An investigation of the factors regulating house mouse (*Mus musculus*) and ship rat (*Rattus rattus*) population dynamics in forest ecosystems at Lake Waikaremoana, New Zealand.

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Sunset in Wairau Arm, Lake Waikaremoana, New Zealand.

Photo by Pete and Judy Morrin

For Derek

General abstract

Factors regulating the eruptive population dynamics of house mice, *Mus musculus*, and ship rats, *Rattus rattus*, were investigated over 29 months in mixed forest at Lake Waikaremoana, New Zealand. Mice and rats are generally present at low density, but erupt periodically following synchronous southern beech (*Nothofagus* spp.) seeding. A range of factors proposed as important in shaping the population dynamics of these species was investigated. These included rodent diet and habitat use, and the roles of food availability and predation pressure. Changes in rodent population dynamics were investigated using three relative density estimates: footprint tracking tunnels; and two kill trapping indices. Tracking tunnels gave reliable density estimates, but were influenced by sampling effort and habitat type. Rats had an opportunistic, omnivorous diet, and had no measurable detrimental effects of stomach parasite infection. Rats were generally more common in forest with the most food, but became equally abundant in all areas following widespread synchronous tree seeding. Rats were more numerous in areas with predators removed. Mice were found in all areas following *Nothofagus* seeding. Mice became scarce as food levels dropped, suggesting that the forest habitat does not contain enough food to support them in most years. The roles of food limitation and predation in shaping rodent population dynamics were investigated initially by computer modelling. The model showed that predators could not prevent a rodent population eruption, nor limit peak prey-population density. However, predation may be important during the decline and low phases of the eruption. The predictions of the model were tested in a large-scale field experiment. Predators were removed from a 750 ha peninsula in the study area. Rodent population dynamics during an eruption were compared in large areas with and without predators present. Predators did not prevent a prey eruption or limit peak population size as predicted by the computer model. There was evidence that predators limited prey populations during the post-eruption low phase, but the role of predation during the rodent decline remains unclear. Thus, the eruptive population dynamics of mice and rats in forest ecosystems in New Zealand are driven primarily by spatial and temporal variation in food supply, with predation by a single common predator potentially important during the crash and low phases following a population eruption.

Thesis Format

The chapters of this thesis are presented in a self-contained paper format. Each chapter consists of an Abstract, Introduction, Methods, Results, Discussion, and Reference section. Inevitably, this does lead to some repetition, especially in the reference lists, but allows each section to become more focused on a specific topic, and more easily followed.

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But hey, enough of my yacking.

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Chapter 1: General Introduction

1.1 Introduction

While the population dynamics of small mammal communities have been extensively described and classified (Krebs *et al.* 1973; Gilwicz 1980; Lidicker 1988; Newsome 1990), the mechanisms underlying and driving these dynamics are not well understood. A vast number of hypotheses that attempt to explain small mammal population dynamics have been proposed (for reviews, see Batzli 1992; Krebs 1996), but so far they have failed to provide the unifying laws many early ecologists hoped underpinned the science.

Early studies of the population dynamics of small mammals (including members of the orders Rodentia, Lagomorpha, Marsupialia, the predatory families Vivveridae, Mustelidae, and some members of the Felidae and Canidae), perhaps naïvely, looked for single factors that would explain the stable, cyclic or eruptive population dynamics exhibited by these species. While this simplifies the questions asked, difficulties can arise in explaining any deviation from the proposed hypothesis if more than one factor is involved (Lidicker 1988).

Most frequently, studies of the population dynamics of small mammal species have focused on the roles food quality or quantity (Flowerdew and Gardner 1978; Bomford 1987; Bomford and Redhead 1987; Craig and Bunn 1989), predation (Pearson 1966; Henttonen *et al.* 1987; Norrdahl and Korpimäki 1995; Reid *et al.* 1995; Korpimäki and Norrdahl 1998) or individual differences between members of the community (Chitty 1960; Boonstra and Rodd 1983; Gilwicz 1990; Blackburn *et al.* 1998) play in determining the observed population dynamics. Recently, there has been a growing realization that a population will interact with a range of biotic and abiotic factors at a higher, lower, or similar trophic level, that may vary spatially and temporally to shape the ecology of a species (Lidicker 1988; Desy and Batzli 1989; Krebs *et al.* 1995; Krebs 1996). Very rarely does a single factor explain the behaviour exhibited by the population. An understanding of the ecology of a species therefore becomes more a

question of, for example, the relative importance of bottom up versus top down regulation (Matson and Hunter 1992), or the relative importance of food limitation and predator limitation (Linden 1988; Krebs 1996), rather than a question of which single factor controls a particular species or system.

1.2 Classes of small mammal population dynamics

Small mammal population dynamics are generally divided into three categories (Table 1.1): 1). Stable populations. These are characterized by a regular, annual variation in numbers, from a low at the start of the breeding season, to a peak following juvenile dispersal. 2). Cyclic populations. These go through a regular multi-annual cycle of increase, peak, decline and low phases (Krebs *et al.* 1973), with a period between peaks of 3-4 years for a number of microtine species (Krebs 1996), and 8-10 years for snowshoe hares in North America (Krebs *et al.* 1986; Sinclair 1986). 3). Eruptive populations. These exhibit low density for a variable length of time before a change in extrinsic factors allows a short-lived population eruption (Newsome *et al.* 1989; Murphy 1992; Pech *et al.* 1992).

