Norway rats were trapped in the Waikato and Rotorua regions, at sites which included a privately operated piggery, native bush next to a stream and at a factory adjacent to an effluent pond. Cage traps baited with peanut butter were checked daily. Captured rats were transported back to the university animal house facilities, where they were sexed and weighed. They were placed in individual cages and left for 2 weeks to habituate.

Husbandry

Individual home cages were approximately 1m x 1m x 1m, with a mesh ground floor and also a shelf they could sit on. The rats were fed every second day, a mixture of standard rat pellets plus carrot, and apple, and water *ad lib*. They were provided with a nest tube containing nesting material such as hay and newspaper. Rats of the two species were kept in separate rooms with a 12 hour light – dark cycle. The room temperature ranged between 14 and 21°C.

Trials

A total of 11 Norway rats (5 females and 6 males) and 12 ship rats (6 females and 6 males) were available for this experiment. Female Norway rats weighed an average of 231 grams; the males 318 grams. Female ship rats weighed an average of 121 grams and males 127 grams.

Two outdoor aviary-style pens were used for these trials, one specifically for ship rats and one for Norway rats, each measuring 3.1 m x 4.0 m x 2.2 m. The pens had concrete floors, with wire mesh walls and ceilings, and a nest box, food and water, at ground level.

Stands of three different heights were used (two 1.0 metre, two 1.5 metres and one 2.0 metres) which represented a range of low trees in which rats might forage. At the top of each stand, a small platform was placed where the rat could sit, and which could also support a container holding one gram of peanut butter. Five stands were placed in each pen, representing an artificial forest (Figure 1). Because the planed timber stands were narrower, smoother and presumably harder to climb than real trees, footholds were provided up four of these stands by nails set 7cm apart up the stand.

Three different widths of rope (4mm, 6mm and 8 mm) (Figure 2), were used to link the stands to each other, to simulate the interlocking branches of trees. The ropes were all approximately 100 cm long. The artificial forest also had a 140 cm long horizontal swinging bamboo pole attached to the ceiling of the pen, (Figure 1), on which the rats could run across the gap between the two 1.5 m stands.

Infra red lighting enabled the cameras, linked to 12 hour time lapse video players, to record the activity of the rats every night from 5pm until 7am. Cameras were placed in the uppermost corner of the pen to ensure the nest box and all the stands were seen. Thin aluminium sheets were placed on the sides of the pens from floor level to approximately 2 metres high to make it more difficult for the rats to climb the wire mesh and gain access to the cameras.

Each rat spent a total of five nights alone in the pen. The first night was the habituation night, while the second night was recorded. In the morning, the food containers were collected and any peanut butter left was weighed. Various other treatments occupied the other three nights, as discussed in Chapter Three. Once a rat had completed the five night experiment, it was removed from the pen and the pen mopped with hot soapy water to remove all traces of rat scent. All experiments were approved by the University of Waikato Animal Ethics committee, protocol number 741.

Figure 1. The artificial forest (S Foster)

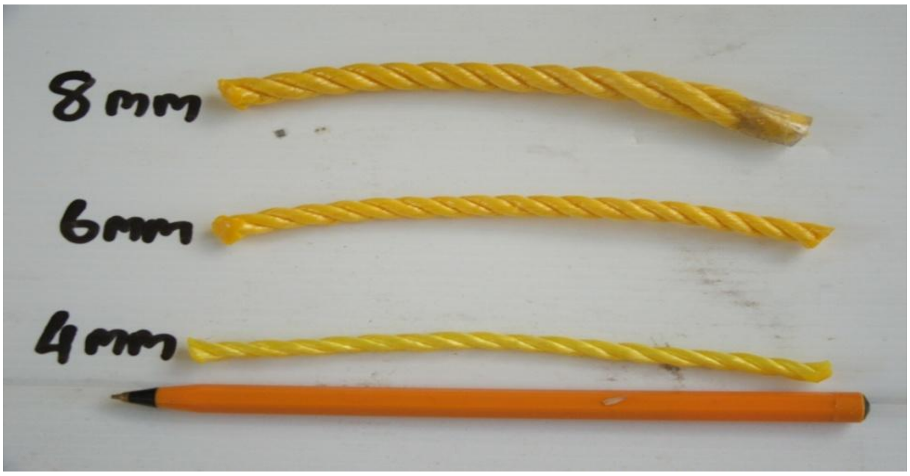

Figure 2. The three widths of rope used (S Foster)

The information collected from the video footage was:

- Time taken to climb up and down the stands
- Frequency of climbing throughout the night
- Time taken to traverse the different thicknesses of rope
- Frequency of traversing the rope throughout the night
- The time until the first obstacle was completed from sunset, as Norway rats are mainly nocturnal and ship rats are nocturnal (Innes 2005a; Innes 2005b).
- Amount of time spent on the ground versus on the stands; this was done by randomly selecting ten intervals of five minutes, and noting where the rat was positioned in the pen during that time.

Students t tests were used to test for differences between species (sexes pooled) in: average time to traverse ropes of each thickness; average time it took to climb up and down each of the stands in the artificial forest; average time each species spent on the ground versus on the stands; average time taken until the first obstacle was attempted after sunset; average time taken to cross the bamboo pole and average frequency of climbing throughout the night.

RESULTS

Traversing the ropes

Rats of both species took less time to cross the widest rope, compared to the thinnest rope, and crossed it most often, but the fastest average transit time by Norway rats was still slower than the slowest average transit time by ship rats (Table 1; Figure 3). Significance was detected between species in speed of crossing the 4mm and 8mm wide ropes with both P values being less than 0.05. Significance could not be determined for the 6mm rope width.

Table 1. Number and duration of crossings of ropes of various widths made by captive wild ship rats and Norway rats

Rope Width	4 mm		6 mm		8 mm	
Rat Species	Ship	Norway	Ship	Norway	Ship	Norway
No. of crossings	3	8	6	1	294	98
Av. traverse time	4.3	24.0	5.3	11.0	2.9	7.8
SE	0.30	2.80	1.10	0.00	0.04	0.60
t value	4.15		-		13.23	
p value	0.0024		-		<0.0000	

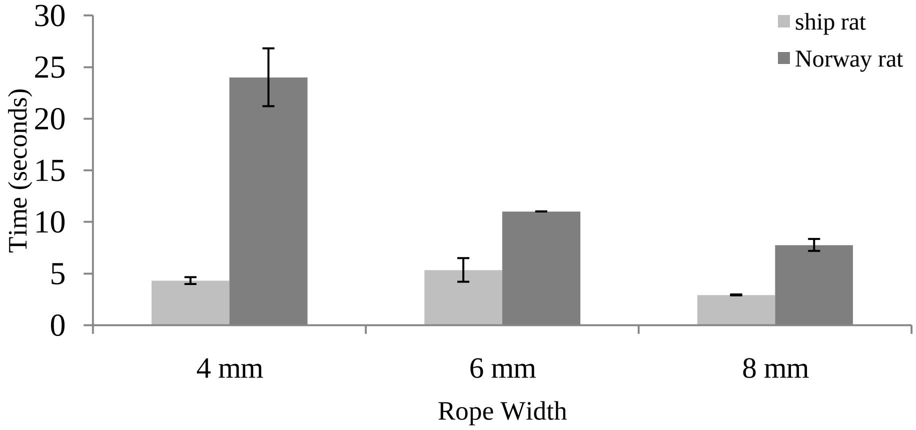

Figure 3. Average time (seconds) for each species to traverse the ropes

Climbing up and down the stands

Ship rats were significantly faster than Norway rats in climbing up and down all the heights. P values for all the differences in average times shown in Table 2, Table 3 and Figure 4 were less than 0.05.

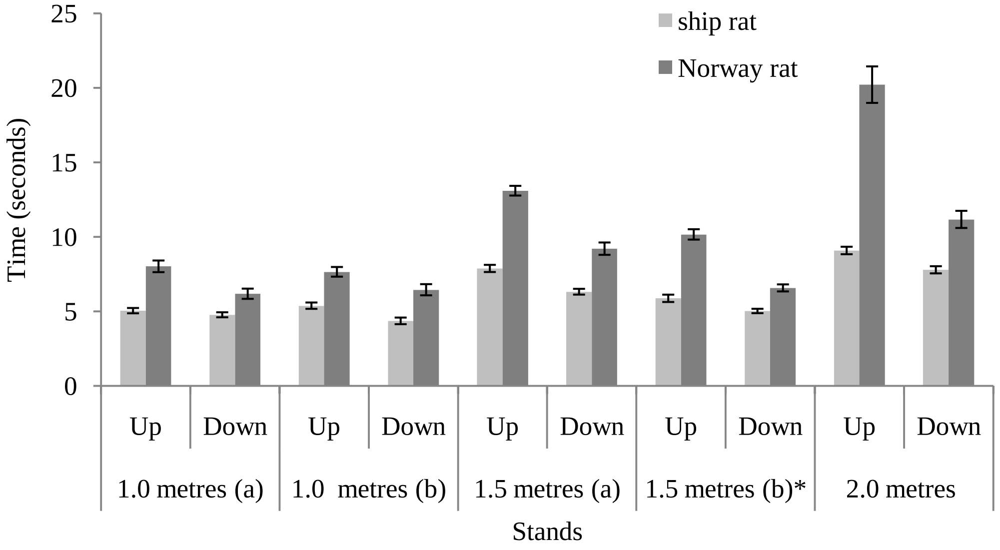

Figure 4. Average time (seconds) for each species to climb up and down all the stands in the artificial forest. The * indicates the 1.5 metre stand with no nails

The average frequency of climbing up and down stands of each height during one night was calculated (Table 4, Table 5, and Figure 5). The only significant difference between species was in the number of times they climbed up the 2.0 metre stand (P value < 0.05). Ship rats on average climbed up the 2.0 metre stand 13.8 times, while Norway rats on average only climbed it 3.0 times (Table 4, Figure 5).

Table 2. Average climbing speeds up the various stand heights for captive wild ship rats and Norway rats in the artificial forest. The * indicates the stand with no nails

Stand	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Rat Species	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway
Total no. of crossings	63	41	42	36	92	163	128	80	151	33
Av. time (seconds)	5.05	8.02	5.38	7.65	7.88	13.10	5.88	10.16	9.09	20.22
SE	0.18	0.39	0.21	0.32	0.24	0.33	0.25	0.35	0.25	1.23
t value	6.93		5.85		12.90		10.05		8.90	
p value	<0.000		<0.000		<0.000		<0.000		<0.000	

Table 3. Average climbing speeds going down the various stand heights for captive wild ship rats and Norway rats in the artificial forest. The * indicates the stand with no nails

Stand	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Rat Species	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway
Total no. of crossings	52	39	36	33	135	97	117	77	125	42
Av. time (seconds)	4.77	6.18	4.36	6.45	6.32	9.21	5.03	6.57	7.79	11.17
SE	0.18	0.34	0.22	0.37	0.19	0.41	0.15	0.24	0.24	0.58
t value	3.70		4.80		6.32		5.58		5.42	
p value	<0.000		<0.000		<0.000		<0.000		<0.000	

Table 4. Average frequency of climbing up the various stand heights for one night, for captive wild ship rats and Norway rats in the artificial forest. The * indicates the stand with no nails

Stand	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Rat Species	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway
Av. freq. for one night	5.9	3.27	3.82	3.27	7.82	14.82	10.18	7.27	13.82	3.00
SE	2.06	1.29	1.17	0.82	1.94	4.07	2.75	1.74	3.52	0.87
t value	1.08		0.38		1.55		0.89		2.98	
p value	0.29		0.71		0.14		0.38		0.007	

Table 5. Average frequency of climbing down the various stand heights for one night, for captive wild ship rats and Norway rats in the artificial forest. The * indicates the stand with no nails

Stand	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Rat Species	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway
Av. freq. for one night	4.91	3.09	3.27	3.09	10.64	8.82	9.82	7.00	9.55	3.82
SE	0.99	1.31	1.04	0.80	2.72	2.38	2.53	1.66	3.35	1.08
t value	1.11		0.14		0.50		0.93		1.63	
p value	0.28		0.89		0.62		0.36		0.12	

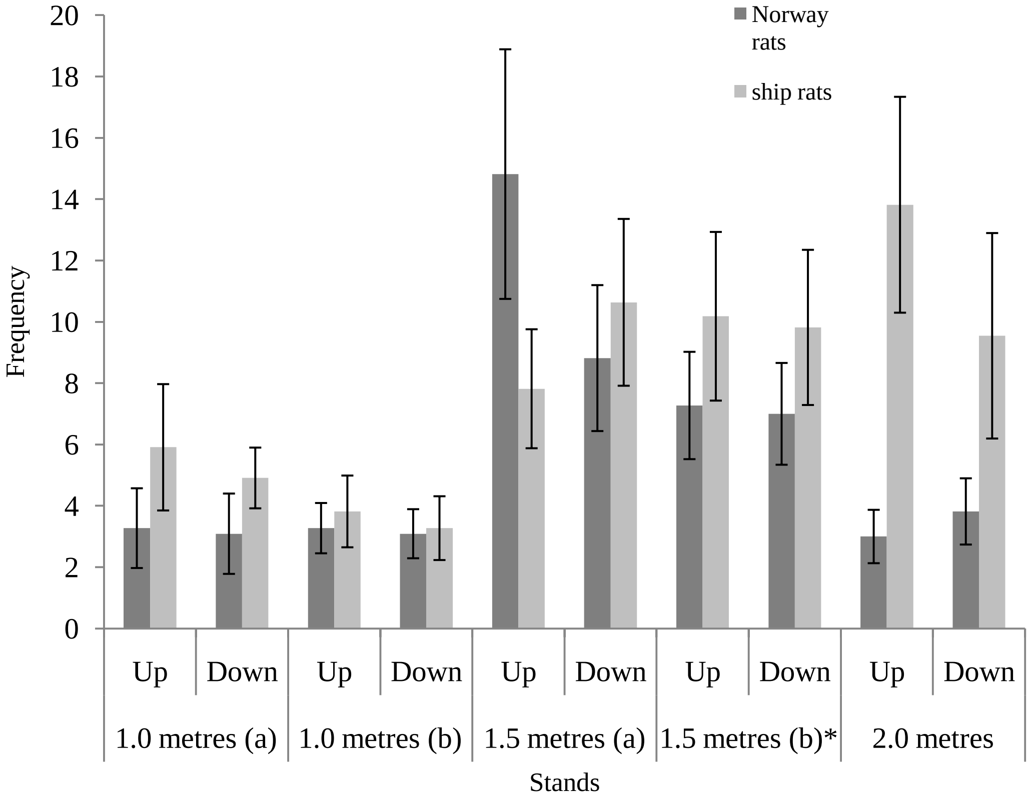

Figure 5. Average frequency with which captive wild Norway and ship rats climbed up and down the various stand heights throughout the night, in the artificial forest. The * indicates the stand with no nails

Time spent on the ground versus the stands

Records of activity in the artificial forest were split into two areas: (1) on the ground, either in the nest box or out on the floor, and (2) climbing the stands or spending time sitting on top of the stands. Ship rats spent significantly more time on average (24.1%) on the stands above ground level than the Norway rats did (9.2%) (t=3.59; P=0.001). Norway rats spent significantly more time on the ground on average (90.8%) than ship rats did (75.9%), (t=-3.59; p=0.001) (Table 6, Figure 6).

Table 6. Average percentage of time captive wild ship rats and Norway rats spent on the ground versus the stands in the artificial forest

	Ground		Stand	
Rat Species	Ship	Norway	Ship	Norway
Av. % of time spent	75.88	90.78	24.14	9.22
SE	2.96	2.92	2.96	2.92
t value	3.59		3.59	
p value	0.001		0.001	

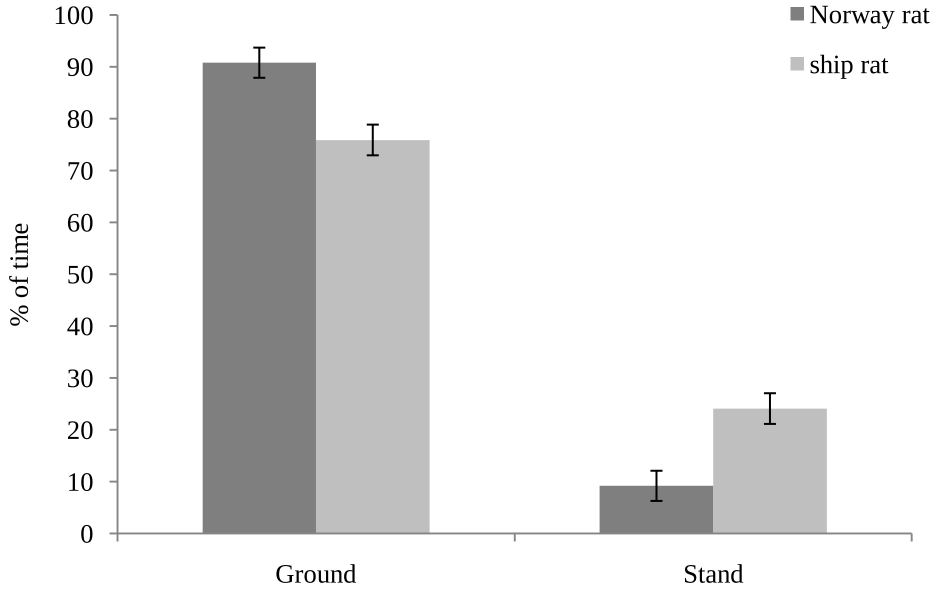

Figure 6. Average percentage of time captive wild ship rats and Norway rats spent on the ground versus the stands, in the artificial forest

Time taken to attempt the first obstacle

Ship rats were much quicker to explore attempting the first obstacle on average 39.7 minutes after sunset, while Norway rats attempted the first obstacle, on average 97.1 minutes after sunset (Figure 7; t=2.48, p= 0.022). The video footage showed that the majority of ship rats attempted the first obstacle straight after leaving the nest box, while the majority of Norway rats spent some time exploring the ground before attempting any obstacles.