Eruptive population dynamics are the least common and least widely studied of the classes of population behaviour exhibited by small mammal species (Newsome 1990). The eruptive system is most commonly seen in disturbed or modified habitat (e.g. mice, *Mus musculus*, in agricultural regions of Australia, Newsome 1969; Newsome 1970; Sinclair *et al.* 1990), in systems with introduced *r*-selected (MacArthur and Wilson 1967) species (e.g. rabbits, *Oryctolagus cuniculus*, in semi-arid Australia, Newsome *et al.* 1989; Pech *et al.* 1992), or where energy inputs into the system are irregular (e.g. bank voles, *Clethrionomys glareolus*, in Denmark, Jensen 1982; ship rats, *Rattus rattus*, and house mice in New Zealand forests, Fitzgerald 1978; King 1983; Fitzgerald *et al.* 1996).

Table 1.1 Characteristics of stable, cyclic and eruptive small mammal population dynamics. 'Regularity of input' refers to how frequently energy (in the form of plant or animal food) is supplied into the bottom of the system. 'Generality of dynamic' refers to how many small mammal species present in the community show the particular class of population dynamic.

Parameter	Stable populations	Cyclic populations	Eruptive populations
Period of fluctuation	Annual cycle, with peak following juvenile dispersal[1]	Multi-annual, 3-4 year period in lemmings and voles[2], 8-10 years in snowshoe hare[3]	Variable duration; period of low density, followed by eruption (every 3-4 years in New Zealand forests[4])
Amplitude of fluctuation	Small regular[2]	Large (26-100 fold increase), regular amplitude[3,5]	Small in low phase, large in eruption (10-20 fold increase)[4,6]
Generality of dynamic	Most if not all species in community[7]	Many species in synchrony[8]	Few or many[9]
Regularity of energy input	Annual production[10]	Annual production[3,11]	Variable, usually 3-4 years[4,6]
Role of predation	Year-round generalist predators. High predation pressure, possible predator limitation[5,7]	Mix of generalist and specialist predators. Time-lags in predation pressure possible[5,12,13]	Unclear, predators may limit in the low phase, may not affect the size of eruption[14]

1. (Montgomery 1989) 2. (Krebs *et al.* 1973; Taitt and Krebs 1985) 3. (Boutin *et al.* 1995) 4. (King 1983; Fitzgerald *et al.* 1996) 5. (Hanski *et al.* 1991) 6. (Jensen 1982) 7. (Erlinge *et al.* 1983) 8. (Henttonen *et al.* 1987) 9. In northern beech forests in Denmark, bank voles (*Clethrionomys glareolus*) erupt following synchronous beech seeding but yellow-necked fieldmice (*Apodemus flavicollis*) do not (Jensen 1982), In comparison, in semi arid Australia, both introduced European rabbits (*Oryctolagus cuniculus*) and native rodents and marsupials increase in number following drought-breaking rains (Newsome *et al.* 1989). 10. (Batzli and Pitelka 1983; Lindroth and Batzli 1984) 11. (Lidicker 1988) 12. (Korpimäki *et al.* 1991) 13. (Krebs 1996) 14. (Newsome *et al.* 1989; Sinclair *et al.* 1990; Pech *et al.* 1992).

In comparison to stable and cyclic populations, eruptive populations are driven primarily by variation in food supply (bottom up regulation) (Jensen 1982; Newsome *et al.* 1989), with variation in the size of the energy input determining the size of the population eruption (Fitzgerald *et al.* 1996). The role of predators in these systems has not been clearly elucidated. Work in Australia has shown that predators may be able to keep low-density populations in a "predator pit" from which they cannot escape until a change in food supply provides sufficient energy for widespread breeding and an eruption to high density (Sinclair *et al.* 1990; Pech *et al.* 1992). The predator limitation of pre-eruption populations appears to be due to density dependent changes in the functional response of the resident predators (Sinclair *et al.* 1990), although the predator functional response cannot compensate for the large numerical response in the prey species to increased food during the eruption. It is not clear, however, what role predators play in the peak, decline and crash phases of the eruption. Peak prey populations are influenced by an ephemeral energy input, and are not sustainable, so the question becomes one of what role predation plays in the crash phase, and does the presence of predators affect the timing, duration or magnitude of a crash that theory predicts will occur irrespective of any predator induced mortality?

1.3 Small mammal predator/prey systems in New Zealand.

New Zealand is globally unique in having a large land mass and large endemic flora and fauna that, prior to human colonization (c.1000 years b.p.), contained no terrestrial mammals (King 1990a). Humans have introduced a range of small mammal species (Table 1.2) that are now present in various combinations in most natural and modified habitats in New Zealand. The three most common small mammal species in forest ecosystems in New Zealand now are the house mouse (Plate 1.1), the ship rat (Plate 1.2), and the stoat (*Mustela erminea*) (Plate 1.3), with weasels (*M. nivalis*) and cats (*Felis catus*) present in low numbers (King 1990a).

In southern beech (*Nothofagus* spp.) and mixed *Nothofagus*-Podocarpacae forests in New Zealand, house mice, ship rats and stoats constitute an eruptive predator-prey

Plate 1.1 The house mouse, *Mus musculus*. Photo R. Whitford.

Plate 1.2 The ship rat, *Rattus rattus*, photographed in front of a snap-trap cover, Treatment area 1, Lake Waikaremoana, New Zealand. The rat shown is the black colour morph *R.r.rattus*.

Plate 1.3 Stoat, *Mustela erminea*. New Zealand animals are significantly larger than British animals from which New Zealand populations originated. Photo: P. Morrin.

Table 1.2 Characteristics of common small mammals introduced into New Zealand. Prey and predator species are listed chronologically by date of introduction. Data from King (1990a).

Species introduced	Date/mode of introduction	Current distribution	Population dynamics	Conservation threat
Prey Species				
Kiore (*Rattus exulans*)	c.1000 years b.p/ polynesian settlers	Restricted on mainland New Zealand	Previously widespread and eruptive in mainland beech forest	Minor
House mouse (*Mus musculus*)	1820s / European settlers	Common in commensal situations, present in most forested habitats	High density populations in commensal situations, eruptive in beech forest	May affect seed and seedling set, and some invertebrates. Support predators in beech forest
Norway rat (*R. norvegicus*)	Late 1700s/ European explorers and settlers	Moderate numbers in commensal situations, rare in natural ecosystems	High density populations in commensal situations, unclear in natural situations	Minor on the mainland, may threaten seabird populations
Ship rat (*R. rattus*)	Mid 1800s / European settlers	Common in commensal, forested and agricultural systems	Variable; stable population dynamics in mixed/broadleaf forests/eruptive in beech forest	Major seed, invertebrate and bird predators. Support predator populations
Predator Species				
Cat (*Felis catus*)	Late1700s / European explorers and settlers	Common in commensal situations, grasslands; low density in forest systems	Regular annual variations, limited by ship rat and rabbit numbers?	Threat to a number of grassland and coastal species
Weasel (*Mustela nivalis*)	1880s / European pastoralists	Localized, common following beech seeding	Generally rare, increase following mouse eruptions	Unclear
Stoat (*M. erminea*)	1880s / European pastoralists	Widespread in forest and grassland	Stable in podocarp forest, eruptive in beech forest	Implicated in the decline of a range of native fauna
Ferret (*M. furo*)	1880s / European pastoralists	Common in agricultral and native grasslands	Stable, linked to rabbits on grassland	Locally important predators of grassland species

assemblage (Fitzgerald 1978; King 1983; Fitzgerald *et al.* 1996). Populations of mice and rats exhibit short-term eruptions following synchronous southern beech seeding, which in turn leads to short term increases in predator densities (King 1990b), before prey and predator densities crash back to pre-eruption levels (Murphy 1992).

In comparison to the Northern Hemisphere systems from which they came, these species represent a very simple predator/prey system that lacks many of the multitude of intricate trophic interactions found in Northern Hemisphere, or Australian, small mammal communities.

There are several reasons why the New Zealand small mammal assemblage provides excellent opportunities for studying the interactions between potential population limiting or regulating factors:

1. The small number of species involved. In most forest communities, there are only two rodent prey species (house mice and ship rats), and one common predator (the stoat). As a result, causal relationships between predators and prey can more clearly be seen, and are not greatly confounded by factors such as prey switching by predators, or strong inter-specific competition between prey.

2. The identity of species involved. Globally, New Zealand presents the only situation where house mice and ship rats are present as the only rodent species common in a forested ecosystem, and where their only common predator is the stoat. As a result, the predator-prey association does not share a common evolutionary history, and the interactions between the species are not clouded either by arguments invoking possible past competition between species (the ghost of competition past; Connell 1980) or by a common co-evolved predator/prey system (Krebs and Davis 1993). The system therefore provides an excellent opportunity to study the relative importance of multiple factors in determining population dynamics of small mammal species, and allows us to test the applicability of predator/prey theory in a "human initiated", natural community.

3. Management implications. Currently, endemic New Zealand species are threatened by predation from introduced small mammals, especially the ship rat and stoat (see Innes 1990; King 1990b). Efforts to reduce the threat to native species are often focused at the species level, and take the form of targeted predator control. Investigation into the ecology of the small mammal assemblage can thus help to recognize the potential impacts of removing or controlling one component of the predator:prey system, and highlight any implications for native species that this manipulation may have.

While the small mammal community in New Zealand forests presents an excellent opportunity to study the factors driving these systems, there are still many aspects of the ecology of the species involved that we do not understand.

The exact nature of the responses of rodents to increased energy at the start of an eruption has not been fully established. While the amplitude of the mouse response to the beech seedfall is significantly correlated with the size of the seedfall (Fitzgerald *et al.* 1996), it is not clear if mice respond to shed beech flowers, the seed itself, or to increased numbers of invertebrates that feed on the seed (Murphy 1992; Fitzgerald *et al.* 1996). The mechanism of the response to the beech seeding in ship rats is also unclear. Beech seed may be too small to constitute profitable food, so rat population increases may be triggered by something other than seed density *per se*.

The social structure, diet, and behaviour of ship rats in beech forest has been poorly studied. Ship rats are more common in broadleaf or mixed forest than in beech forests (Innes 1990) and although it has been suggested that this is due to increased habitat diversity in broadleaf-mixed forest over beech forest, the underlying mechanisms have not been determined.

Similarly, it is not clear what role predators play in the eruptive system in New Zealand. King (1983; 1985) suggested that predation by stoats may hasten the decline in house mouse populations following the peak phase of a population eruption, a phenomenon that has been demonstrated with red fox (*Vulpes vulpes*) predation on declining rabbit populations in Australia (Newsome *et al.* 1989).

Therefore, New Zealand presents a relatively simple predator/prey system in which to test theories of the interaction between predator and food limitation of small mammal populations. However, there are aspects of the underlying ecology of the species involved that must be clarified if an accurate understanding of the system is to emerge.

1.4 Aims of the study

The primary objective of the study was to identify the factors that determine the eruptive population dynamics of rodents in forest communities in New Zealand. Given current knowledge of the ecology of house mice and ship rats (Innes 1990; Murphy and Pickard 1990) and stoats (King 1990b) in New Zealand, and current small-mammal population ecology theory (Lidicker 1988; Newsome 1990; Krebs 1996; May 1999), the study had three specific aims:

1. To identify the diet of ship rats in mixed forest, and investigate the role of variation in food availability and diet flexibility in the eruptive population dynamics of ship rats.

2. To investigate the influence of food availability, and forest structure and composition, in determining the habitat use of ship rats in mixed forest in New Zealand.