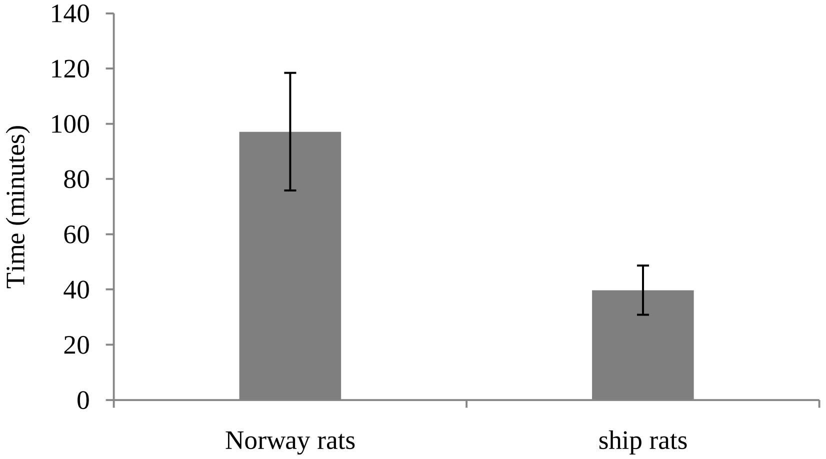

Figure 7. Average time after sunset before the first obstacle was attempted by wild captive Norway rats and ship rats in the artificial forest

Crossing the bamboo pole

Ship rats crossed the bamboo pole quicker than Norway rats (7.4 seconds compared with 11.6 seconds; Figure 8), but not much more often (25 versus 22). This difference in time was significant (t=-2.91, p=0.005).

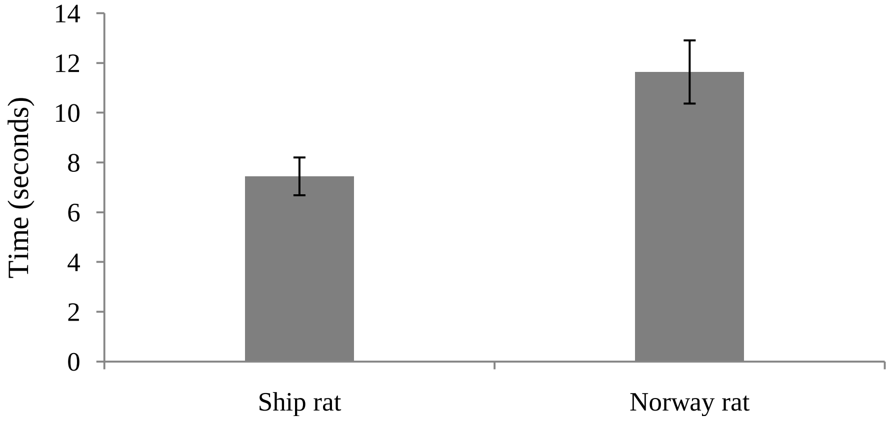

Figure 8. Average time for wild captive ship rats and Norway rats to cross the bamboo pole in the artificial forest

DISCUSSION

The ship rat is known to be extremely agile (Innes 2005b) and this could give them a competitive advantage when utilising above-ground resources in native forest in New Zealand, such as fruit and birds' nests on the ends of thin branches. The Norway rat is usually described as primarily ground-dwelling (Innes 2005a), which could be a disadvantage in this type of habitat. The work in this chapter aimed to test the null hypothesis that there are no significant differences between the two species in the efficiency with which they can access above-ground forest resources.

The results, as expected, failed to support the null hypothesis. Ship rats were significantly faster at crossing the 4mm and 8mm wide ropes strung between the stands. They also were significantly faster than Norway rats climbing up and down each of the stands in the artificial forest. I conclude that ship rats are significantly better adapted to climbing than are Norway rats. It is also interesting to note that ship rats were able to climb up the 1.5 metre stand with no nails faster, on average, than the 1.5 metre stand with nails. A study by Yabe *et al.* (1998) supports this conclusion. They conducted a histological study of the paw pad lamellae of the *Rattus* species. They found the paw pads of the Norway rat had a thin corneous layer, shallow lamellar pits and broad lamellae which are common in digging animals, while the ship rat paws had a thick corneous layer, steep lamellar pits and narrow lamellae which are consistent with a climbing animal.

The longer tail of the ship rat may improve the balance of the rats as they are crossing branches. It was observed on the video footage that the tails of the ship rats were flicking around as they were traversing the ropes and bamboo pole; however Norway rats tails did not seem to be making the same movement patterns. Mares and Lacher (1987) observed that in many arboreal mammals, the tail is elongated which seems to help with arboreal type behaviours. This pattern has also been observed in squirrels. Arboreal non gliding forms tend to have the longest tails, followed by the gliding forms, and lastly ground dwelling forms that tend to have the shortest tails (Essner. Jr 2002).

Norway rats have much larger body weights than ship rats, so subsequently it takes more effort and is expensive in energy to climb. The food gained from climbing may not be as profitable for Norway rats as it is for ship rats. Persson (1985) argues that smaller animals will have the advantage in exploitation competition due to their lower absolute food requirements, than larger animals. In New Zealand, Norway rats may be at a disadvantage in the forest as some of the food available (arthropods and seeds) are small and hard to find, which makes it more energetically demanding for Norway rats, to find them, compared with the smaller rat species (Harper 2006).

However, that does not mean Norway rats cannot climb. In contrast to published accounts, the Norway rats used in this experiment were quite capable of climbing when they chose to do so. All 11 used in this experiment climbed the majority of the stands in the artificial forest, even though they were much slower than ship rats and some looked quite awkward. Likewise, the two Norway rats observed by Mellgren *et al.* (1984) in an experiment on optimal foraging theory and travel requirements, climbed to all the platforms presented to them (platforms that varied from 30 cm to 2.1 metres above the ground supporting various densities of prey). Both of the Norway rats used by Mellgren *et al.* (1984) were climbing higher than the Norway rats in the pens in this study.

Huck and Price (1976) looked at the effect of the post-weaning environment on the climbing behaviour of wild and domestic Norway rats. They observed that wild Norway rats climbed the test apparatus, even after being denied early climbing experiences, while domestic Norway rats only climbed if exposed to early climbing experiences. The authors concluded that these results may have been due to three reasons: (1) the domestic Norway rats were larger so climbing was more difficult for them, (2) the wild and domestic Norway rats may have been responding differently to a novel environment, and (3) differences in the advantage of being able to climb in the field versus the laboratory may have affected their behaviour.

Creel (1913) compared the climbing ability of Norway rats, ship rats and the alexandrines form of the ship rat, and concluded that the Norway rat was capable of climbing the same obstacles as the other two species. Lastly, Hill *et al.* (1983) recorded Norway rats climbing a blackberry bush to eat fruit, to at least 3 metres above the ground.

Tests in captivity do not necessarily show what wild animals do when not in captivity, so it remains unclear whether Norway rats climb in the wild as well as our captive ones. Some previous studies suggest they do not. Lovegrove (1996) compared the survival of the Saddleback *(Philesturnus carunculatus)* on three New Zealand offshore islands. On Kapiti Island, Norway rats and Kiore were present. Nests less than one metre above the ground were destroyed significantly more often than nests above one metre, while on Cuvier and Little Barrier Island, which only had Kiore present, nests at all heights were equally vulnerable. This difference is a characteristic signal of the damage done by ground dwelling Norway rats.

Lovegrove (1992) also looked at predation on the saddleback and the implications for the management of this species. In one experiment, artificial nest boxes were constructed 1.5 metres above the ground on a smooth vertical surface, assuming that ground-foraging Norway rats could not access these nest boxes. Birds which nested in the boxes had a much higher chance of surviving than those which did not use them. These studies suggest that Norway rats generally do not climb in the wild, but are not conclusive.

Greater utilisation of the artificial forest by ship rats was also shown in the amount of time each species spent on the stands versus on the ground. Ship rats spent significantly more time above the ground, on the stands, whereas Norway rats spent significantly more time on the ground. Likewise, Key and Woods (1996) tracked individuals of both species, in sites of sympatry and allopatry, in the Galapagos Islands. They used the spool-and-line method to determine the amount of time each species spent in the forest canopy. They found that Norway rats rarely climbed, and more often moved along the cracks of lava rocks and under rocks, while ship rats spent significantly more time in the canopy.

A study by Hooker and Innes (1995) found similar results in New Zealand forest. Ship rats were radio tracked in the Pongakawa Ecological Area of Rotoehu Forest, New Zealand. Hooker and Innes (1995) found 26% of all fixes were in vegetation of the 0-2 metre height class, 56% in the 2-8 metre height class and 18% in the over 8 metre height class. Rat day nest sites were found, all above ground level, especially in epiphytes and tree hollows. Rats were observed, running along supplejack vines and climbing up and down trees.

Perry *et al.* (2009) found that ship rats in the Orongorongo Valley near Wellington, in mixed beech-podocarp-broadleaf forest, spent more time in the subcanopy and canopy than on the ground (87% of fixes recorded there). By contrast, Dowding and Murphy (1994) found ship rats more often on the ground, in Kauri forest, Northland. They reasoned that this may have been due to (1) the sub canopy layer of the forest being relatively open and sparse, or (2) that the food source being harvested by the rats at the time may have been on the forest floor.

There are always limitations to the results gained from captive-based trials. Possibly the reason why Norway rats climbed during this trial was that it was a unique and novel environment, or because the effort of climbing is worth making only when there is very little food at ground level, as in a bare concrete pen. Results from any trials involving wild caught animals need confirmation in a more natural setting. However captive based trials are useful to test hypotheses before implementing the same test in a large scale experiment in the wild.

Exploitation competition for food resources in the forest environment between these two species still needs to be confirmed. Petren and Case (1996) defined five factors which must be established before this interaction can be concluded as happening: (1) the two species must share a limiting resource, (2) the reproduction and survivorship of the species must be limited by the availability of the shared resource, (3) one species must negatively affect the other species acquisition of this resource, (4) decreased resource acquisition by the inferior species must cause a change in distribution or abundance, and (5) interference type behaviours must be ruled out during interactions.

CONCLUSION

Tests on captive wild caught rats showed that ship rats were much more efficient at utilising above-ground resources in an artificial forest habitat in New Zealand, by being more efficient at accessing the artificial above-ground structure. This might give them a competitive advantage, in native forest, in New Zealand, resulting in the displacement of Norway rats. However, the result that Norway rats can climb in captivity, needs to be re-examined in natural habitats, in the wild.

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CHAPTER THREE

Interference competition between *Rattus norvegicus* and *R. rattus*

ABSTRACT

Interference competition has been proposed as one of two interacting mechanisms governing the current distribution of Norway and ship rats in New Zealand. Ship rats are the most abundant species in native forest, while Norway rats are largely restricted to riparian habitats, wharves, rubbish tips and farm buildings. However in countries such as Britain and USA, the situation is reversed and Norway rats are more abundant, than ship rat in most habitats.

The aim of this phase of work was to gather evidence from wild rats in captivity that may help understand the likely outcome of interference competition, should it

occur in the wild. Firstly, inter - and intra - specific staged encounters were carried out in a tank with a partition in the middle, and the rats' responses to each other recorded, on camera, and secondly, the structural conditions found in New Zealand native forest were simulated by placing individual rats in aviary style pens, with stands supporting food rewards at various heights, and ropes of various widths linking the stands together. The scent of the opposite species was supplied either indirectly, by contamination of the food containers, or directly, by placing a live caged individual on the ground underneath one of the stands. The subject rat's activities were recorded remotely for approximately 12 hours during the night.

Ship rats tended to be more disturbed by the presence of a Norway rat or the scent of a Norway rat, than Norway rats were to the presence of a ship rat, but few results from the artificial forest experiments were significant.

During the staged encounters, two (of 12) Norway rats exhibited aggressive behaviour towards ship rats, while none of the ten ship rats exhibited aggressive behaviour towards Norway rats. The Norway's' aggressive behaviour appeared to be ignored by the ship rats, at least while they were protected by the partition. Ship rats were much more social towards other ship rats, than Norway rats were to other Norway rats.

Further testing of these reactions, with larger sample sizes is needed to get a clearer idea of the relationship between these two species.

INTRODUCTION

Interspecific competition is observed when "individuals of one species suffer a reduction in fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of another species" (Begon *et al.* 1996 p. 265). Previous studies on interspecific competition have shown that it can have an impact on the habitat use, and relative population sizes of sympatric species (Eccard and Ylonen 2003). Interspecific competition commonly takes one of two forms, depending on how the common resource is distributed.

Exploitation competition is observed when one species is better than another, at harvesting a given type of resource. This is an indirect interaction, and arises only if the resource is in limited supply (Harris and Macdonald 2007). Interference competition is observed when one species is physically preventing another from accessing a resource, either through territory defence or aggressive encounters, whether the dominant species is using the resource or not (Keddy 1989; Smith & Smith 2001; Harris and Macdonald 2007). The dominant species in these interactions tends to be the larger of the two (Morse 1980; Persson 1985). After this interaction, the dominant species will be able to monopolise more resources, which will support greater growth for the dominant, increase resource acquisition and cause further damage to the subordinate species (Keddy 1989). Interference competition is generally easier to detect than exploitation competition because the interactions are directly observable (Petren and Case 1996).

Ziv *et al.* (1993) conducted an enclosure study to explain the mechanism of interspecific competition between two gerbil species *Gerbillus allenbyi* and *G. pyramidum*. In the enclosures with no *G. pyramidum, G. allenbyi* preferred to forage in the early part of the night, but in the enclosures where *G. pyramidum* was present, *G. allenbyi* was foraging during the second half of the night. *G. pyramidum* also excluded *G. allenbyi* from the preferred habitat, the semi stabilised dune habitat. The authors concluded that interference behaviour from *G.*

pyramidum is the mechanism behind the interspecific competition between these two species.

The Norway rat *R. norvegicus* was transported to New Zealand from about 1770 with the early European explorers, and with early settlers up to about 1865. After about 1865, the ship rat *R. rattus* arrived with the later European settlers, and soon spread right throughout the country. During this time the previously widespread Norway rat became restricted in distribution (Moors 1985; Yom-Tov *et al.* 1999; Harper *et al.* 2005; Innes 2005a; Innes 2005b). The Norway rat is the largest of the three rats in New Zealand, with weights averaging 200-300 grams, while ship rat weights average 120-160 grams (Atkinson and Towns 2005).

Currently, ship rats are found throughout New Zealand, inhabiting a wide range of forest types (Atkinson 1973; Taylor 1978b). They are most abundant in diverse, mature, lowland podocarp-broadleaf forests, from the coast to the tree line, but not in the alpine tussock (Innes 2005b). By contrast, Norway rats are largely confined to farm buildings, riparian sites, coastlines, rubbish tips, and wharves (Atkinson 1973; Taylor 1978b; Innes 2005a).

Norway rats tends to be ground-dwelling and are rarely seen climbing above 3 metres. They are also known for their burrowing and swimming abilities (Atkinson 1973; Thorsen *et al.* 2000), while ship rats are primarily arboreal and spend most of the time in the forest canopy, occasionally coming down to the forest floor to forage (Atkinson 1973; Hooker and Innes 1995; Lindsey *et al.* 1999). Perry *et al.* (2009) found that ship rats in the Orongorongo Valley near Wellington, in mixed beech-podocarp-broadleaf forest, spent more time in the subcanopy and canopy than on the ground (87% of radio fixes recorded there). Norway rats are known predators of ground dwelling birds, while ship rats have a serious impact on perching birds (Atkinson 1973; Thorsen *et al.* 2000).

A prediction from competition theory is that one species will be displaced from a habitat when an ecologically similar species arrives (Begon *et al.* 1996), and this seems to have happened to Norway rats, when ship rats arrived in New Zealand. In contrast, ship rats were the displaced species, when Norway rats arrived in Britain and the USA (Ecke 1954; Taylor 1978a; Innes 2001).

This situation is further complicated by the introduction of mustelids at approximately the same time as ship rats were spreading throughout New Zealand (Atkson 1973). Taylor (1978b; 1984) proposed that predation by mustelids was the reason why Norway rats are excluded from lowland podocarp forest, and the observed distribution of Norway rats is where they can seek refuges from this predation. However this idea needs further testing.

My hypothesis is that the two species have different advantages in a constantly shifting balance between exploitation competition, and interference competition, which governs their current distribution in New Zealand. Previous literature suggests that ship rats are more agile (Atkinson 1973; Brooks and Rowe 1979) so are expected to be superior in exploitation competition, especially in native forest, while Norway rats are larger, and more aggressive (Atkinson 1973; Dzhemukhadze 2007) so are expected to be superior in interference competition, when the two species encounter each other on the ground.

My first experiment (Chapter Two) suggests that ship rats may have advantages in exploitation competition compared to Norway rats, especially in forests when resources are above the ground, at the end of thin branches, and are limited in quantity. The aim of the second experiment described in this chapter was to test the reverse side of my hypothesis that gives the advantage to Norway rats during face to face encounters and regardless of resources (interference competition).

The larger size and aggressive nature of Norway rats is assumed to give them superiority during interactions on the ground, which led me to predict that (1) if interference competition affects the behaviour of the two species, the ship rat will exhibit submissive behaviour during encounters with Norway rats, while Norway rats will display aggressive behaviour towards ship rats, (2) the behaviour of a ship rat will be more strongly affected by the presence of a Norway rat than will the behaviour of a Norway rat, in the presence of a ship rat.

METHODS

Trapping

Representatives of both species were trapped in the wild. The ship rats were trapped in the Waikato district in a large garden on the outskirts of Hamilton and at the waterworks reserve in the Te Miro district. The Norway rats were trapped in the Waikato and Rotorua regions, at sites which included a privately operated piggery, bush next to a stream and at a factory adjacent to an effluent pond. Cage traps baited with peanut butter and carrot were checked every day. Captured rats were transported back to the university animal house facilities, where they were sexed and weighed. They were placed in individual cages and left undisturbed for 2 weeks to habituate to captivity.

Husbandry

Individual home cages were approximately 1m x 1m x 1m, with a mesh ground floor and a shelf they could sit on. The rats were fed every second day, a mixture of standard rat pellets plus carrot, and apple, and water *ad lib*. They were provided with a nest tube containing nesting material such as hay and newspaper. Rats of the two species were kept in separate rooms with a 12 hour light dark cycle. The room temperature ranged between 14 and 21°C.

Staged Encounters

A total of 12 Norway rats (6 female and 6 male) and 10 ship rats (5 female and 5 male) were available for this experiment. The average weight of the male Norway rats was 254 grams, and 243.5 grams for the females, while the male ship rat’s average weight was 134.6 grams and 132.2 grams for the females. An old fish tank (80cm x 30 cm x 50 cm), was modified as an encounter arena, by adding a clear perspex divider, in the middle, to prevent the rats from making contact. A lid was built with two sliding doors to get the rats in and out. Water and sawdust were placed in the tank during the trials (Figure 1).

Figure 1. The tank used for the staged encounters, with the video camera that recorded all events (S Foster)

One encounter ran for 90 minutes; the first 30 minutes was the habituation period, when the rats could not see each other, followed by 60 minutes when the rats could interact through the partition. All trials were carried out at night and each rat was placed in the tank only once per night. In total, eight types of inter – and intra – specific encounters were completed, two replicates per paired combination (Table 1). Each individual rat was used for a maximum of two trials. Animals fitting the predetermined criteria were picked at random to participate in each encounter.

Table 1. The eight different paired combinations used for the staged encounters between captive wild ship rats and Norway rats

Intraspecific	Interspecific
Norway rat male/ Norway rat male	Ship rat male/ Norway rat male
Norway rat female/ Norway rat female	Ship rat male/ Norway rat female
Ship rat male/ ship rat male	Ship rat female/ Norway rat female
Ship rat female/ ship rat female	Ship rat female/ Norway rat male

Artificial forest experiments

A total of 11 Norway rats (5 females and 6 males) and 12 ship rats (6 females and 6 males) were available for this experiment. The female Norway rats chosen weighed an average of 231 grams; the males 318 grams. Female ship rats weighed an average of 121 grams and the males 127 grams.

Two outdoor aviary style pens were used for these trials, one specifically for ship rats and one for Norway rats, each measuring 3.1 m x 4.0 m x 2.1 m. The pens had concrete floors, with wire mesh walls and ceilings.

Stands of three different heights were used (two 1.0 metre, two 1.5 metres and one 2.0 metres) to represent a range of low trees, in which rats might forage. At the top of each stand, a small platform was placed where the rat could sit, which also supported a container holding one gram of peanut butter. The rats also had access to standard rat pellets, carrot and water *ad lib*, on the ground next to the nest box, while they were in the enclosures.

Five stands were placed in each the pen, to represent an artificial forest (Figure 2). Because the planed timber supports were narrower, smoother and presumably harder to climb than real trees, footholds were provided for four of these stands by nails set 7cm apart up the stand.

Three different widths of rope (4mm, 6mm and 8mm) (Figure 3), were used to link the stands loosely to each other, to simulate the interlocking branches of trees. The ropes were all approximately 100 cm long. The artificial forest also had a 140 cm long horizontal swinging bamboo pole attached to the ceiling of the pen, along which the rats could run across the gap between the tops of the two 1.5 metre stands.

Infra red lighting enabled the cameras, linked to 12 hour time lapse video players, to record the activity of the rats every night from 5pm until 7am. Cameras were placed in the uppermost corner of the pen to ensure all the stands and the nest box could be seen. Thin aluminium sheets were placed on the sides of the pens from floor level to approximately 2.0 metres high to make it more difficult for the rats to climb the wire mesh and gain access to the cameras.

Each rat spent a total of 5 nights in the pen. They stayed in the pen the entire time, residing in the nest boxes during the day. The first night was the habituation night, and various treatments occupied the four other nights, all recorded (Table 2). Each morning, the food containers were collected from the tops of the stands, and any remaining peanut butter was weighed.


Figure 2. The artificial forest (S Foster)

Figure 3. The three widths of rope used (S Foster)

Deer scent was obtained from deer urine collected off a livestock truck. The food containers were rinsed with the urine and left to air dry before the peanut butter was placed in it. The rat scent was gathered by placing the food containers in the home cages of the required rat species for 48 hours. For condition three, a rat was placed in a small cage with nesting material and food, somewhere in the artificial forest, underneath one of the stands. The two scented food containers were randomly placed on two of the stands each treatment night, while the caged rat was randomly placed each night underneath one of the stands for the treatment night. This meant that the scent of the opposite species was above the ground, while an actual rat in a cage was on the ground, underneath one of the stands.

Table 2. The four conditions to which captive wild ship rats and Norway rats were exposed in the artificial forest

Condition	Description
1	Obstacles with no scent or other rat species present (Chapter one)
2	Obstacles with red deer scent (urine) present placed on the food containers, on two of the stands
3	Obstacles with the other rat species present
4	Obstacles with the scent of the other rat species placed on the food containers, on two of the stands

Once a rat had completed the five night experiment, it was removed from the pen and the pen mopped with hot soapy water to remove all traces of rat scent. All experiments were approved by the University of Waikato Animal Ethics committee, protocol number 741.

The information collected from the video footage included:

- Time taken to climb up and down the stands
- Frequency of climbing throughout the night
- Time taken to traverse the different thicknesses of rope
- Frequency of traversing the rope throughout the night
- The time until the first obstacle was completed from sunset, as Norway rats are mainly nocturnal and ship rats are nocturnal (Innes 2005a; Innes 2005b).
- Amount of time spent on the ground versus on the stands; this was done by selecting ten intervals of five minutes and noting the rat movements during that time period.

Data Analysis

Staged Encounters

The position of each rat in the tank and the behaviour being exhibited were noted once every minute. If an interaction was observed, the animal that began the interaction and the animal that ended the interaction were recorded. An interaction was defined as when both rats in the tank were looking at each other and carrying out similar behaviours directed to each other through the partition, or when one rat was actively trying to engage the other rat into an interaction. Behaviours seen are defined and described in detail (Table 3), and placed into three categories: baseline, exploring and interaction behaviours.

A Multivariate Analysis of Variance (MANOVA) was completed, in which the response variables were the percentage of time used for three main categories of behaviour (base, exploring and interaction behaviours) during the encounters, and the explanatory variables were the species and sex of the rat in question and the species and sex of the rat on the other side of the partition. Univariate tests were used to determine where any differences were coming from. These compared the mean time spent in activity for any given combination of rat species, with the mean time spent in that activity for the combination of rats of identical types. The Univariate test was a perturbatation simulation, with 10,000 simulations per test. Student t tests were carried out to compare the number of interactions begun and ended by rats of each species during the inter- and intra- specific encounters.

Artificial forest

Data from condition one (Chapter two) are used in this data analysis to compare with the other three conditions. Student t tests were carried out to see if there were any significant differences between conditions for each species, looking at:

- The time spent on the ground versus above the ground
- Frequency of climbing
- Time taken since sunset until the first obstacle was completed

Table 3. Classification of the behaviours exhibited by captive wild ship rats and Norway rats during the staged encounters

Baseline Behaviours	
Sleeping	The rat is in a still position and the eyes are shut
Sitting	The rat is sitting but the head is still occasionally moving
Drinking water	The rat is drinking water from the bowl in the tank
Grooming/Scratching	The rat is using either its teeth or its feet to groom and/or scratch itself
Exploring behaviours	
Stretching against the wall of the tank	The rat has its two back feet on the ground and the front two feet on the side of the tank, and the body is stretched up high
Sniffing the ground	The rat has its head down and sniffing the sawdust and/ or moving the sawdust around the tank
Jumping	The rat is jumping without touching the sides of the tank
Walking	The rat has all four feet on the ground and is walking around the tank
Interaction behaviours	
Aggression	The rat is crouched down on the ground, the hair on its neck is on end, the tail is moving from side to side, and the ears are laid back
On the divider	This can either be an interaction behaviour or exploring behaviour; this

	depends on when it is exhibited during the trial. The rat has its two back feet on the ground and the two front feet are resting on the divider; the body is either stretched high or bunched.
Sniffing the other rat	The rat has all four feet on the ground, its nose is pressed up to the divider and the other rat on the other side is doing the same.
Sniffing the divider	This can either be an interaction behaviour or exploring behaviour; this depends on when it is exhibited during the trial. The rat has all four feet on the ground but is close up to the divider and sniffing the divider.
Motionless	The rat has stopped a previous activity and frozen, no movement is observed.

RESULTS

Staged encounters

The total number of interactions per paired combination was plotted (Figure 4). Ship rat males paired with another ship rat male had the highest number of interactions at 131, while the lowest number was for Norway rat females versus another Norway rat female (only 2 interactions in total).

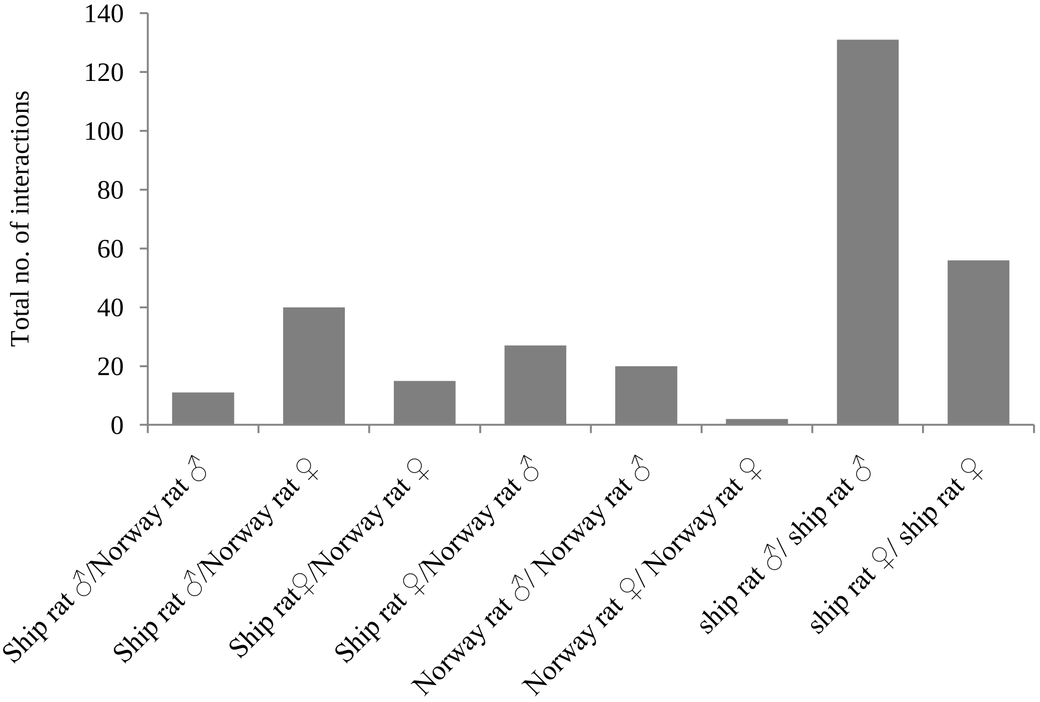


Figure 4. Total number of interactions exhibited through the partition between paired combinations of captive wild ship rats and Norway rats

An animal was observed beginning an interaction, if it was the first of the pair to position itself as close as possible to the other rat, as this was when the interaction began. The rat that ended an interaction was the one which moved away from the other rat, or starting a different behaviour unrelated to the interaction. Norway rats more often initiated interactions, while ship rats more often ended them (Figure 5).

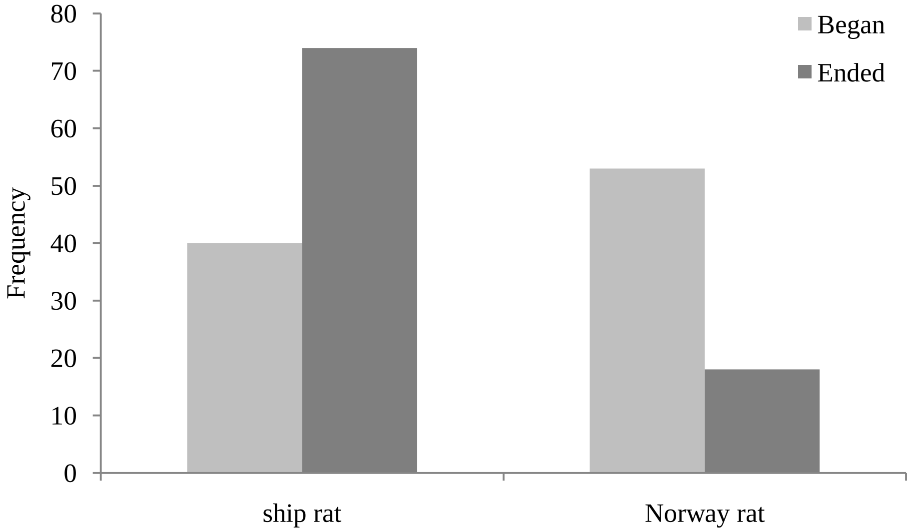


Figure 5. Total number of interactions began and ended by captive wild ship rats and Norway rats during paired staged encounters

Student t tests were used to check if either species behaved differently during four categories of interspecific versus intraspecific encounters. In three of the four categories, there were significant differences in the number of times each species began and ended interactions, according to whether the other rat belonged to its own species or not (Table 4).

Table 4. Student t test results examining possible differences between captive wild ship rats and Norway rats behaving differently in intra- and inter-specific paired staged encounters

	Began				Ended			
Rat Species Combination	Ship		Norway		Ship		Norway	
	inter	intra	inter	intra	inter	intra	inter	intra
Av.	5	23.3	6.6	2.7	9.2	23.1	2.2	2.7
SE	2.01	5.39	2.03	1.27	3.13	5.49	0.96	2.05
t value	3.68		2.44		2.75		0.21	
p value	0.007		0.04		0.02		0.84	

Student t tests were used to check for any differences between species in the number of times they began and ended interactions during interspecific and intraspecific encounters. Ship rat began significantly more interactions with their own species, than Norway rats did, as well as significantly ending more interactions both with other ship rats and with Norway rats. Both species were equally willing to begin interactions with the opposite species (Table 5).

Table 5. Student t test comparing the behaviour of captive wild ship rats and Norway rats reacting to each other during inter- and intra- specific paired encounters

	Began				Ended			
Combination	Inter		Intra		Inter		Intra	
Rat Species	Ship	Norway	Ship	Norway	Ship	Norway	Ship	Norway
Av.	5	6.6	23.3	2.7	9.2	2.2	23.1	2.7
SE	2.01	2.03	5.39	1.27	3.13	0.96	5.49	2.05
t value	1.52		4.25		2.7		3.51	
p value	0.17		0.003		0.03		0.009	

There was evidence that the behaviour of a rat depends on the combination of the species/sex of that rat and the species/sex of the rat on the other side of the partition. The multivariate analysis of variance (MANOVA) found differences significant at the 5% level between the reactions of a rat of a given sex and species and those of a rat of the opposite sex and species (P= 0.03395) (Table 6).

Table 6. Output from Multivariate Analysis of Variance (MANOVA) testing to see if the rat's behaviour is different according to the rat on the other side of the partition

	Df	Pillai	Approx F	num Df	den Df	Pr (>F)
Species Sex	3	0.57269	1.5729	9	60	0.14421
Opp Species Sex	3	0.3256	0.81165	9	60	0.60740
Species Sex: Opp Species Sex	5	0.9875	1.96275	15	60	0.03395*
Residuals	20					

Signif. Codes: 0'***' 0.001 '**' 0.01 '*' 0.05'.' 0.1 ' ' 1

Univariate tests were then carried out to compare the mean time spent in a given activity by one combination of opposite types of rats, compared with the time spent in that same activity by a combination for rats of identical types. Ship rat males spent significantly more time exhibiting base behaviour with Norway rat males, than with other ship rat males (P= 0.0436). Norway rat females exhibited base behaviour for a shorter amount of time when paired with ship rat males, than with other Norway rat females (P=0.0244), spent less time exploring in the presence of a ship rat male than other Norway rat females (P= 0.0401) and spent more time interacting with ship rat males, than with other Norway rat females (P= 0.0094).

The percentage of time each rat spent in the area on its own side of the partition was calculated for both interspecific and intraspecific encounters (Figure 6 and Figure 7). The results are quite variable, and only two encounters were set up for each paired combination. This criterion was not useful in determining which species is socially dominant.

Ship rats interacted more often with each other, than Norway rats did with each other (Figure 8 and 9). Baseline behaviours (Table 3) were always the most common behaviour recorded; by comparison, little time was spent on exploring, and interacting behaviours.

The four most common types of interaction behaviours observed during interspecific and intraspecific encounters, are shown as stacked bar graphs (Figure 10 and Figure 11). The only two rats to show aggressive behaviour were a male and a female Norway rat, both towards male ship rats. No aggressive behaviour was exhibited by rats of either species during the intraspecific encounters.

The interactive behaviour most often observed in both intraspecific and interspecific encounters was described as “on the divider”. The rats were either both up on their hind feet with their front feet at the top of the partition facing each other, or one was exhibiting that posture, trying to get the attention of the other rat.