3. To identify the role of predators in the eruptive population dynamics of rodents in a New Zealand forest ecosystem, and investigate any interactions between variation in food supply and predation pressure in shaping rodent population dynamics.

1.5 The study area

The study was conducted at Lake Waikaremoana (38° 47′ S 177° 05′ E), situated at the south-eastern corner of Te Urewera National Park (212,000 ha), in the North Island of

New Zealand (Figure 1.1). This study was run in conjunction with a larger project (McLennan 1997) investigating the dynamics of the small mammal/predator system, and the implications this has for the threatened northern brown kiwi (*Apteryx australis mantelli* Bartlett).

The lake covers 5,170 ha, and is 582 m a.s.l. The catchment is steep and almost entirely forested with old growth podocarp (Podocarpacae) and southern beech (*Nothofagus* spp.) forests (Plate 1.4). The lake margin is covered with a mix of introduced grasses, sedges, and regenerating manuka (*Leptospermum scoparium*) scrub (McLennan *et al.* 1996).

Large-scale predator trapping was carried out from May 1995 to the end of the study in March 1998 on Puketukutuku peninsula (750 ha), in an attempt to increase northern brown kiwi recruitment rates (McLennan 1996; Basse *et al.* 1999). Trapping targeted stoats, which have been shown to be significant predators of juvenile kiwi (McLennan *et al.* 1996), but also caught other mammals present in the area in low numbers, including weasels, ferrets (*Mustela furo* L.), feral cats and ship rats.

1.6 The study

Any study of population or community ecology depends on an ability to accurately census the population of interest, and to record changes in population density or dynamics. For many small mammal communities, especially in complex environments where direct enumeration is not possible, this necessitates the use of relative density indices. In studies of rodents and predators in New Zealand, this has been attempted using trap capture rates, and more recently, through the use of footprint tracking tunnels (King and Edgar 1977) to measure changes in activity and abundance. However, relative indices are subject to a number of biases that may affect their reliability. Therefore, before using relative density indices to investigate changes in rodent populations following predator reduction, I tested the reliability and

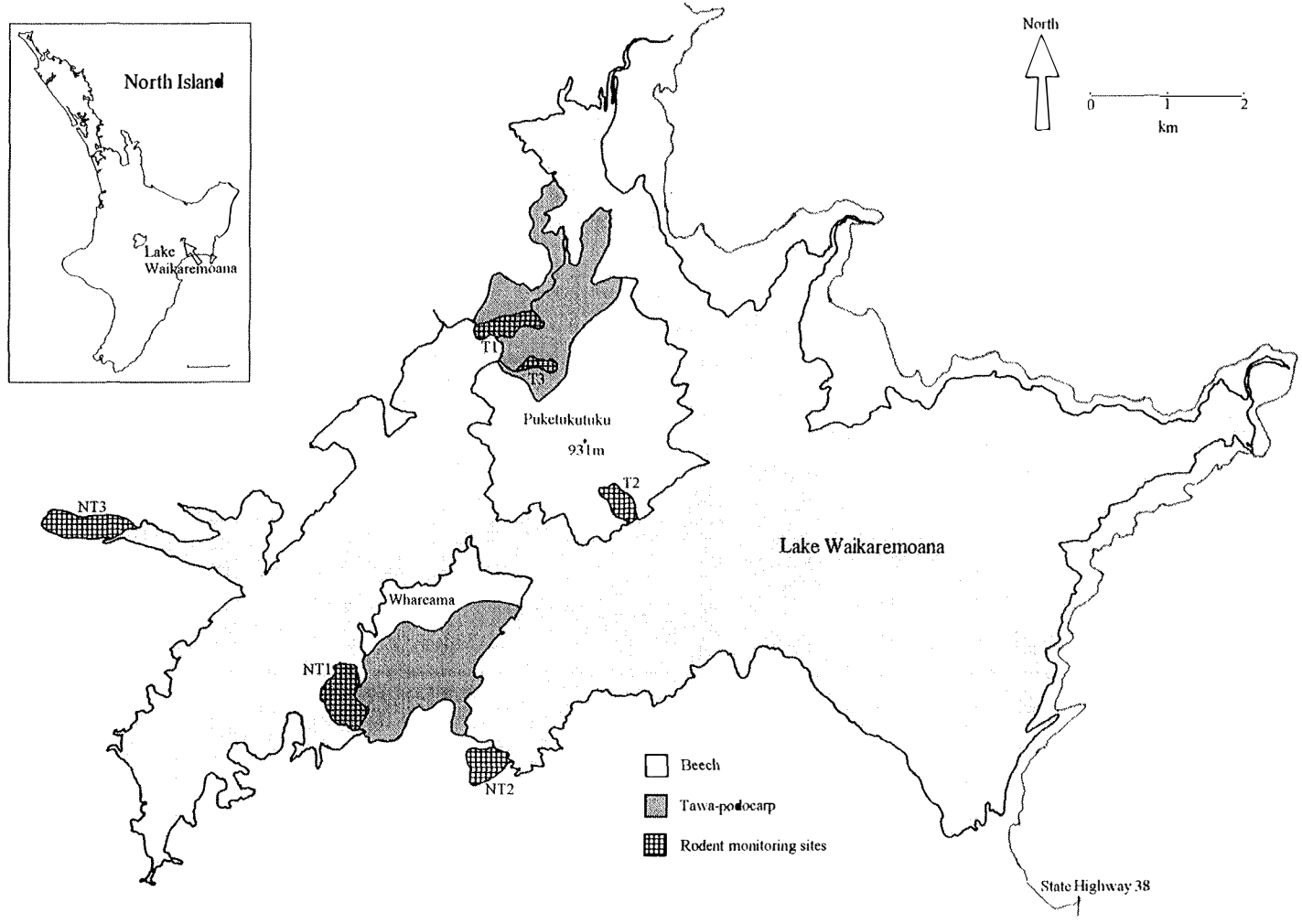

Figure 1.1 Map of the study area at Lake Waikaremoana, Te Urewera National Park, North Island, New Zealand. Predators were trapped on Puketukutuku peninsula (750 ha) from May 1995 to March 1998. T1, T2 and T3 refer to rodent-monitoring areas on the treatment peninsula, while NT1 and NT2 refer to non-treatment areas on Whareama peninsula (450 ha), and NT3 to a non-treatment area in Maraunui bay, where no predator removal was conducted. Scale on the small figure represents 100 km.