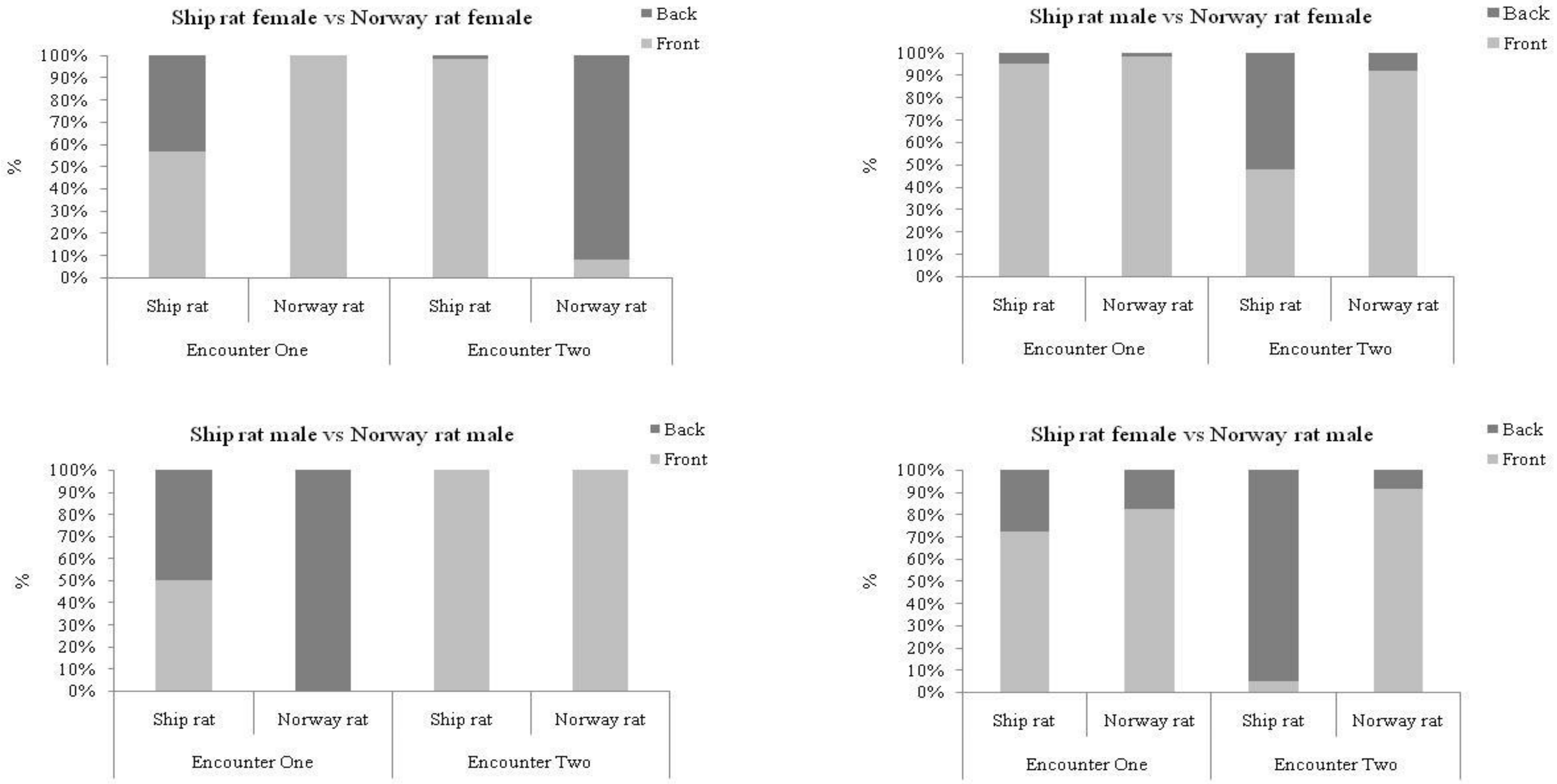
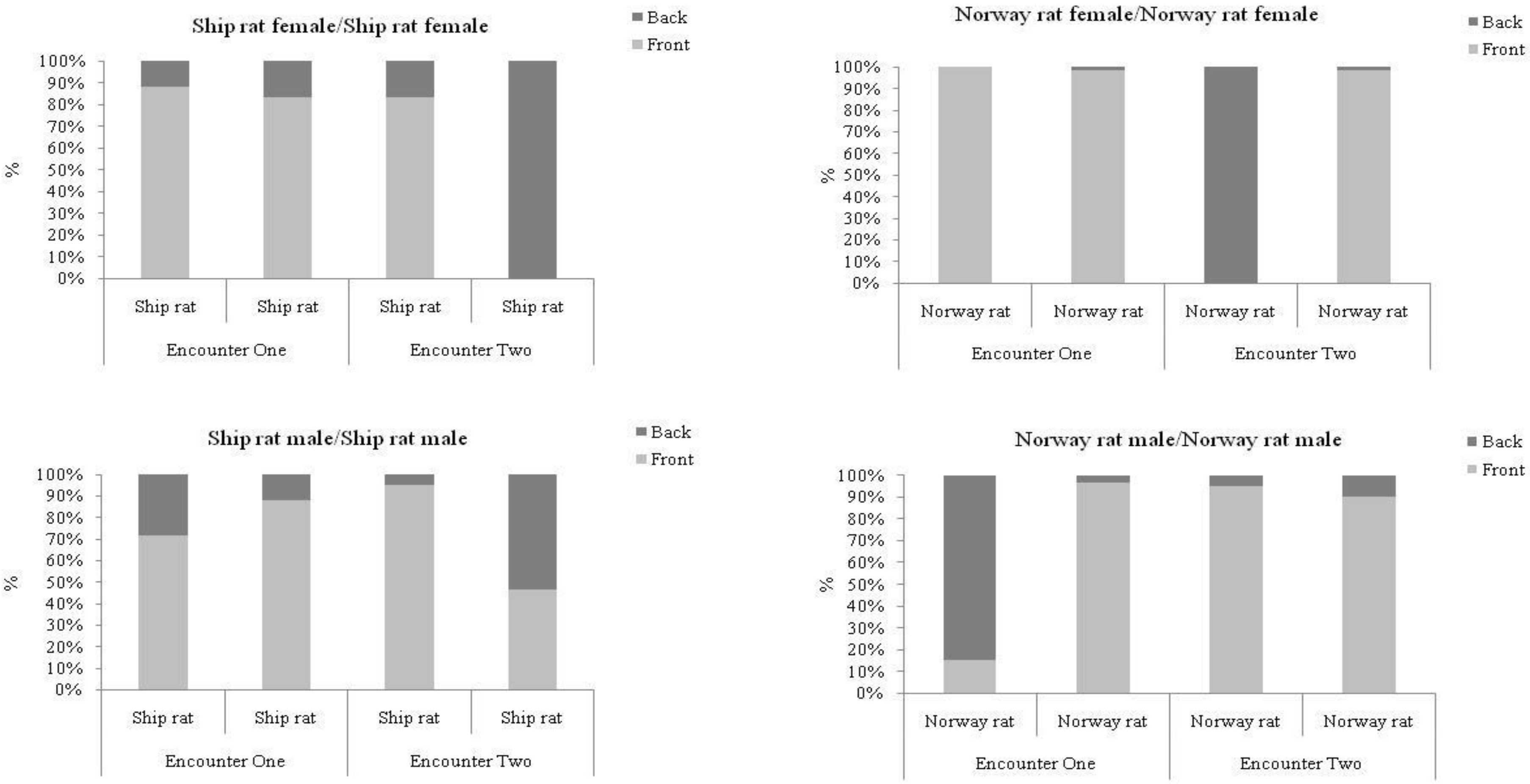


Figure 6. Percentage of time captive wild ship rats and Norway rats spent in the front and back of the tank during the interspecific encounters


Ship rat female/Ship rat female

Norway rat female/Norway rat female

Ship rat male/Ship rat male

Norway rat male/Norway rat male

Figure 7. Percentage of time captive wild ship rats and Norway rats spent in the front and back of the tank during the intraspecific encounters

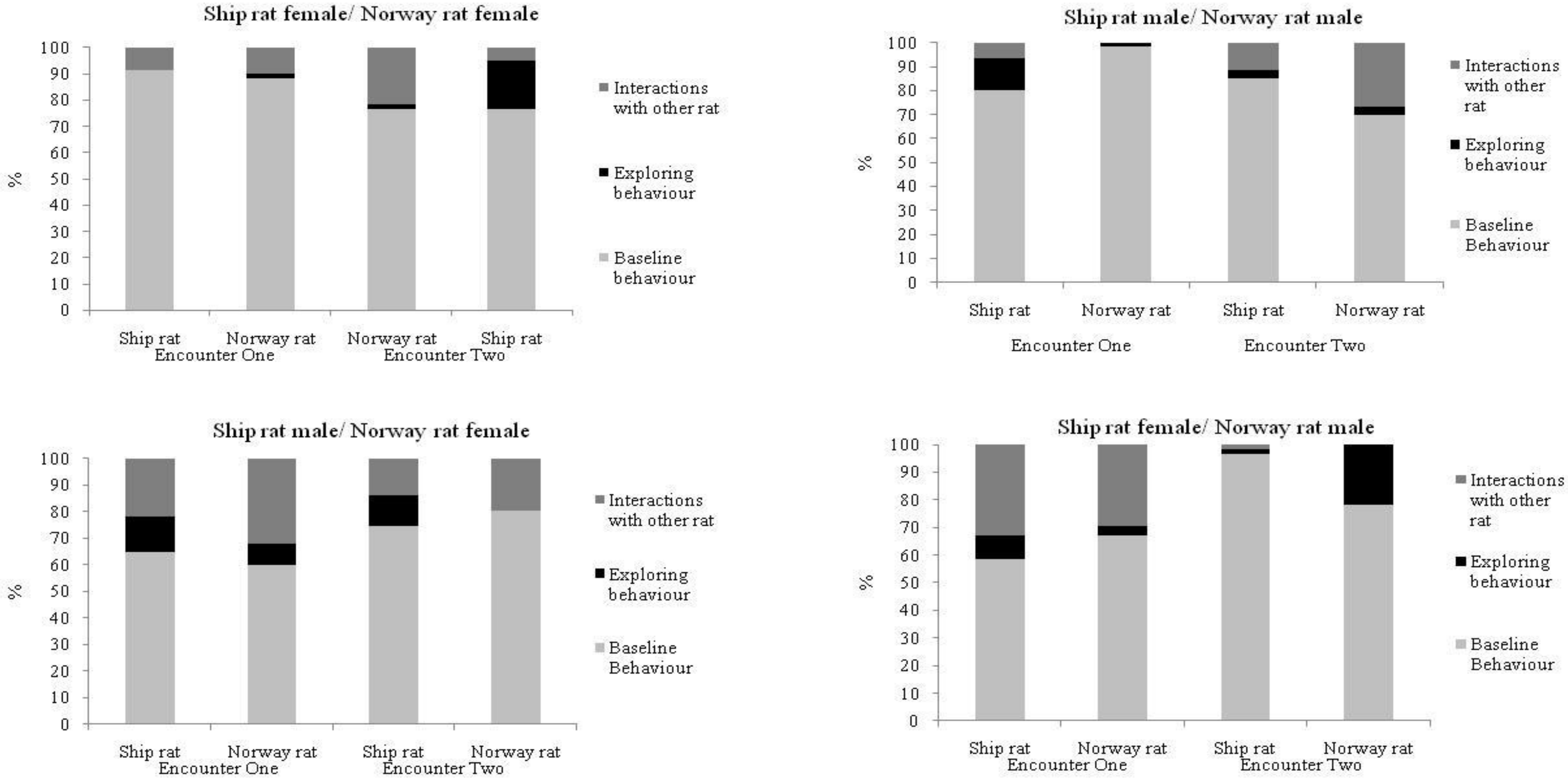


Figure 8. Percentage of time captive wild ship rats and Norway rats spent on the three main activities during the interspecific encounters

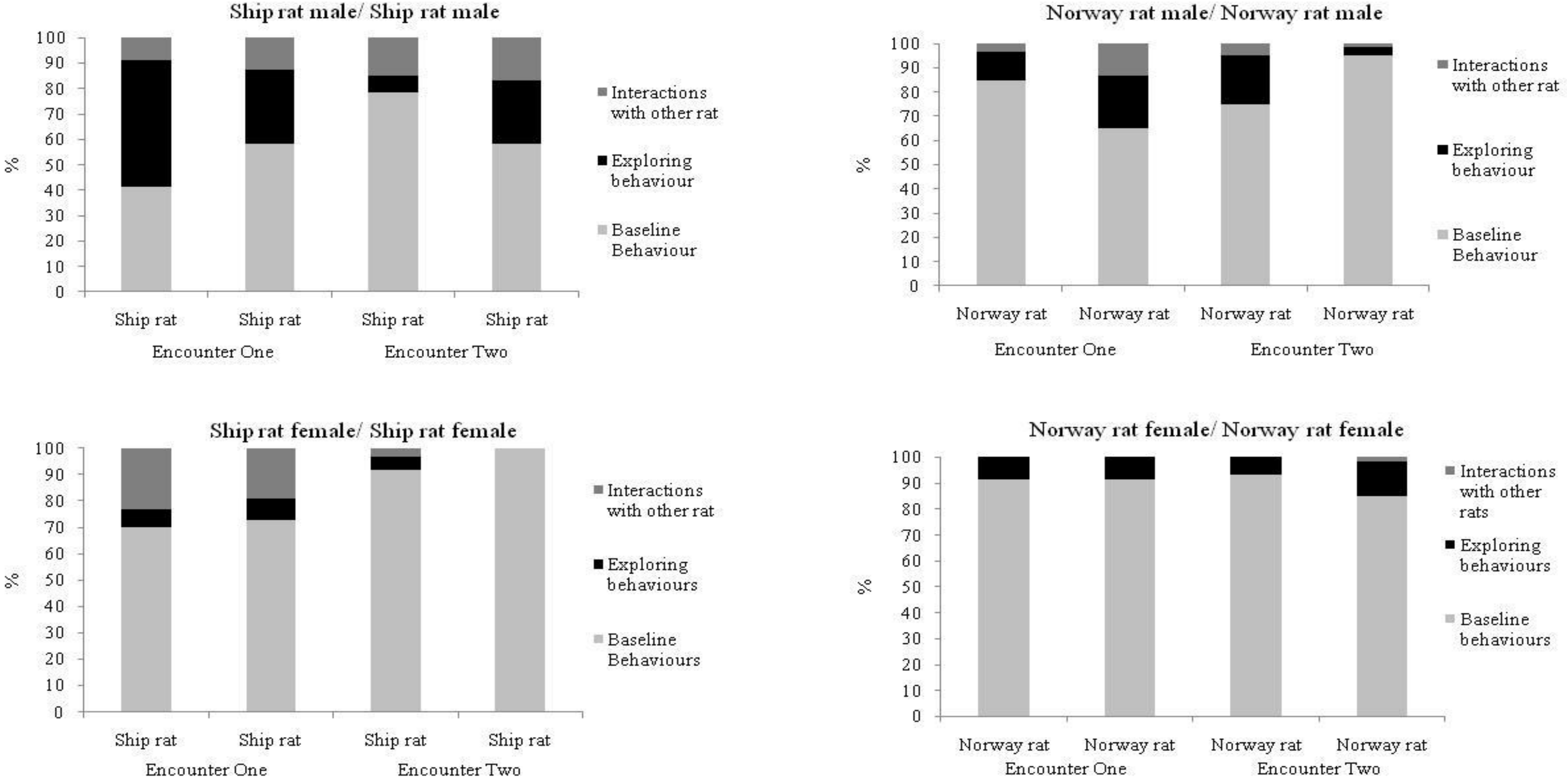


Figure 9. Percentage of time captive wild ship rats and Norway rats spent on the three main activities during the intraspecific encounters

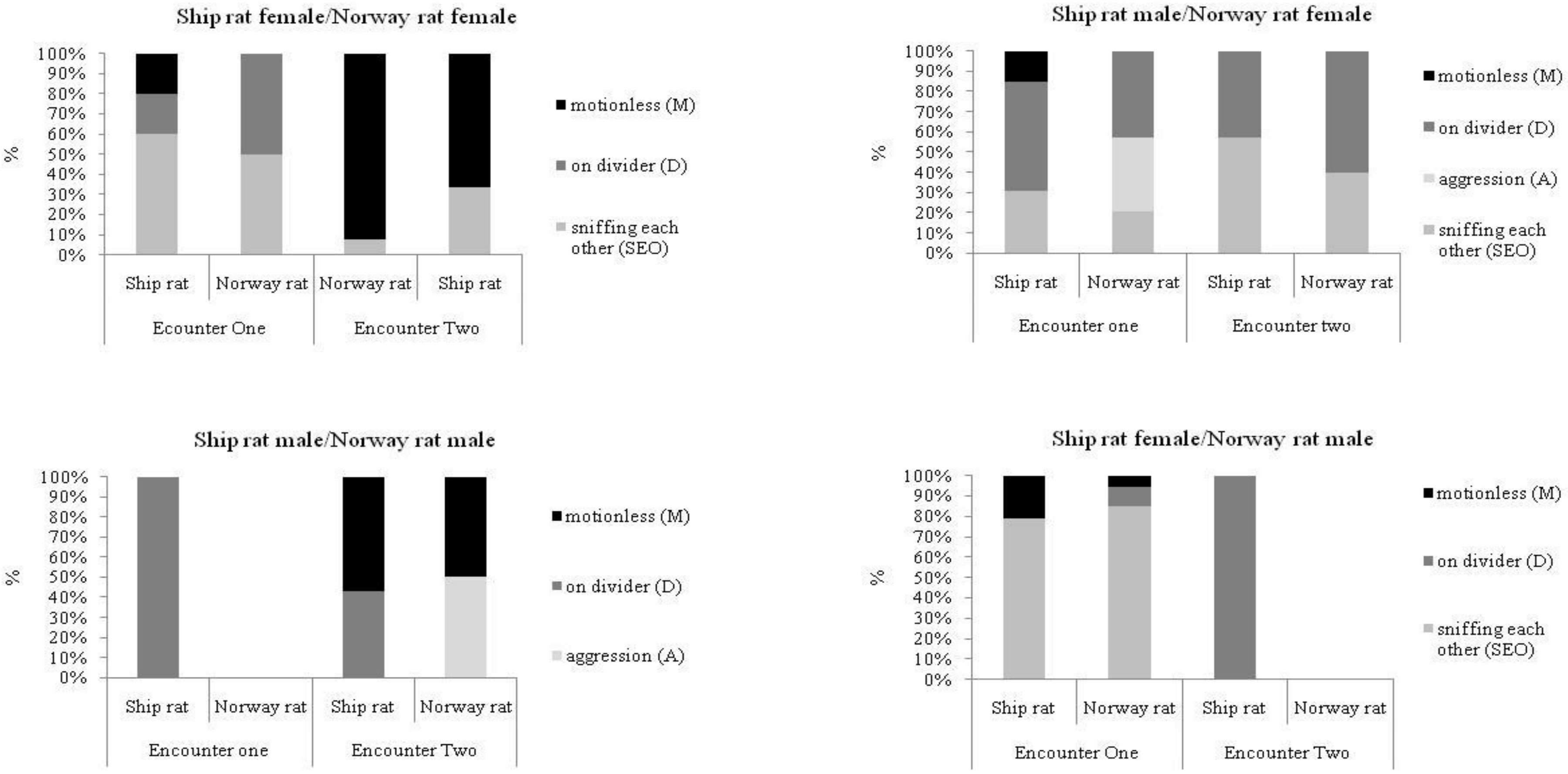


Figure 10. Interactive behaviours exhibited by the captive wild ship rats and Norway rats during the interspecific encounters

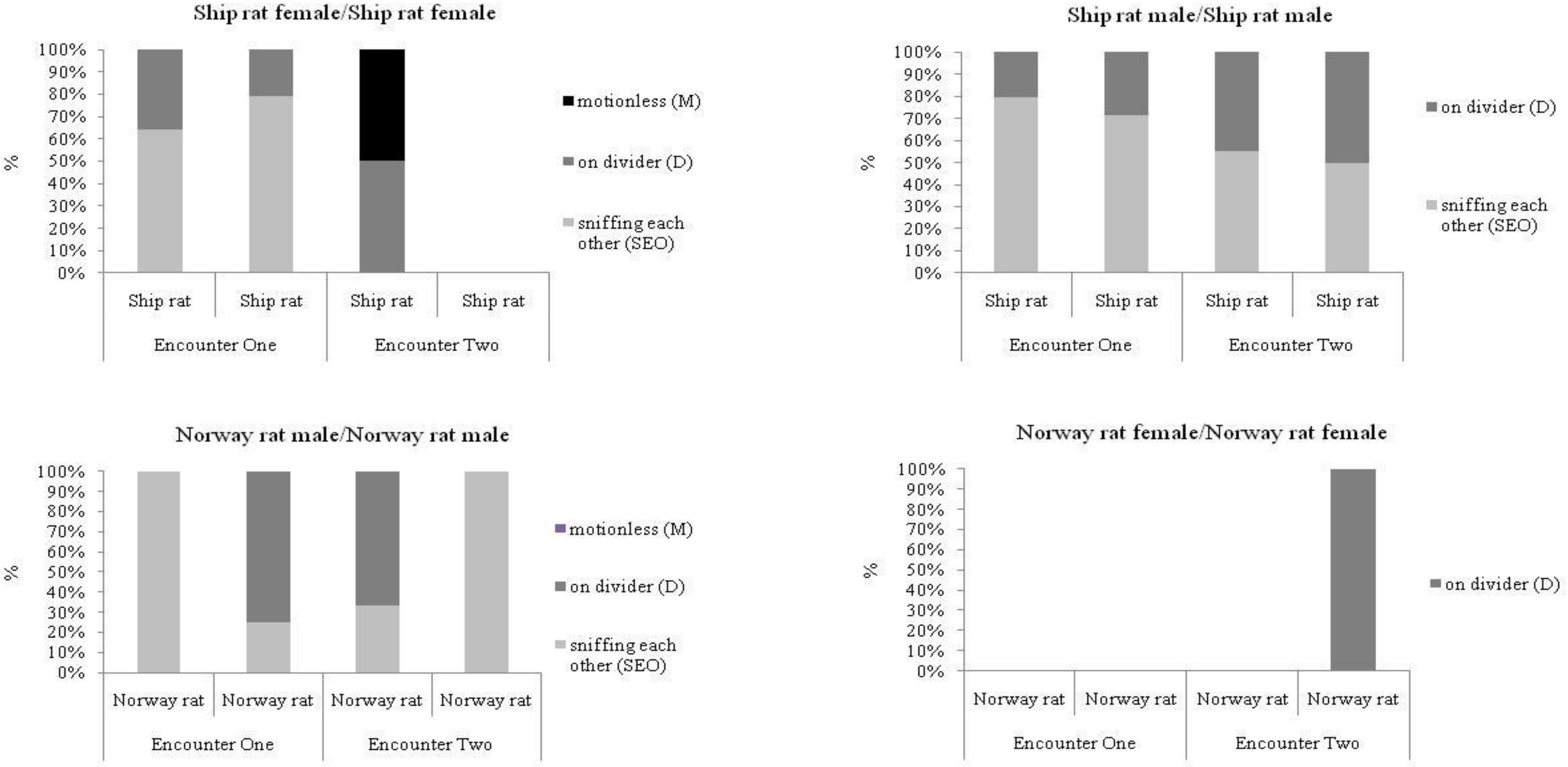


Figure 11. Interactive behaviours exhibited by the captive wild ship rats and Norway rats during the intraspecific encounters

Artificial forest experiments

Condition two (deer scent: Table 2) was not included in this analysis as there were no significant differences in results between conditions one (no scent) and two (red deer scent) in any aspect of behaviour examined.

Norway rats' reaction to ship rats in the artificial forest

Time spent on the ground versus the stands

No significant differences in results were detected in the time spent by the Norway rats on the ground versus up the stands, in the presence of a ship rat, or ship rat scent (condition three and four) (Table 7, Table 8 and Figure 12), compared to condition one (no ship rat).

Table 7. Average % of time spent on versus above the ground with no ship rat present and a ship rat present in the artificial forest for captive wild Norway rats

Condition	Ground 1	Ground 3	Stand 1	Stand 3
Av. % of time spent	90.8	91.4	9.2	8.6
SE	2.92	2.20	2.92	2.20
t value	0.16		0.16	
p value	0.87		0.87	

Table 8. Average % of time spent on versus above the ground with no ship rat present and the scent of a ship rat present in the artificial forest for captive wild Norway rats

Condition	Ground 1	Ground 4	Stand 1	Stand 4
Av. % of time spent	90.8	94.5	9.2	5.5
SE	2.92	1.72	2.92	1.72
t value	1.09		1.09	
p value	0.29		0.29	

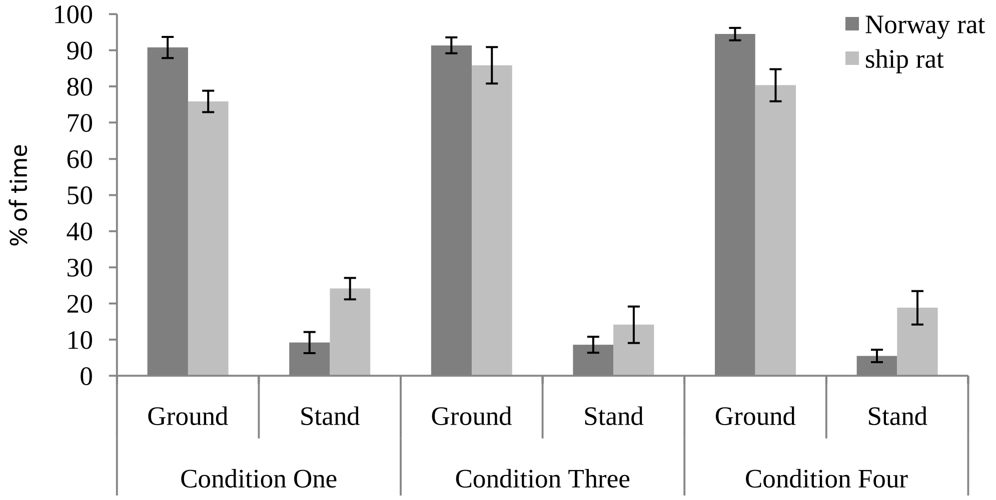


Figure 12. Percentage of time each species spent on versus above the ground in the artificial forest with no rat of the other species present, scent of the other species present or an actual rat of the other species present

Frequency of climbing

Norway rats appeared to be unaffected by the presence of a ship rat or ship rat scent in the artificial forest (condition three and four), as no significant differences in the average climbing frequency were detected (Table 9, Table 10, Table 11, Table 12, Figure 13 and Figure 14), compared to condition one (no ship rat).

Table 9. Average frequency of climbing up the various stand heights for the captive wild Norway rats: no ship rat present versus a ship rat present in the artificial forest. The * indicates the stand with no nails

Stands	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Condition	1	3	1	3	1	3	1	3	1	3
Av. freq.	3.3	3.4	3.3	4.4	14.8	14.5	7.3	6.9	3.0	1.6
SE	1.29	1.67	0.82	1.12	4.07	4.03	1.74	2.02	0.90	0.50
t value	0.06		0.82		0.05		0.14		1.35	
p value	0.95		0.42		0.95		0.89		0.19	

Table 10. Average frequency of climbing down the various stand heights for the captive wild Norway rats: no ship rat present versus a ship rat present in the artificial forest. The * indicates the stand with no nails

Stands	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Condition	1	3	1	3	1	3	1	3	1	3
Av. freq.	3.1	2.2	3.1	4.4	8.8	7.5	7.0	7.6	3.8	1.9
SE	1.31	0.63	0.80	1.22	2.39	2.51	1.66	1.49	1.08	1.19
t value	0.59		0.91		0.38		0.27		1.20	
p value	0.56		0.37		0.71		0.79		0.25	

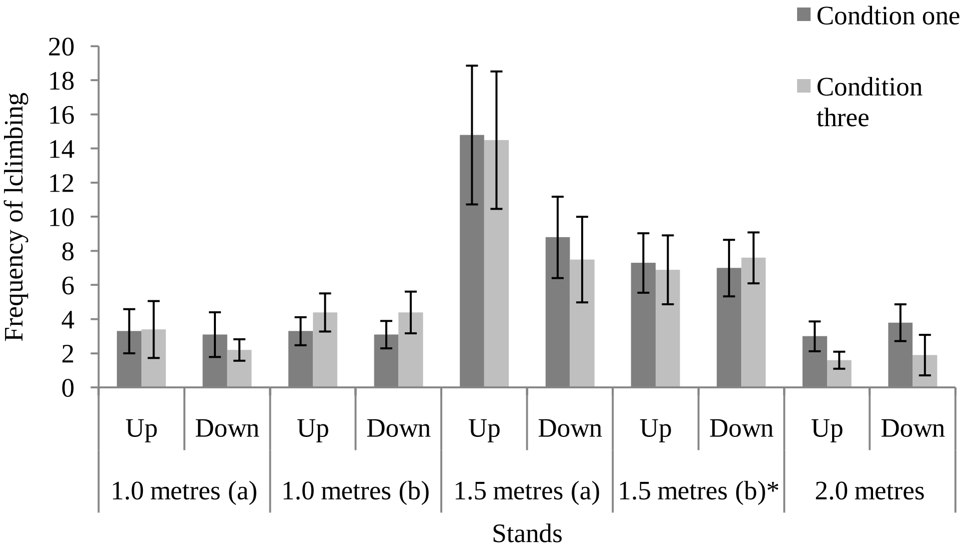


Figure 13. Average frequency of climbing for captive wild Norway rats: no ship rat present versus a ship rat present in the artificial forest. The * indicates the stand with no nails

Table 11. Average frequency of climbing up the various stand heights for captive wild Norway rats: no ship rat present versus the scent of a ship rat present. The * indicates the stand with no nails

Stands	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Condition	1	3	1	3	1	3	1	3	1	3
Av. freq.	3.3	3.5	3.3	2.6	14.8	9.2	7.3	8.4	3.0	3.4
SE	1.29	0.79	0.82	0.61	4.07	1.80	1.74	1.63	0.90	0.68
t value	0.12		0.62		1.27		0.46		0.33	
p value	0.91		0.54		0.22		0.65		0.75	

Table 12. Average frequency of climbing down the various stand heights for captive wild Norway rats: no ship rat present versus the scent of a ship rat present. The * indicates the stand with no nails

Stands	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Condition	1	3	1	3	1	3	1	3	1	3
Av. freq.	3.1	3.0	3.1	2.4	8.8	6.4	7.0	7.5	3.8	4.2
SE	1.31	0.54	0.80	0.58	2.39	1.10	1.66	1.55	1.08	0.90
t value	0.06		0.74		0.93		0.24		0.26	
p value	0.95		0.47		0.36		0.81		0.80	

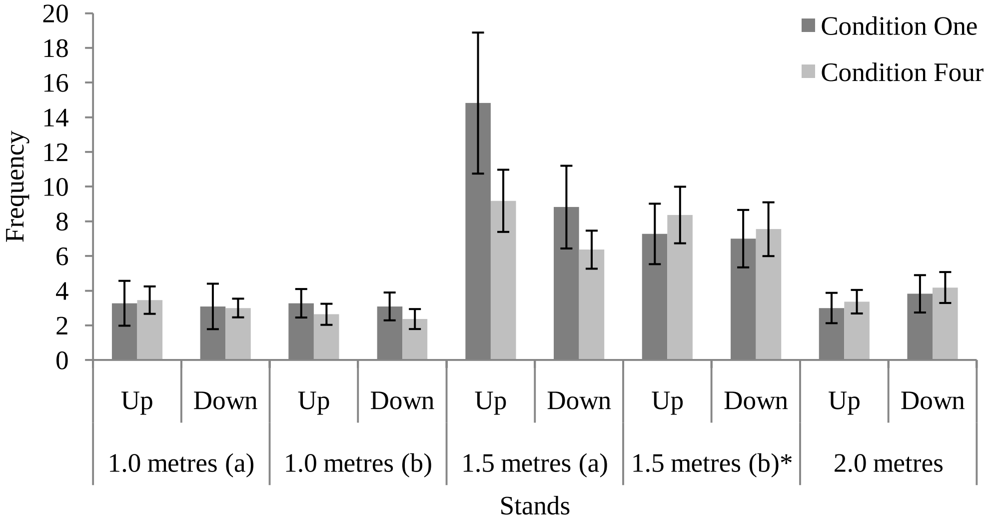


Figure 14. Average frequency of climbing during one night for captive wild Norway rats with ship rats not present versus the scent of a ship rat present in the artificial forest. The * indicates the stand with no nails

Time taken until first obstacle attempted

Norway rats tended to take less time to attempt the first obstacle, in the presence of a ship rat or the scent of a ship rat (conditions three and four), compared to condition one (no ship rat); however these results were not significant (Table 13 and Figure 15).

Table 13. Student t results for Norway rats in the time taken to attempt the first obstacle after sunset, comparing when no ship rat was present against when the scent or an actual ship rat was present in the artifical forest

Condition	1	3	1	4
Av. time taken	97.1	96.3	97.1	86.5
SE	21.30	54.40	21.30	46.06
t value	0.01		0.21	
p value	0.99		0.84	

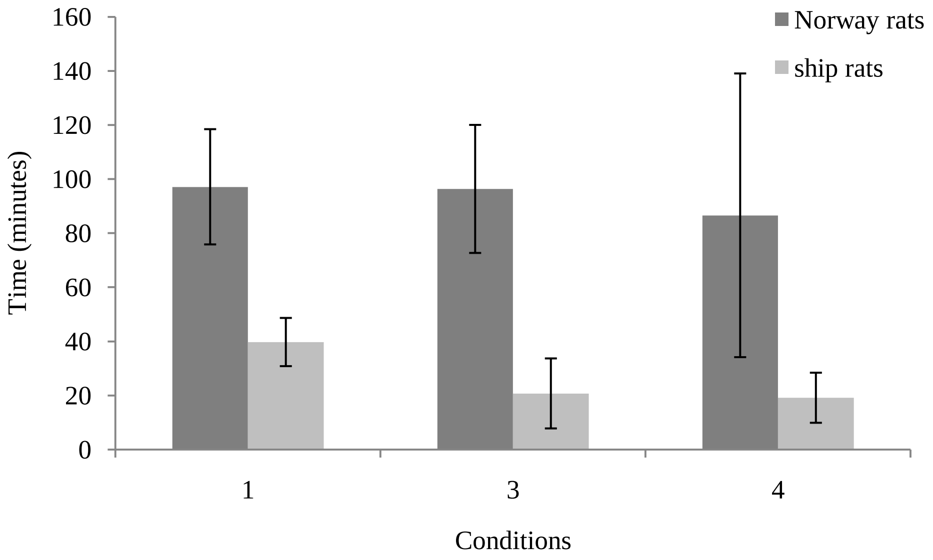


Figure 15. Average time taken until the first obstacle was attempted for captive wild ship rats and Norway rats with the other species not present, the scent of the other species present, or the scent of the other species present

Ship rat's reaction to Norway rats in the artificial forest

Time spent on the ground versus the stands

No significant differences in results were detected in the time spent by the ship rats on the ground versus up the stands, in the presence of a Norway rat, or

Norway rat scent (condition three and four) (Table 14, Table 15 and Figure 16), compared to condition one (no Norway rat).