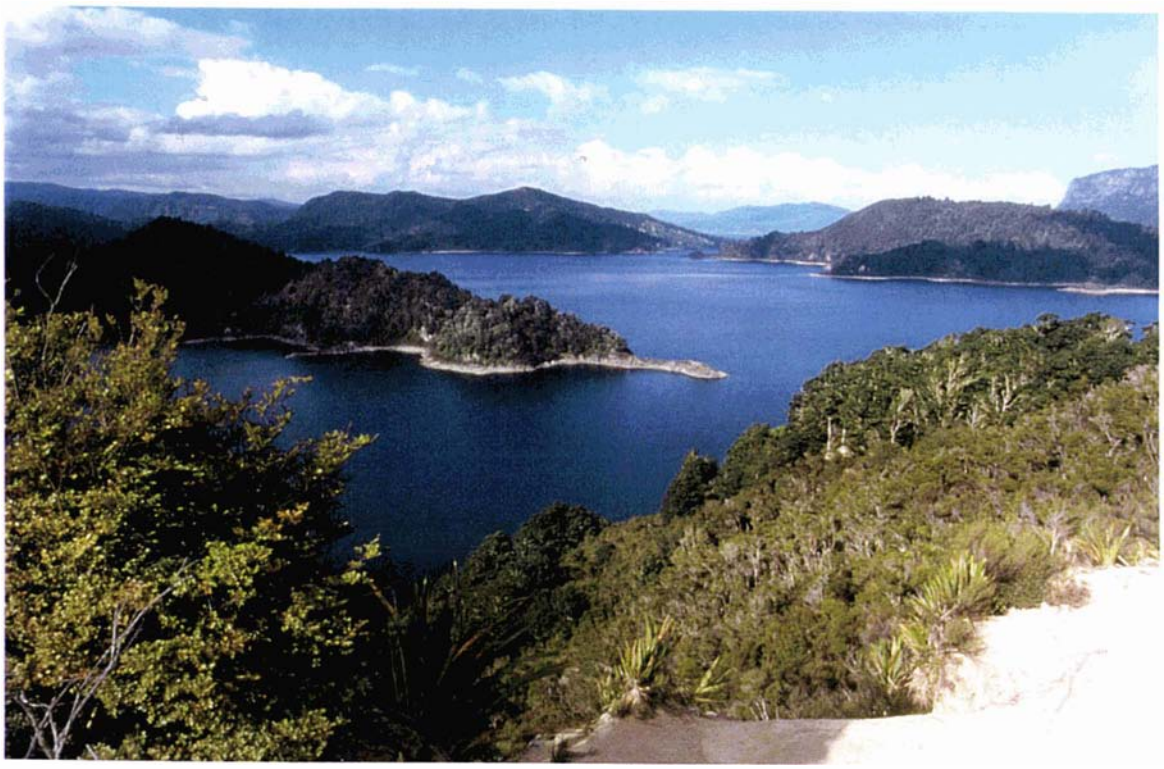

Plate 1.4 View of Wairau arm of Lake Waikaremoana, New Zealand. Puketukutuku, the treatment peninsula is in the middle-distance, while Whareama peninsula, the non-treatment area, is on the right, with the Panekiri Bluffs behind.

repeatability of density estimates obtained from density indices commonly used in New Zealand (Chapter 2; Calibration of tracking tunnels, snap traps and Fenn traps: Do they tell the same story?).

The ability to persist in a wide range of habitats, and respond to an unpredictable resource such as the irregular energy input from synchronous beech seeding, suggests that ship rats have a fairly catholic diet that can respond to changes in food availability and quality. An omnivorous diet has been reported elsewhere in the ship rat, both in New Zealand (Best 1969; Daniel 1973; Innes 1979; Gales 1982) and internationally (Clark 1980; 1982). An investigation of such diet flexibility is an important step in understanding the factors that govern small mammal populations, especially in understanding how large changes in food availability during a beech masting affect ship rat and mouse populations. Therefore, in Chapter 3 (Diet and diet selection in ship rats in mixed forest at Lake Waikaremoana, New Zealand), I present data on the food consumed by ship rats caught in the study area over an 18 month period, and compare this to estimates of food availability in the environment. Chapter 3 also presents data on infection rates of stomach parasites in rats caught during the study, to investigate if parasite loads might influence population density or dynamics.

In Chapter 4 (Habitat use of house mice and ship rats in a mixed forest mosaic at Lake Waikaremoana, New Zealand), I investigate the distribution of house mice and ship rats among two broad forest types at Lake Waikaremoana. I test whether mice and rats are habitat specialists (confined to a small subset of microhabitats) or habitat generalists (associated with broad-scale environmental gradients).

Given the primary importance of changes in food availability in driving the irregular eruptions of rodents in New Zealand forests (King 1983; Murphy 1992; Fitzgerald *et al.* 1996; Chapter 3, this study), the question remains, what role do predators play, if any, in the rodent population dynamics? In Chapter 5 (A computer simulation of rodent and predator population dynamics in an eruptive system) I present a synthesis of the current understanding of the small mammal assemblage in New Zealand forests, through the construction of a computer model of house mouse, ship rat and stoat population dynamics. The model was constructed using current knowledge on rodent and predator biology and ecology in New Zealand and elsewhere, and was used to

generate a number of predictions regarding the role of predators in a primarily food-driven system. It serves to highlight what we do not currently know, as much as what we do know, about the biology and ecology of rodents and their predators in New Zealand.