Table 14. Average % of time spent on versus above the ground with no Norway rat present and a Norway rat present in the artificial forest

Condition	Ground 1	Ground 3	Stand 1	Stand 3
Av. % of time spent	75.9	85.9	24.1	14.1
SE	2.96	5.04	2.96	5.00
t value	1.71		1.71	
p value	0.10		0.10	

Table 15. Average % of time spent on versus above the ground with no Norway rat present and the scent of a Norway rat present in the artificial forest

Condition	Ground 1	Ground 4	Stand 1	Stand 4
Av. % of time spent	75.9	80.3	24.1	18.8
SE	2.96	4.30	2.96	4.60
t value	0.80		0.94	
p value	0.42		0.36	

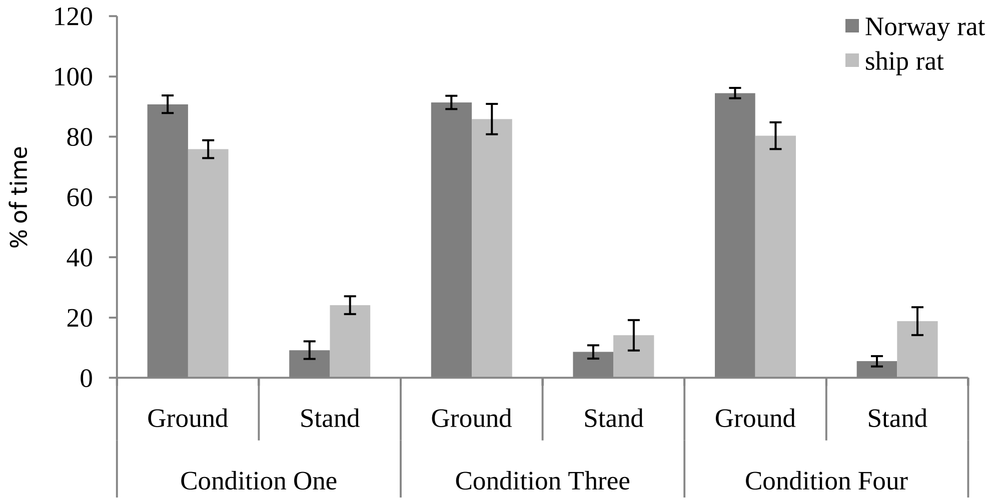


Figure 16. Percentage of time each species spent on the ground versus above the ground for all conditions

Frequency of climbing

When a Norway rat was present on the ground in the artificial forest (condition three), ship rats tended to climb the stands less often, although the difference was significant only in the average frequency ship rats climbed down the 1.0 metre (a) stand (P=0.047). The scent of a Norway rat above the ground in the artificial forest had no affect on the average climbing frequency of the ship rats (Table 16, Table 17, Table 18, Table 19, Figure 17 and Figure 18).

Table 16. Average frequency of climbing up the various stand heights for captive wild ship rats: no Norway rat present versus an actual Norway rat present in the artificial forest. The * indicates the stand with no nails

Stands	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Condition	1	3	1	3	1	3	1	3	1	3
Av. freq.	5.9	2.4	3.8	1.9	7.8	7.7	10.2	6.0	13.8	9.2
SE	2.06	0.96	1.17	0.67	1.94	2.43	2.75	1.01	3.52	3.39
t value	1.56		1.41		0.03		1.77		0.95	
p value	0.13		0.17		0.98		0.09		0.35	

Table 17. Average frequency of climbing down the various stand heights for captive wild ship rats: no Norway rat present versus an actual Norway rat present in the artificial forest. The * indicates the stand with no nails

Stands	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Condition	1	3	1	3	1	3	1	3	1	3
Av. freq.	4.9	2.0	3.3	1.9	10.6	7.2	9.8	4.8	9.5	6.7
SE	0.99	0.96	1.04	0.61	2.72	2.02	2.53	1.03	3.35	2.99
t value	2.11		1.11		1.02		1.83		0.63	
p value	0.047		0.28		0.32		0.08		0.54	

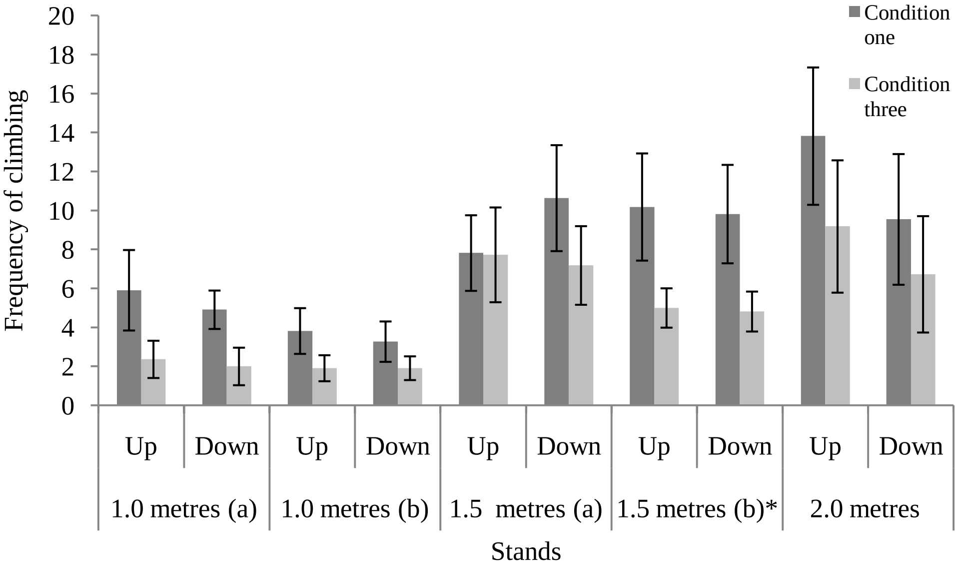


Figure 17. Average frequency of climbing for captive wild ship rats with a Norway rat not present versus an actual Norway rat being present in the artificial forest. The * indicates the stand with no nails.

Table 18. Average frequency of climbing up the various stand heights for captive wild ship rats: no Norway rat present versus the scent of a Norway rat present in the artificial forest. The * indicates the stand with no nails

Stands	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Condition	1	3	1	3	1	3	1	3	1	3
Av. freq.	5.9	5.7	3.8	3.4	7.8	7.8	10.2	11.3	13.8	6.9
SE	2.06	1.58	1.17	1.02	1.94	1.88	2.75	2.15	3.52	2.07
t value	0.09		0.26		0.03		0.33		1.72	
p value	0.93		0.80		0.98		0.74		0.10	

Table 19. Average frequency of climbing down the various stand heights for captive wild ship rats: no Norway rat present versus the scent of a Norway rat present. The * indicates the stand with no nails

Stands	1.0 metres (a)		1.0 metres (b)		1.5 metres (a)		1.5 metres (b)*		2.0 metres	
Condition	1	3	1	3	1	3	1	3	1	3
Av. freq.	4.9	5.8	3.3	3.9	10.6	8.7	9.8	10.8	9.5	7.3
SE	0.99	1.6	1.04	1.15	2.72	1.85	2.53	2.14	3.35	1.94
t value	0.49		0.41		0.61		0.28		0.58	
p value	0.63		0.68		0.55		0.78		0.57	

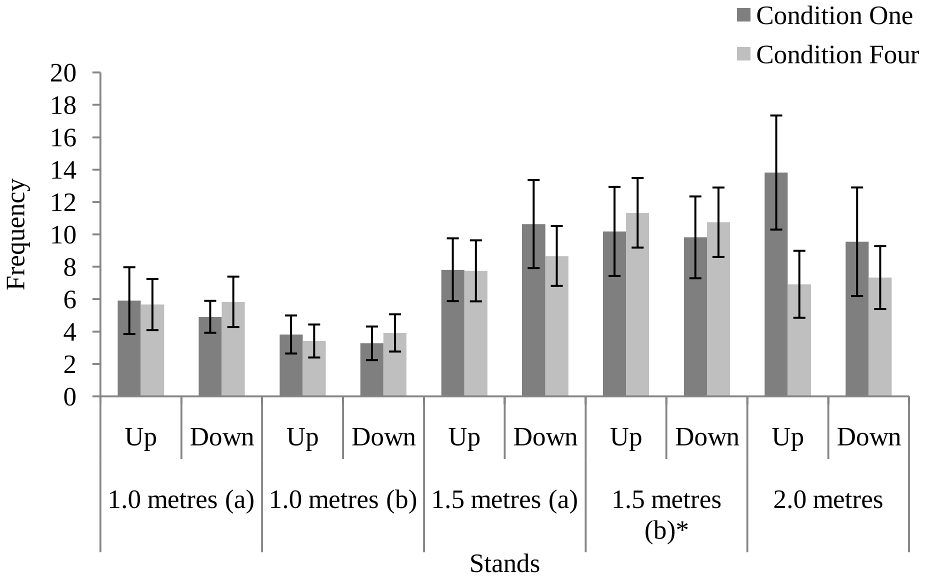


Figure 18. Average frequency of climbing during one night for captive wild ship rats with no Norway rat present versus the scent of a ship rat present in the artificial forest. The * indicates the stand with no nail

Time taken until first obstacle attempted after sunset

Ship rats on average were significantly faster to attempt the first obstacle (P=<0.05), when the scent of a Norway rat was present above the ground in the artificial forest (condition four), compared to condition one, no scent (Table 20 and Figure 19). They were also faster to attempt the first obstacle, when a Norway rat was present (condition three), compared to condition one (no Norway rat), though this difference was not significant.

Table 20. Student t results for ship rats in the time taken to attempt the first obstacle after sunset, comparing when a Norway rat was not present with when one was through either scent or actually being present in the artifical forest

Condition	1	3	1	4
Av. time taken	39.7	20.2	39.7	19.1
SE	8.91	9.26	8.91	4.03
t value	1.48		2.17	
p value	0.15		0.04	

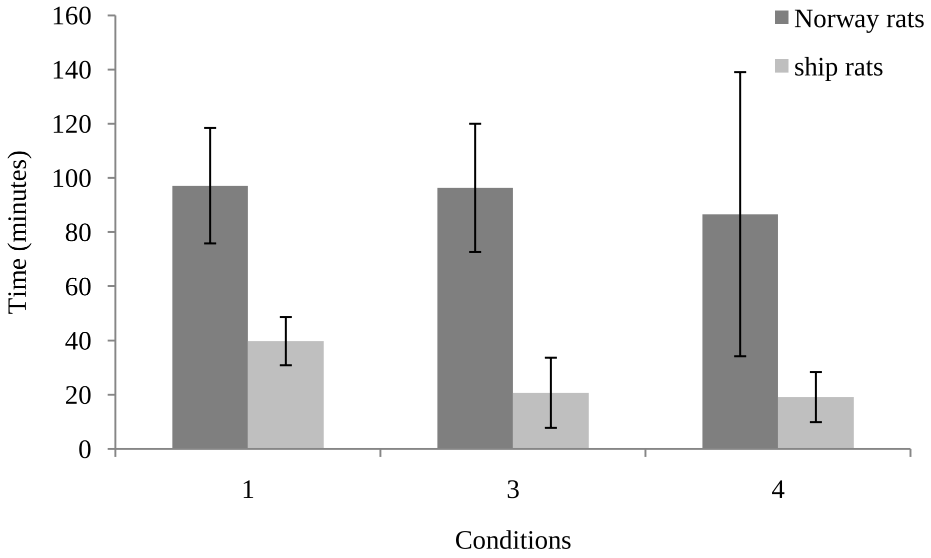


Figure 19. Average time taken until the first obstacle was attempted for captive wild ship rats and Norway rats with no rat of the other species present, scent of the other species present and an actual rat of the other species present

DISCUSSION

Interference type behaviours such as aggression are generally less risky and expensive for the larger of two combatants so it is expected that larger species might use these types of behaviours in response to competition, from smaller, closely related animals that are superior in exploiting a common resource (Persson 1985).

Norway rats are known for their large size and aggressive nature (Dzhemukhadze 2007) so it was expected that they would have an advantage when they interact with ship rats on the ground, which could be sufficient to compensate for their disadvantage in competing with the smaller, but more agile ship rats for resources above the ground. The work described in this chapter aimed to test that hypothesis.

In support of this, two (of 12 tested) Norway rats displayed a significant degree of aggressive behaviour towards ship rats in the staged encounters, while none of the ten ship rats displayed any, and Norway rats also appeared to be less disturbed by the presence of a ship rat on the ground in the artificial forest, than ship rats were by the presence of a Norway rat on the ground.

During the artificial forest experiments, both species responded to the presence of the other rat species (either their scent or a live rat in a cage) by tending to spend more time on the ground versus above the ground, than they did when there was no sign of the other species nearby. The video footage showed that ship rats spent a lot of time circling and interacting with the caged Norway rats, and they climbed the stands less often than they did when in the arena alone, whereas the Norway rats tended not to spend as much time interacting with the caged ship rats. None of these differences in behaviour and time budgets are large enough to be significant.

From the video footage of the staged encounters, it was observed that the ship rats appeared to ignore any aggressive behaviour from the Norway rats so long as they were protected by the partition. By contrast, the aggressive behaviour of the

Norway rats was clear: they were crouched low on the ground, the hair on their back was on end, the ears were laid back, the tail was whipping from side to side, and their complete focus was on the ship rat, on the other side of the partition. Barnett (1963) observed similar characteristic signals of aggression, especially the raising of the hair on the rats' backs.

Ship rats were seen to end more interactions than Norway rats but this cannot be interpreted as a sign that they were scared or chased off by the Norway rats. Ship rats appeared to have small attention spans, and the high frequency of ending interactions observed was simply because the ship rats often changed their behaviour spontaneously. This was the opposite of the Norway rat's behaviour. Some of the Norway rats would spend long periods of time just watching the ship rat moving around.

The sociability of each species can be inferred from the total number of interactions exhibited during each staged encounter. The pairs with the highest number of interactions were ship rat males versus ship rat males, while the least interactive pairs were Norway rat females versus Norway rat females. Vestal (1977) compared the interactive behaviour of pairs of laboratory-strain Norway rats with those of pairs of *Mus musculus, Peromyscus leucopus and P. maniculatus* in a 1 metre diameter open arena. Norway rats had the highest number of interactions when paired with a conspecific stranger, but no direct comparison can be made to the work described here on wild caught Norway rats.

Boreman and Price (1972) looked at the social dominance in wild (laboratory reared first generation offspring of wild caught parents) and domestic (mixture of Sprague Dawley, Long Evans, Wistar and Holtz-man inbred strains) Norway rats and their hybrids. They found that domestic Norway rats were dominant over both wild, and hybrid Norway rats in both competitive and spontaneous interactions. One explanation offered was that the larger body size of the domestic Norway rats may itself bestow social dominance. The authors also observed that wild Norway rats interacted the least with conspecifics, which agrees with the results in this chapter. Allen (1977) observed that wild Norway rats exhibited more attack, threatening and running away behaviours towards conspecifics, than domestic and hybrid Norway rats did to conspecifics. The domestic Norway rats were also more active, especially in exploring behaviours during conspecific encounters.

Studies looking at social dominance during interactions between Norway rats and ship rats have produced varied results, and these generally depend on whether the Norway rats tested were wild or laboratory born. Sridhara *et al.* (1980) found that laboratory-born Norway rats are not dominant over ship rats, through a series of staged encounters. They defined the encounters between the two species to be neutral or amicable, and observed little aggressive behaviour.

Wild born Norway rats tend to be dominant over ship rats during social encounters. Takahashi and Blanchard (1982) placed a wild Norway rat into a colony of wild ship rats and vice versa. Resident Norway rats were more aggressive towards the intruder ship rat than the resident ship rats were to an intruder Norway rat. Barnett (1958) observed that intruder ship rats placed in a colony of Norway rats, were aggressively attacked (Figure 20), resulting in the intruder ship rat being killed or exhibiting submissive behaviour, but when an intruder Norway rat was placed into a colony of ship rats, any aggressive behaviour exhibited by the ship rats did not have any effect on the behaviour of the intruder Norway rat. Barnett (1958) concluded that a ship rat would not usually be able to defeat a Norway rat in an aggressive fight.

Work carried out by Barnett and Spencer (1951) supports this hypothesis. Two established colonies of Norway rats and ship rats were freely allowed to mingle. At the conclusion of the experiment it was found that the Norway rats had successfully invaded the nest boxes of the ship rats. More ship rats died during the experiment than Norway rats. The authors did not see the deaths of these ship rats but theorised that they may have died through lack of food and stress from having no safe refuges to avoid the Norway rats.

Figure 20. An artistic impression of a male *Rattus norvegicus* biting a male *Rattus rattus* during an interspecific encounter (From K. Vogt & F. Specht. Die Saugetiere. 1883, as cited in Barnett, 1963, p. 95).

The behaviour of wild rats may not always be predictable from captive observations but for the ship rat versus Norway rat interaction a single large scale but uncontrolled natural experiment supports the conclusions of captive observations. The ship rat was once widespread in Britain, but appears to have been displaced as the Norway rat spread throughout Britain during the 18th century (Atkinson 1973). Ship rats are now found only on Lundy Island in the Bristol Channel, where Norway rats are also present, and on the Shiant Islands, in the Outer Hebrides, where Norway rats are not present (McDonald *et al.* 1997). In other countries the ship rat is known as the roof rat, because their ability to live within the roof structure of a building gives them an advantage over the Norway rats which occupy the floor levels (Taylor 1975).

Animal ethics is (rightly) becoming increasingly important in governing research proposals, and because of this, I was not allowed to stage encounters between rats free to harm each other. The partition separating the rats in my observations may have altered their behaviour compared with what might have naturally been observed in the wild. It is difficult to predict what might have happened if the rats had been allowed to make contact during the encounters, but older studies such as those by Barnett and colleagues (Barnett 1963), done under conditions no longer permitted suggest that the ship rats would probably have been injured. Alternative methods are needed to confirm this prediction, without unnecessary stress or harm to the subject animals. Larger sample sizes would also be useful to help smooth out the variability in the data.

CONCLUSION

These data are consistent with the prediction that Norway rats will be superior in interference competition over ship rats; however the results are not conclusive. In the artificial forest, both species were aware of the opposite species, however few significant results were detected. During the staged encounters, ship rats protected by the partition seemed to ignore the aggressive behaviour exhibited by the Norway rats. Further refinement of the methods used, and an increase in sample sizes, may allow a more accurate picture of the relationship between these two species.

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CHAPTER FOUR

Arboreality of *Rattus norvegicus* and *R. rattus* in native forest

ABSTRACT

A balance of exploitation competition and interference competition may contribute to governing the current distribution of ship rats and Norway rats in New Zealand. In this balance, it is hypothesised that in native forest, ship rats will be superior in exploitation competition, especially in the trees, while Norway rats will be superior in interference competition, when they encounter each other on the ground.

From this hypothesis, two predictions can be made on the habitat use of both these species when they are found together in native forest: (1) ship rats will be found more often in the sub canopy and canopy, and (2) Norway rats will be found more often on the forest floor. The aim of this phase of the project was to determine the ratio of ship rats and Norway rats captured on the forest floor, versus 2.0 metres above the ground, in places where both species coexist.

Rahui Island on Lake Waikareiti was suggested to be an ideal location for a field trial, as both species are known to have been there in the past, and the entire island was covered with native beech forest. To test this idea, 17 trapping stations, consisting of a Victor snap trap on the ground and one on top of a 2.0 metre stand, were placed every 30 metres along a transect, totalling 480 metres across the island.

Unfortunately the number of rats trapped was extremely low, so no conclusive results could be attained. 20 ship rats were trapped on the forest floor, and 3 2.0 metres above the ground, while only one Norway rat was trapped, on the forest floor. Further research is needed to get a better idea of the arboreality of these two species in areas of sympatry, in native forest.

INTRODUCTION

Interspecific competition is observed when "individuals of one species suffer a reduction in fecundity, survivorship or growth as a result of resource exploitation or interference by individuals of another species" (Begon *et al.* 1996, p. 265). Previous studies on interspecific competition have shown that it can affect the habitat use and relative population sizes of sympatric species (Eccard and Ylonen 2003). Interspecific competition commonly takes one of two forms; depending on the how the common resource is distributed.

Interference competition is observed when one species is physically preventing another from accessing a resource, either through territory defence or aggressive encounters (Keddy 1989; Smith and Smith 2001; Harris and Macdonald 2007). The dominant species in these interactions tend to be the larger of the two (Morse 1980; Persson 1985). During such an interaction, the more dominant species will be able to monopolise more resources, which will support greater growth for the dominant, increase resource acquisition and cause further damage to the subordinate species (Keddy 1989). Interference competition is easier to detect than exploitation competition as the interactions are directly observable (Petren and Case 1996).

Interference competition was concluded to be the mechanism behind the decline of the *Nesoryzomys swarthy,* rice rat in the Galapagos Islands, in the presence of the *Rattus rattus* ship rat. Harris and Macdonald (2007) carried out a press and food supplementary experiment with these two species. During the press experiments, ship rat abundance was experimentally decreased; this was followed by an increase in immigration of female rice rats into the grids. Rice rat numbers did not change throughout any of the food supplementation grids; however ship rat numbers increased dramatically. Harris and Macdonald (2007) concluded that interference competition by ship rats was the mechanism behind the population decline in rice rats in that area.

Exploitation competition is observed when one species is better than another at harvesting a given type of resource. This is indirect and the resource has to be in limited supply (Harris and Macdonald 2007). Animals are responding to the resource level, which in turn is being affected by the other competitors, in that habitat (Begon *et al.* 1996).

An example of exploitation competition was found in two species of gecko, in Hawaii, the native asexual gecko *Lepidodactylus lugubris*, and the sexual gecko *Hemidactylus frenatus* during enclosure studies. Petren and Case (1996) found that the reason why populations of *L. lugubris* decline in the presence of *H. frenatus* is because of differences in the ability of both species to exploit food resources. *H. frenatus* depletes insect resources to a very low level which reduces resource acquisition by *L. lugubris.* This causes a reduction in the body condition, survivorship and fecundity of the *L. lugubris.*

The Norway rat *R. norvegicus* was transported to New Zealand, from 1770, with the early European explorers and settlers, up to about 1865. After about 1865, the ship rat, *R. rattus* arrived with the later European settlers, and soon spread right throughout the country. During this time the previously widespread Norway rat became restricted in distribution (Moors 1985; Yom-Tov *et al.* 1999; Harper *et al.* 2005; Innes 2005a; Innes 2005b).

The Norway rat is much larger, with weights averaging 200-300 grams, than ship rats, who average 120-160 grams (Atkinson and Towns 2005). Currently, ship rats are found throughout New Zealand, inhabiting a wide range of forest types (Atkinson 1973; Taylor 1978b). They are most abundant in diverse, mature lowland podocarp-broadleaf forests, from the coast to the tree line, but not in the alpine tussock (Innes 2005b). By contrast, Norway rats are largely restricted to farm buildings, riparian sites, coastlines, rubbish tips, and wharves (Atkinson 1973; Taylor 1978b; Innes 2005a).

Norway rats tend to be ground dwelling, and are rarely seen climbing above three metres. They are also known for their burrowing and swimming abilities (Atkinson 1973; Thorsen *et al.* 2000), while ship rats are primarily arboreal and spend most of the time in the forest canopy, occasionally coming down to the forest floor to forage (Atkinson 1973; Hooker and Innes 1995; Lindsey *et al.* 1999). Norway rats are known predators of ground dwelling birds, while ship rats have impacted perching birds (Atkinson 1973).

My hypothesis is that there is a balance of exploitation competition and interference competition, which contributes to governing the current distribution of ship rats and Norway rats in New Zealand. In this balance, ship rats are expected to be superior in exploitation competition, especially in native forest, while Norway rats will be expected to be superior in interference competition, when they encounter each other on the ground.

From this hypothesis, two predictions can be made on the habitat use of both these species when they are found together in native forest: (1) ship rats will be more often found in the sub canopy and canopy, and (2) Norway rats will be more often found on the forest floor. The aim of this phase of work was to determine the ratio of ship rats and Norway rats captured on the forest floor, versus two metres above the ground.

Results of previous work (Chapter Two) suggest that Norway rats can climb if they choose to. This information was gathered using a method that captured wild rats and placed them in an artificial environment. Because they may behave differently in the wild, it is essential this concept is tested in nature.

METHODS

Study site

This field work was carried out on Rahui Island on Lake Waikareiti, in the Te Urewera National Park in the East Coast Conservancy. The lake is approximately 5 kilometres north east of Lake Waikaremoana, has six islands which are named Te Kahaatuwai, Motungarara, Te Onoatahu, Motutorutoru, Te Arakoau and lastly Rahui Island, which is one of the largest at 26.6ha (Figure 1). Rahui Island is unique, as it has its own lakelet named Tamaiti.

The lake is free from introduced aquatic weeds and pollution so has remarkably clear water. Rahui Island has no possums, and there is little possibility of deer once being present because the steep sides of the island would make landing difficult. To make landing easier for visitors, a landing platform and ladder has been put in place. The island has a relatively tall forest canopy, dominated by silver (*Nothofagus menziesii)* and red (*N. fusca*) beech with some mountain beech (*N. solandri* var. *cliffortioides*) (Figure 2). Other common species include Hall's totara (*Podocarpus hallii*), miro (*Prumnopitys ferruginea*) and toatoa (*Phyllocladus toatoa*). The dominant sub canopy species include tawari *(Ixerba brexiodes*) and kamahi (*Weinmannia racemosoa*) (Merrett & Shaw 1999).

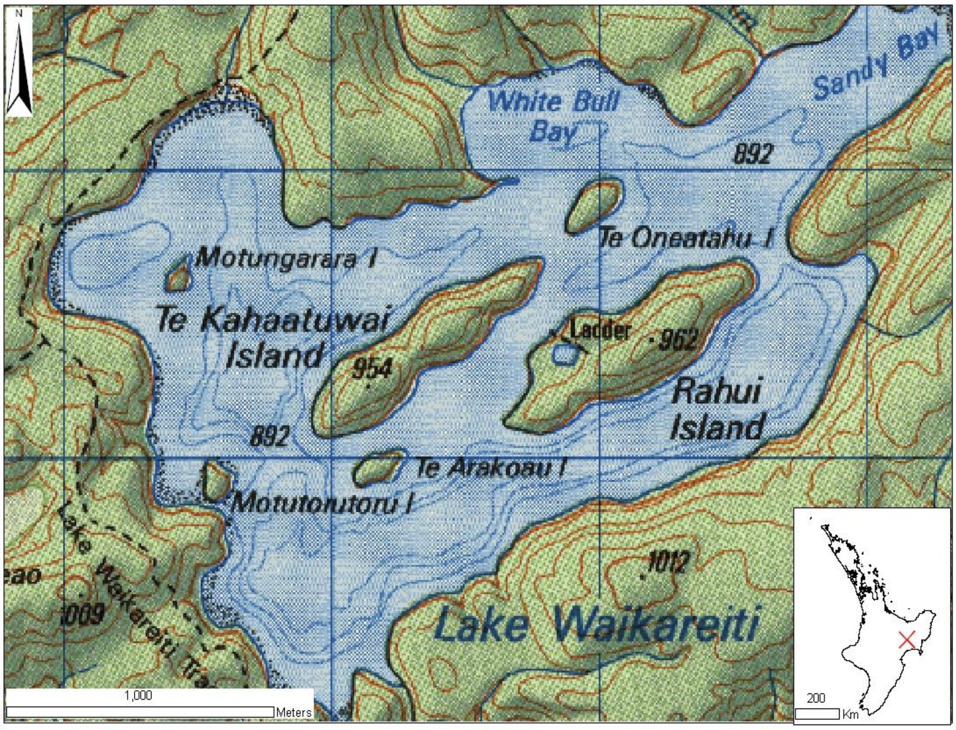

Figure 1. Lake Waikareiti. The red cross indicates the lake in the North Island (from Maptoaster)

Figure 2. The forest on Rahui Island (S Foster)

Trapping

Traps were set along a 480 metre line used in the previous year for a rodent study (Figure 3). Every 30 metres, a station was placed, with a total of 17 stations. Each station had two Victor snap traps, with covers (to prevent by-catch), one set on the ground and one set up on a platform two metres above the ground (Figure 4). These were the same 2.0 metre stands (only slightly modified), used in the experiments discussed in Chapter Two and Three. The platforms on top of the stands were made larger to allow the traps and covers to fit on them. The stands consisted of a 2.0 metre pole placed into the ground next to the nearest suitable tree, at each 30 metre mark. The traps on the 2.0 metre stands were accessible either by climbing up the pole or from the branches of the tree it was next to.

After setting up, these stands and traps were left in place for approximately 18 days to enable the rats to overcome any neophobic reactions they may have to the stands, traps and covers. On the 5th of November 2009, the traps were baited with peanut butter and set for four nights.

The traps were checked every day, captured rats were identified to species, sexed, and weighed. Approximately one week later, the traps on top of the stands were set for a further three nights. In this session, only the traps above the ground were set, in case animals were being trapped first on the ground level, before entering the above ground traps. Captured rats were identified to species, sexed, and weighed. All work undertaken was approved by the University of Waikato Animal ethics committee, protocol number 766. Iwi permission was granted by the Lake Waikaremoana Hapu Restoration Trust.

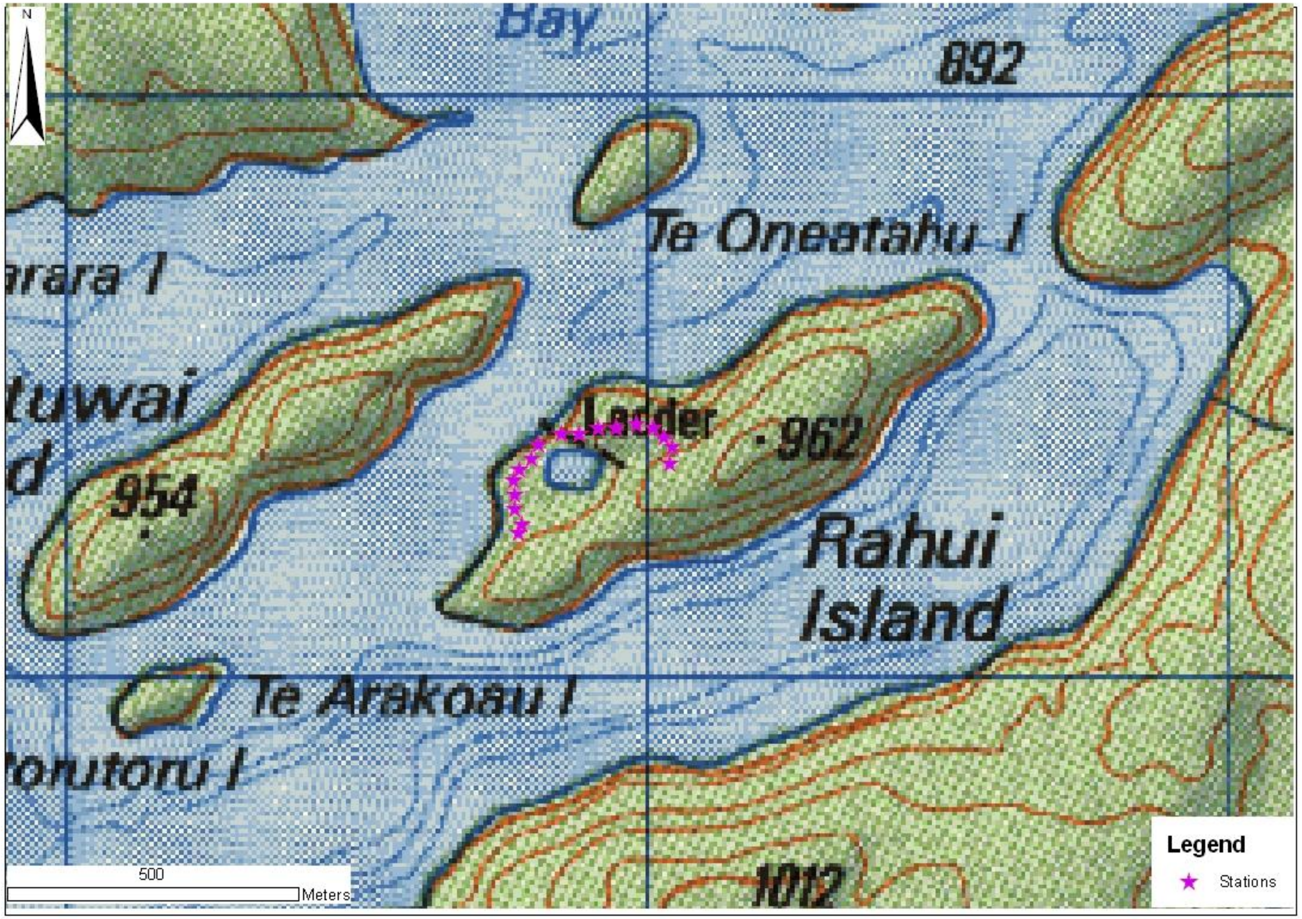

Figure 3. Rahui Island showing the locations of the stations (from Maptoaster)

Figure 4. A station (C Bryan)

RESULTS

The first trapping session (with all 36 traps set both on the ground and above the ground), yielded a total of 21 rats; one was a Norway rat, and the rest were ship rats. The average ship rat weight in this first trapping session was 166 grams, while the weight of the Norway rat was 300 grams. All the rats were caught in the traps on the ground (Table 1).

Table 1. Results from first trapping session, with all traps set

	Norway rats		Ship rats	
	Ground	Above ground	Ground	Above ground
No. trapped	1	0	20	0
Average weight (grams)	300	-	166	-
No. of males	0	-	12	-
No. of females	1	-	8	-

The second trapping session (with only the traps above the ground set), yielded no Norway rats, and three ship rats. The average weight of these rats was 143.3 grams. Also during this trapping session, two mice were caught with an average weight of 35 grams (Table 2).

Table 2. Results from second trapping session with only the traps above the ground set

	Norway rats	Ship rats	Mice
No. trapped	0	3	2
Average weight (grams)	-	143.3	26
No. of males	-	2	1
No. of female	-	1	1

DISCUSSION

The total number of rats captured was disappointing, compared with the numbers of both species recorded in a study conducted in October 2008, by the Department of Conservation (King 2008). Commensal populations of Norway rats are known to be extremely neophobic (Atkinson 1973), so it may be that more were present than what was caught, however wild populations on islands, tend to be extremely non neophobic. Taylor and Thomas (1993) reported no neophobia in the Norway rats, on Breaksea and Hawea Islands as over 80% of the bait was taken the first night of poisoning and almost 100% taken during the next three nights.

The change in capture success may have been because: (1) the populations declined as food became scarce because of the high population numbers or (2) the winter of 2009 was known to be particularly cold, so there may have been increased mortality throughout the population.

The results gained from this trapping study are not conclusive, because so few rats were captured. Ship rats were trapped only on the forest floor, when both ground level and 2.0 metre above ground traps were set, while only one Norway rat was trapped on the ground level traps. When only the traps 2.0 metres above the ground were set, only three ship rats were trapped, with no Norway rats trapped. Much more research is needed to clarify the questions asked.

These results, so far as they go, are consistent with other studies looking at the habitat use of these two species in forest. Key and Woods (1996) tracked individuals of both species, in sites of sympatry and allopatry, in the Galapagos Islands. They used the spool and line method, to determine the amount of time each species spent in the forest canopy. They found that Norway rats rarely climbed, but more often moved along the cracks of lava rocks and under rocks, while ship rats spent significantly more time in the canopy.

This segregation of habitat in areas where both species exist together does not only happen in the forest. Ecke (1954) reported the spread of Norway rats into Southwest Georgia, slowly replacing ship rats. Personal observations by Ecke (1954) noted that in buildings where both species coexisted, the more arboreal ship rat was found in the upper storeys of the buildings, while Norway rats were found in the basements.

Habitat segregation also happens in captivity. Barnett and Spencer (1951) established populations of ship rats and Norway rats, and allowed them to mingle, to observe the interspecific behaviour between the two species. They found that, by the second day after integration, the majority of the Norway rats had invaded ship rat’s nests and the ship rats had retreated to the roof and a ledge approximately 10 feet off the ground.

A study by Cavia *et al.* (2009) looked at the rodent diversity in the city of Buenos Aires. They found that ship rats were most abundant in sites with a high proportion of vertical complexity, such as large industrial and residential buildings, as the ship rats were able to climb and build nests in the upper storeys of these buildings.

Previous studies in New Zealand, suggest Norway rats do not climb in the wild. Lovegrove (1996) compared the survival of the Saddleback *(Philesturnus carunculatus)* on three New Zealand offshore islands. On Kapiti Island, Norway rats and kiore were present. Nests below one metre were destroyed significantly more often than nests above one metre while on Cuvier and Little Barrier Island, which only had kiore present, nests at all heights were equally vulnerable. This difference is a characteristic signal of the damage done by ground dwelling Norway rat’s.