In Chapter 6 (The role of predators in ship rat and house mouse population eruptions: Drivers or passengers?) I test a number of predictions regarding the role of predators in a population eruption generated from the literature and the computer model developed in Chapter 5. Large-scale predator reduction was carried out in the study area, and the role of predation in prey population dynamics was tested by comparing the responses of ship rat and house mouse populations in areas with and without predator reduction.

Chapter 7 presents a synthesis of the factors influencing the eruptive population dynamics of rodents in New Zealand mixed forests. Specifically, I discuss the relative importance of food availability, habitat heterogeneity and predation pressure in determining eruptive rodent population dynamics.

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Chapter 2: Calibration of tracking tunnels, snap traps and Fenn traps: Do they tell the same story?

2.0 Abstract

Density indices of free-living populations of ship rats (*Rattus rattus* L.) in mixed forest in New Zealand obtained using footprint tracking tunnels and two kill-trapping indices were compared. Tracking tunnels and snap-trap estimates of rat density were tightly correlated when run over five consecutive nights on a 9 ha trapping grid. Tracking rates and snap-trap capture rates were not significantly correlated when run along a trapping line for a 12 month period, although tracking rates and the total number of rats caught in a trapping session were significantly correlated. Time series analysis showed that rat density indices from tracking tunnels and Fenn-traps were significantly correlated when run for 27 consecutive months in a rat population with moderate density. Time series analysis showed that tracking rates and Fenn-trap capture rates over a 27 month period were negatively related in a low density rat population. The findings highlight the importance of habitat, sample size and target species behaviour in influencing relative density indices obtained from tracking tunnels, snap-traps, and Fenn-traps. I suggest that tracking tunnels should be used to compare relative abundance within similar habitat types, and to only compare population trends between habitats. Tracking tunnels should always be complemented with a second density index.

2.1 Introduction

In the majority of studies of small mammal populations, difficulty in measuring absolute abundance necessitates the use of relative density measures. Obtaining a measure of absolute abundance requires that the study area can be completely covered, that all individuals can be recognised and counted, and that contagion effects do not bias the estimate of population size (Caughley 1977; Pollock *et al.* 1990). In comparison, relative density measures are less costly and time consuming to conduct, do not rely on exhaustive enumeration of all individuals in a population, and, in most situations, can provide similar amounts of information as direct counting (Caughley 1977).

The choice of density estimate or index will depend on the question to be addressed, and the biology of the species under investigation. Studies investigating population parameters such as reproductive or survival rates are best tackled with mark-recapture techniques (Pollock *et al.* 1990; Lebreton *et al.* 1992). In comparison, questions pertaining to relative changes in population size following perturbation to the system can often best be answered with relative density indices, such as track deposition rates (King and Edgar 1977; Korpimäki *et al.* 1991; Reid *et al.* 1995; Korpimäki and Norrdahl 1998).

Despite their widespread and frequent use in all areas of ecology and population biology, relative density indices are susceptible to a number of biases. Problems previously noted include saturation of the indexing technique allowing non-linear relationships to develop (Tanaka 1960; Caughley 1977), and modification of responses of the target species to the indexing method by competitors or predators (Brown *et al.* 1996). There is also a tendency for relative indices to measure activity as well as abundance (Sheppe 1965; Sarrazin and Bider 1973; King and Edgar 1977). This can increase variability in the index, and may reduce the wide scale applicability of any conclusions. In the worst case, this may limit the applicability of the conclusions to only the system under study.

In New Zealand, footprint tracking tunnels (King and Edgar 1977) are a widely used small-mammal density index (Plate 2.1). Tracking tunnels rely on ink-pads and paper

Plate 2.1 End view of footprint tracking tunnel, Non-treatment area 3, Lake Waikaremoana, New Zealand. The peanut-butter bait can be seen on the end of the tunnel, and the prints of a ship rat are recorded on the tracking paper inside.

to record target species tracks, and by extrapolation, abundance, and have largely replaced the use of kill-trapping as the primary rodent index employed (Innes *et al.* 1995). Brown *et al.*(1996) compared density estimates of ship rat (*Rattus rattus* L.) and house mouse (*Mus musculus* L.) populations using footprint tracking tunnels and removal trapping from a trapping grid. They found a tight relationship between the two indices over the short, intensive time frame of the experiment, but noted that the relationship may not be as tight under different experimental protocols, or if run at a different time or location. Brown *et al.* (1996) are the only authors known of to have tested indices of ship rat and mouse relative density.

Further investigation of the relationship between relative indices and measures of absolute abundance of rodents in New Zealand is clearly needed. In recognition of this, I compared ship rat density estimates obtained from tracking tunnels and trapping, under three experimental situations.

1). A removal trapping grid similar to Brown *et al.*'s (1996) was run in similar forest, but later in the year.

2). Density estimates obtained along a trapping- and indexing-line run earlier through the same habitat were compared, allowing the investigation of the influence of running these indices on a trap-line, rather than in a grid situation.

3). Ship rat density estimates obtained from the tracking tunnel line were compared with two established Fenn-trap predator-trapping lines that were run continuously from January 1996 to March 1998. This included a rodent population eruption that occurred, following synchronous southern beech (*Nothofagus* spp.) seeding in autumn 1995 (Dr C. Ward, pers. comm.).

4). The indicated magnitude, and rates of change, in the rat populations obtained from tracking tunnels and Fenn-traps run in beech forest from January 1996 to March 1998 were also compared.

Thus I had four tests of the reliability of the tracking tunnel indexing technique, using two trap types, and two trap arrangements.

2.2 Methods

2.2.1 Study area

The study was conducted at Lake Waikaremoana (38° 47′ S 177° 05′ E,), situated at the south-eastern corner of Te Urewera National Park (212,000 ha), in the North Island of New Zealand. This study was part of a larger project investigating the dynamics of the rodent/mustelid predator/prey system, and the implications this has for the threatened northern brown kiwi (*Apteryx australis mantelli* Bartlett).

2.2.2 Trapping grid indexing

I followed the methods of Brown *et al.* (1996), and used the Zippin removal method of density estimation (Zippin 1958). In June 1998, a 300 x 300 m grid was established in an area of tawa-podocarp forest on Puketukutuku peninsula. The grid was approximately 600 m from the edge of the lake, at an altitude of 80-100 m above lake level. Single Ezeset Supreme™ rat traps (Plate 2.2) baited with peanut butter were placed at 25 m intervals across the grid. Three types of trap cover were used: 1) plastic, a 40 cm section of 20 cm diameter Novaflow™ drainage tubing; 2) wire, a "tent" of "chicken wire" approximately 40 cm x 20 cm x 20 cm, and secured by a metal hoop; and 3) natural, fallen logs, fern fronds, or other vegetation. Trap covers were sequentially alternated along each transect line of the grid. Twenty-six tracking tunnels were placed in four lines at 50 m intervals along transect lines 100 m apart. Each tracking tunnel was within 1-2 m of a snap-trap.

Traps and tracking tunnels were placed on the lines on 21 June 1998, and run for five consecutive nights from the 23-28 June 1998. Traps were set on the afternoon of the 23 June, and subsequently checked between 0800 and 1200 h each morning. The location, species, colour morph (for *Rattus rattus*) and sex of any animals caught were recorded. Any sprung traps were recorded, re-baited with peanut butter if required, and reset.

Plate 2.2 Snap trap set under a "natural" cover on the trapping grid run in June 1998 at Lake Waikaremoana, New Zealand. The metal hoop securing the trap can be seen in the foreground. The trap was unsprung with the bait gone when checked.

Plate 2.3 Ship rat caught as a by-catch in a Fenn trap, Lake Waikaremoana, New Zealand. The metal cover to prevent non-target captures has been lifted back, and the hens' egg bait can be seen.

The topography of each trap site was recorded as ridge, face, gully (Brown *et al.* 1996), with the addition of terrace (flat area with slope < 20°) and streambed. Whether the site was under either a tawa (*Beilschmiedia tawa*) or tree fern (Cyatheaceae and Diksoniaceae) sub-canopy was also recorded. All carcasses were kept for autopsy in the laboratory. Each animal was weighed and measured as per (Cunningham and Moors 1983), and the age of individuals was determined using reproductive indices (Daniel 1972) and tooth wear criteria developed for *R. rattus* (Karnoukhova 1971; Innes 1990) and for *M. musculus* (Lidicker 1966).

The effective trapping area was calculated by adding a boundary strip, as per Brown *et al.* (1996), using the same estimate of an average home-range radius of 56 m (Hooker and Innes 1995) for the width of the boundary. For this study, this gave an effective area of 17 ha.

2.2.3 Trapping line monitoring

In December 1996, rodent snap-traps were placed on an established trap-line in tawa-podocarp forest on the 750 ha Puketukutuku peninsula that juts into Lake Waikaremoana (Area T1, Figure 1.1). Forty single Ezeset Supreme™ rat traps were placed at stations 50 m apart along the trap-line, giving a total length of 2 km. Each trap was covered with a plastic trap cover similar to that used on the trapping grid and secured by a pin at either end to exclude non-target animals. Traps were baited with peanut butter, and run for three consecutive nights every six weeks between January and December 1997. During each trapping session traps were set in the evening of the first day, and checked between 0800 and 1000 h the next morning. The details of any capture were recorded as for the trapping grid. Any sprung traps were recorded, re-baited if required, and reset. At the end of the trapping session all traps were sprung, and left in place until the next trapping session. Captures per hundred trap nights (C100/TN) were corrected for sprung traps by subtracting half a trap night for every sprung trap recorded (Cunningham and Moors 1983).

Single tracking tunnels (King and Edgar 1977) were placed at 100 m intervals along the trap-line. Tunnels were run for a single night, usually within 2-3 nights prior to

the snap-traps, although on one occasion the tracking tunnels were run two weeks before the snap-trap indexing. Tracking tunnels were baited with peanut butter, set in the evening, and checked the following morning. Tracking rates are expressed as the percentage of tunnels tracked by a given species.

2.2.4 Fenn-trapping lines

As part of a large-scale predator control program, predator-monitoring transect lines were established in September 1994 through the bush and around the coastline on Puketukutuku peninsula. In May 1995, Mk 4 and Mk 6 Fenn kill traps (FHT Works, Redditch, England) (Plate 2.3) were placed at 150 m intervals along each of the transect lines on this peninsula, and on several additional ridges between transects. Traps were placed at 25 m intervals across the neck of the peninsula in an attempt to intercept any predators moving into the trapped areas. Fenn traps were also placed at each of the coastline stations on Puketukutuku peninsula. All traps were placed under wooden covers to prevent capture of non-target animals, and were baited with either hens' eggs or rabbit meat. Traps were run continuously from May 1995 until March 1998 and were checked every 7-10 days. The species, sex, and capture date and locations of all animals caught were recorded. Captures per 100 trap nights were calculated, and were corrected for sprung traps by halving the number of trap-nights for any traps sprung since the last trapping inspection.