Lovegrove (1992) also looked at the predation of the saddleback and the implications for the management of this species. In one experiment, artificial nest boxes were constructed 1.5 metres above the ground on a smooth vertical surface, assuming that ground foraging Norway rats could not have access to these nest boxes. Birds which nested in the boxes had a much higher chance of surviving, than those which did not use them. These studies suggest that Norway rats generally do not climb in the wild, but are not conclusive.

There are several limitations to this study. The method chosen was deemed to be the most suitable in the time and money constraints upon me at the time. It may have been better to place several lines at least 500 metres apart, or place extra lines on other islands. A different design of trap lines may have been more useful: have all the traps on the ground for one line, while all the traps on another line, above the ground. Traps could be placed higher in the tree canopy

CONCLUSION

In one area where both rat species coexist in native forest, ship rats were occasionally trapped above the ground and mostly on the forest floor, while the only Norway rat was trapped on the ground. These results are weakly consistent with other trapping and radio tracking studies in New Zealand forest, that together are consistent with, but do not prove the hypothesis that ship rats maybe superior at exploitation competition in the forest environment.

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CHAPTER FIVE

General Discussion

OVERVIEW

The general aim of this project was to investigate the hypothesis that coexistence between Norway rats and ship rats is governed by constantly shifting between a balance of different advantages in exploitation competition and interference competition, mediated by habitat which contributes to explaining their current distribution in New Zealand.

Ship rats *Rattus rattus* are more agile so are expected to be the superior competitor in exploitation competition, especially in native forest, while the larger, more aggressive Norway rat *R. norvegicus* will be the superior competitor in interference competition.

Here, I discuss the implications of the findings from Chapters Two, Three and Four and identify areas for future research.

Chapter Two describes tests made to determine which species is superior in climbing ability, as this may be important in exploiting above-ground resources in New Zealand native forest. The specific hypothesis developed for this chapter was that ship rats would be better climbers than Norway rats. To test this, an artificial forest comparable in structure to New Zealand forest was created in aviary style pens, containing stands of various heights, representing a range of low trees that rats may forage on. These were connected to each other loosely via ropes of different widths, to represent interlocking branches. Food rewards were placed at the top of the stands, and individual rats of both species were placed in the pens overnight and their activities video recorded.

As expected, ship rats were significantly faster climbing up and down all the stands than Norway rats, and traversing the various widths of rope. Ship rats also utilised the above-ground habitat more often as they spent more time on the stands, than on the ground, than did Norway rats. However, Norway rats did not avoid climbing as expected, even though there was food available to them at floor level. Norway rats climbed all the heights presented to them, albeit they were much slower and some looked quite awkward.

These results fit the general behavioural descriptions of these two species. Norway rats are ground-dwelling and are known for their burrowing and swimming abilities (Atkinson 1973; Thorsen *et al.* 2000), while ship rats are primarily arboreal and spend most of their time in the forest canopy (Atkinson 1973; Hooker and Innes 1995; Perry *et al.* 2009). These general behavioural differences imply different bird species will be vulnerable to them. Norway rats generally prey upon eggs, young and adult birds, which nest near or on the ground, or in burrows, while ship rats prey upon the eggs or young of perching birds, which live and nest in the forest canopy, as well as birds which nest on the ground (Atkinson 1973; Jones *et al.* 2008).

Chapter Three describes tests looking at which species is superior at interference competition. This was done using two methods. Firstly, inter-and intra-specific encounters were carried out in a tank, with a rat at each end separated by a partition in the middle, and the rat’s responses to each other remotely recorded; and secondly, a caged rat or its scent, was placed in the artificial forest and the responses of a rat of the opposite species which had the run of the enclosure was remotely recorded for approximately 12 hours during the night.

In the staged encounters, ship rats were much more social towards conspecifics, than Norway rats were to other Norway rats. No ship rats (of ten tested) displayed aggressive behaviour towards other ship rats. No (of twelve tested) Norway rats displayed aggressive behaviour towards other Norway rats, but two Norway rats clearly reacted aggressively towards the ship rats on the other side of the partition.

While the ship rats were protected by the partition from any contact with a Norway rat, their behaviour appeared to unaffected by the displays of aggression from the Norway rats, or at least they showed no submissive behaviours, or attempts to escape. The ship rat in one of these encounters spent 100% of the time up the front of the tank, closest to the aggressive Norway rat. By contrast, the behaviour of ship rats free to move around in the artificial forest seemed to be more influenced by the presence of a Norway rat than expected from their behaviour in the tank. Habitat utilisation was decreased by ship rats as they spent more time either in the nest box, or investigating the caged Norway rat. When their situations were reversed, the behaviour of the Norway rats was no different from when they had the enclosure to themselves: they neither avoided the caged ship rat nor attempted to attack it.

Chapter Four focussed on trying to validate the results from Chapter Two and Three in the wild. Rahui Island, on Lake Waikareiti was deemed suitable as it was entirely covered by beech forest, and both Norway rats and ship rats were confirmed to be there, by Department of Conservation observers, the year before. One Norway rat and 20 of 23 ship rats were trapped all on the ground.

DISCUSSION

Ecological theory predicts that interspecific competition will lead to coexistence of two (or more) species either in sympatry (by resource partitioning) or in allopatry (through habitat exclusion). Coexistence can be stable or unstable, depending on the level and distribution of resources available in the habitat. Coexistence that is possible during times of abundance may be restricted during times of low resource levels, because then interspecific competition will become intense and only the superior competitor in the habitat will survive (Begon *et al.* 1996; Harper *et al.* 2005).

Both ship rats and Norway rats have advantages in interspecific competition, and the results from this project are consistent with the hypothesis that each is superior in different respects. The balance of advantages is constantly shifting depending on the habitat they are in. Ship rats have an advantage in exploitation competition in native forest, as they are able to access resources in the tree canopy more rapidly and with less effort. This ability may also give the speed and agility needed to escape any aggressive behaviour from Norway rats, if confronted by one on the forest floor. Norway rats seem to be the superior competitor in situations of interference competition, and they are also able to access resources not available to ship rats because they are good swimmers and burrowers (Atkinson 1973). Their large size and aggressive nature ensures that producing confrontational behaviours is cheap and less risky (Persson 1985). It would therefore be expected that, where both species live together in forest habitat, ship rats would be found more often in the tree canopy, while Norway rats would be more often on the forest floor. The results gathered from Rahui Island are inconclusive as ship rats were trapped both on the forest floor and 2.0 metres above the ground, while only one Norway rat was trapped on the forest floor.

Vertical stratification in structurally complex habitats is a way to reduce interspecific competition between sympatric species (Cameron and Kincaid

1982). Arboreal species can utilise resources in the tree canopy before they become available to ground dwelling competitors on the forest floor (Layne 1970). Before ship rats arrived in New Zealand, Norway rats were abundant right through the country and occupied most habitats, including all native forests, and they survived for decades longer on some islands not reached by ship rats. So there is historical evidence that Norway rats can utilise forest habitats when alone. Why, then, was it displaced from most forests when ship rats arrived (Atkinson 1973)? Why does it still live in certain mainland habitats such as stream sides and rubbish dumps?

Taylor (1978; 1984) suggests that predation by mustelids is the reason for the current distribution of Norway rats in New Zealand. Mustelids are known predators of rats (King and Murphy 2005), and they were introduced at approximately the same time (ca. 1884), as Norway rat numbers began to decline. Atkinson (1973) proposed that ship rats may have been introduced to the North Island, between 1858 and 1865, and to the South Island around 1890, but only remained in ports and towns because of competition from Norway rats similar to the conditions in Europe. Predation from mustelids on Norway rats may have lowered population levels enough that ship rats could move out into the surrounding countryside. However this idea needs further testing, as studies carried out on islands (Harper *et al.* 2005; Harper 2006), where no mustelids are present, still only had low numbers of Norway rats in the forest.

The hypothesis formulated in this thesis, allied with supplementary information, leads to predictions on the expected relative distributions of the two species in sympatry in New Zealand, and to a potential explanation of the current distribution of the remnant populations of Norway rats. I propose that, when large populations of semi arboreal ship rats (agile, light-weight, long-tailed) became established in New Zealand, they preferred to forage in trees, where food and nest sites were abundant and where they could avoid contact with Norway rats. In the process, they lowered the amount of food resources falling down to the forest floor for Norway rats. This decline in resources for the Norway rat (coupled with the predation risk from mustelids), displaced them from this habitat, or restricted them to low population numbers in areas of forest where their burrowing and swimming habits give them a slight advantage.

Yabe (1979) looked at the food habits of both rat species in relation to their ecological distributions, by observing the stomach contents of trapped rats in varying habitats. Norway rats more often ate animal materials, while ship rats more often ate seeds, fruit, and plant material, and this was reflected in the habitats they were trapped in. Norway rats were more often found in urban areas, in a fish market and on an artificial islet, while ship rats were more often found in the forested areas on two islands sampled and in the gardens and parks in residential areas. Miyao *et al.* (1960) measured the large intestinal length and the caecum length against the small intestinal length in rats, calculating the ratios. They observed that the ratio was smaller in Norway rats than ship rats. This difference in physiology may affect the type of foods each species can digest efficiently. Kami (1966) proposed that this difference in physiology may cause the Norway rat to be inferior in utilising a diet high in cellulose or poor in protein, compared to ship rats.

Harper (2006) trapped a high number of Norway rats along the coastline on Pearl Island, and proposed that the high protein marine derived food source may have encouraged them to stay in that habitat. Bettesworth and Anderson (1972) found that 80% of the volume of food found in the stomach contents of Norway rats on Whale Island, in the Bay of Plenty, was the flesh and down of chicks of the grey faced petrel, *Pterodroma macroptera*, with the rest being made up of insect remains, and intertidal invertebrates.

Other studies do suggest that where both species coexist, there is generally habitat segregation, with ship rats preferring the upper half of the habitat, and Norway rats the lower half. In an enclosure study, Barnett and Spencer (1951) found that ship rats moved up into the ceiling of the enclosure when Norway rats were introduced. In the wild, Key and Woods (1996) confirmed this pattern of habitat segregation in areas of sympatry using a spool-and-line method. They found ship rats spent significantly more time in the tree canopy, while Norway rats spent significantly more time on the ground, rarely climbing.

In Britain and USA, Norway rats are more abundant than ship rats, even though the ship rats were first to arrive (Taylor 1975). The British experience was duplicated in Southwest Georgia, where Ecke (1954) described how Norway rats slowly invaded, and displaced ship rats. The two species were found together only in a small number of multiple storey buildings, with ship rats occupying the upper half of the buildings, and Norway rats in the basements. Because there are only a small number of multiple storey buildings in Georgia, Ecke (1954) concluded that both species cannot coexist unless there are sufficient resources for both food and habitat. Where there were no multi storey buildings ship rats could not avoid Norway rats so were displaced. One reason why the outcome of competition is different in Britain and USA is that ship rats are not able to take refuge in the forests, as they are already occupied by several species of efficient arboreal foragers, the tree squirrels of the family *Sciuridae* (Gurnell *et al.* 2008).

The discovery that Norway rats can climb (Chapter Two) is puzzling. The question needs to be asked: why don’t Norway rats climb in the forest like ship rats do? There are several possible answers to this that need to be further researched: (a) they can climb if they choose to, but falling from a height carries a greater risk of injury for a heavier animal, so where ground-based options are available, most individuals prefer to forage there, (b) they were bored with the bare concrete floor in the enclosure, (c) they were able to climb the devices in these experiments but because of some unknown reason, are unable to climb real trees due to differences in texture, shape, etc, (d) larger energetic costs and slower speed of vertical climbing by a heavier rat, and their restrictions to the larger stronger branches, may limit their foraging opportunities in the canopy, especially if the canopy resources have already been diminished by ship rats, and lastly, (e) predation from mustelids.

Body size affects the foraging decisions of rodents. It determines not only prey handling ability, but also the ability to digest low nutrient plant material, speed and the energetic costs of travelling (Price 1983). Smaller mammals have lower total food requirements, but higher per gram (Schmidt-Nielsen 1984), so in sympatric rodent communities including species of different body sizes, the smaller species tends to be the more efficient forager (Rosenzweig and Sterner 1970; Kotler and Brown 1988). This was the case with the gerbil species *G. allenbyi* and *G. pyramidum.* The larger *G. pyramidum* had significantly lower handling time with prey than *G. allenbyi*, but the smaller *G. allenbyi* had a much higher encounter rate with prey, with may give them an advantage over *G. pyramidum* during times of low resource availability (Kotler and Brown 1990).

The larger body size of the Norway rat may give them an advantage during interference encounters with ship rats, but at the price of decreased efficiency in exploitation competition for the resources in the forest canopy. Larger animals can benefit from interference behaviours in response to competition from smaller, closely related animals, as the costs and risks of such behaviours are cheaper for larger animals (Persson 1985). When interspecific competition is asymmetrical, with one species dominant over the other during interspecific encounters, the subordinate species generally becomes restricted to habitats or time periods where interference from the dominant species is not profitable (Case and Gilpin 1974). In this case, ship rats can escape to the tree canopy where it may not be profitable for Norway rats to go.

The interactive effects of both exploitation competition and interference competition are in other species too. Fellers (1987) observed both forms of competition taking place between nine species of ants living in a woodlot in Maryland, USA. The dominant ant species physically prevented the subordinate species from accessing the food whenever they met, but the subordinate species overcame this by being more efficient and quicker at gathering food. The author found that there was an inverse relationship between dominance and the relative speed with which the baits were accessed. The subordinate species was able to locate and use resources rapidly while the dominant species exhibited aggression, territoriality and used poisons. A balance between all forms of interference and exploitation competition in a complex habitat allowed all nine species of ant to coexist.

A similar scenario has been observed in Australian honeyeaters. Ford (1979) proposed the idea that a balance of both interference competition and exploitation competition allows the species to coexist. He hypothesised that the larger species are more efficient at interference competition through aggressive exclusion, while the smaller species are more efficient at exploitation competition, by being able to utilise smaller amounts of nectar, from smaller flowers.

King and Moors (1979) also observed a similar pattern of shifting advantages in interspecific competition with weasels *Mustela nivalis*, and stoats *M. erminea*. Weasels are more efficient at exploitation competition as they can exploit small prey and can breed rapidly, while stoats are superior in interference competition as they are the larger of the two species, but are limited by being able to only produce one litter per year. King and Moors (1979) concluded that this balance between these two species is determined by the heterogeneity of the environment and the distribution of the prey fauna.

Ship rats are less tolerant of cold temperatures than are Norway rats, and seem to be more successful in tropical climates (Taylor 1975). They also tend to prefer structurally complex forests (Harper *et al.* 2005), where their arboreality allows them greater ecological flexibility (Radar and Krockenberger 2006). The warmer climate and variety of vertically complex habitats available to ship rats in New Zealand forests may both give ship rats a significant additional advantage over Norway rats.

An important parallel case was identified by Brown (1971), who looked at the interspecific interactions between two species of chipmunks *Eutamias dorsalis* and *E. umbrinus.* He found that *E. dorsalis* was dominant over *E. umbrinus* in habitat with few trees, because *E. dorsalis* could normally win aggressive encounters, but when the habitat was a complex forest, the primarily arboreal *E. umbrinus* was able to escape through the trees and *E. dorsalis* became the less dominant species in that environment. Brown (1971) noted that this relationship is similar to that of the Norway rat and the ship rat, in that the different abilities to take refuge in trees and buildings by the two species, and their differences in levels of aggression, are important in deciding the outcome of interactions between the two species.

CONCLUSION

The results described in this thesis are consistent with the prediction that the distribution of ship rats and Norway rats in New Zealand could be governed by a shifting balance of exploitation competition and interference competition. Both species are superior at some form of interspecific competition depending on the habitat they are in. Ship rats are apparently the superior competitor in exploitation competition in New Zealand native forest, while Norway rats are superior in interference competition, during encounters on the ground. The balance between these forces is influenced by habitat (complex vertical structures favouring ship rats) and climate (cold climates are favoured by Norway rats). However other factors such as predation may contribute to governing the overall distribution of these two species in New Zealand (Taylor 1978; 1984) but this idea has never been tested.

FUTURE RESEARCH

Diet analysis and intensive behavioural observations of wild rats of both species, comparing areas of sympatry and allopatry, may be able to determine whether the foraging choices of the two rat species vary according to whether the other species is present or not. Where both species coexist, removal experiments, with a controlled distribution of food supplies, may be able to precipitate behavioural changes that could illustrate the finer details of their relationship.

More detailed information is needed on how high Norway rats can climb, when they choose to. All of the eleven Norway rats tested in the enclosure climbed to 2.0 metres, which was the highest stand available (2.0 metres), although not often and not well. Some Norway rats managed to traverse the thinnest rope, even though with difficulty and much less often than did the ship rats, so tests are still needed to determine how thin a piece of rope has to be before they can no longer traverse it. This information may be important to conservationists, when deciding on safe havens for translocated birds. Using more realistic climbing structures, such as real trees may also ensure the results are more reliable and better represent the conditions that would be encountered in native forest by rats.

Body size determines the energetic costs of climbing. Taking physiological measures such as oxygen intake and CO^2 output, when rats of various sizes are active on slopes of increasing incline would help to construct a model of the energetic costs of foraging on versus above the ground for the two species. If the energy expended by a larger rat to climb a tree exceeds the potential reward from the foraging opportunities in the canopy, especially if the canopy resources have already been diminished by ship rats, the reasons why the larger Norway rat do not climb become clearer.

Only two studies to date has been conducted trapping Norway rats on the mainland, which excludes Stewart Island. Innes *et al.* (2001) trapped 43 Norway rats, 34 of which came from a single trap next to a stream at the Pureora Forest

Park, on the edge of an unlogged piece of forest, and lastly Morgan *et al.* (2009) trapped two Norway rats in a gully in Hamilton city. More research is needed on the habitats, behaviour, and ecology of this species, in these habitats, on the New Zealand mainland.

Animal ethics is important in designing humane experiments with animals. In order to design experiments which will produce informative results while also safeguarding experimental animals, it would be helpful to have some new but ethical acceptable experimental designs to look more closely at the natural history of interference competition between these and other species.

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