2.2.5 Correlation between tracking tunnels and Fenn traps

Capture rates on the Fenn trap-lines in tawa-podocarp forest were compared with the tracking tunnels on the trapping line used in the snap-trapping trap-line calibration experiment. The tracking tunnels ran along the 25 m spaced Fenn trap-line for approximately 700 m (7 stations), before cutting approximately 400 m through the bush to intersect with a second trap-line (trap spacing, 150 m) running across the neck of the peninsula. The tracking tunnel line ran back down to the lake edge (700 m, 7

stations), and thus circumscribed an area of approximately 18 ha (Area T1, Figure 1.1).

The tracking tunnels were run each month from January 1996 to March 1998, using the one-night index described previously, and were compared with two density indices calculated from the Fenn trap-lines. A trapping rate was calculated for only those Fenn traps on the sections of trap-lines that had tracking tunnels on them ("Halfline"). The tracking tunnel rate was also compared with the average capture rates for all Fenn traps in podocarp forest.

Density indices were also compared from tracking tunnels and Fenn traps placed in beech forest on Puketukutuku peninsula. A line of tracking tunnels with 100 m spacing was established in December 1995 in beech forest at the far end of the peninsula (Area T2, Figure 1.1). The tracking tunnels ran up a Fenn trapping-line (Fenn line 31, 150 m spacing) for 500 m (5 stations), before looping back down to the lake edge (900 m, 9 stations), enclosing an area of approximately 15 ha. The tracking tunnels were run monthly using the one-night tracking protocol outlined previously. The tracking rate was compared with average Fenn capture rates from Fenn line 31 (900 m, 6 stations) and Fenn line 3 (3150 m, 21 stations), which ran across the peninsula and enclosed both Fenn line 31 and the tracking tunnel line.

2.2.6 Statistical analysis

Differences in capture rates between ages, sexes and locations of rats caught in the snap-trap trapping grid experiment were compared using chi-square (X^2) analysis, with significance levels determined from the X^2 distribution with the appropriate degrees of freedom.

Due to the short time frame and small sample size from the snap-trapping grid and trap-line experiments, the relationship between tracking rates and snap-trap capture rates were compared using linear regression in the SYSTAT 8.0 computer program (SPSS 1998). As the objective of the trapping was to calculate true density given a

relative density measure, tracking rates were classed as the independent variable in the analysis, and snap-trap captures as the dependent.

Differences in numbers of trap-nights run in the two habitats were analysed using an analysis of variance in SYSTAT. Broad scale differences in the density estimate between years on individual indexing lines were analysed using the Genmod procedure in the SAS (SAS Institute Inc 1990) computer program. An individual tunnel could be tracked or untracked, so a binomial distribution was used. The Genmod analysis produces a X^2 statistic that can be compared with the critical value from the X^2 distribution with the appropriate degrees of freedom. An auto-regressive correlation matrix was used in the model, which correlates the trapping data with the previous value only.

The relationship between tracking tunnel and Fenn-trap density indices was compared using a time-series analysis to allow for possible trends and auto-correlation in the data. The tracking and trapping data were first tested for stationarity using the Dickey-Fuller test (Hendry and Doornick 1999). Any paired series that were non-stationary, and thus showed long term trends, were compared using co-integration analysis (Hendry and Doornick 1999), which looks for agreement in long term trends between the data series. Any paired tracking and trapping series that were stationary were compared using linear regression, testing for auto-correlation between the residuals.

Trends in density estimates from the different indices were compared using the Wilcoxon Signed Ranks Test (Zar 1974). The signed rank of the difference between each pair of values is calculated, and the test statistic is calculated as the sum of the ranks with the less-frequent sign. The test statistic (T) is compared with the critical value (T_{crit}) with the appropriate sample size (Zar 1974). For each year (1996 and 1997) the number of months that each index scored rat density higher in either tawa-podocarp or beech forest was calculated, and agreement in overall population trends between tracking tunnels, numbers of rats caught, and captures per 100 trap-nights (C/100TN) were compared.

2.3 Results

2.3.1 Trapping grid

Over the five-night trapping period 121 ship rats were caught on the trapping grid. No house mice were caught. There were no significant differences in capture rate of rats for traps under tawa or tree fern canopy (tawa canopy = 66 rats, tree-fern canopy = 55 rats; $X^2 = 0.001$, $df = 1$, $P = 0.98$), or for captures by site type ($X^2 = 4.208$, $df = 3$, $P = 0.24$). There were no significant differences in capture rates between trap cover types ($X^2 = 3.737$, $df = 2$, $P = 0.15$).

The overall male:female sex ratio was 1:1.03, and did not differ significantly between nights ($X^2 = 2.381$, $df = 4$, $P = 0.67$). The vast majority of rats caught were immature, both on the basis of reproductive classification (83% juvenile), and from tooth wear indices (Age class III or less; 70% juvenile). The proportion of juvenile rats caught each night did not differ over the five trapping nights ($X^2 = 3.439$, $df = 4$, $P = 0.49$).

The number of rats caught on the edge of the grid increased throughout the trapping period, so that by the final night, 89 % of captures were on the edge of the grid.

The minimum density of rats on the grid was calculated to be 7.1 rats ha^{-1} (121 rats in 17 ha), while the regression of nightly catch against cumulative catch generated the equation: Cumulative catch = 139.8 - 2.043 x (nightly catch) ($r_5 = 0.87$, $P < 0.05$). This gives an estimated density of 8.22 rats ha^{-1} (95% C.I. = 5.9 to 10.53 rats ha^{-1}). The regression of percentage tracking rate against the estimated density of rats remaining on the grid is shown in Figure 2.1. A linear regression generated the equation: Density = 0.110 (% tracking rate) - 0.451, and explained 87% of the variation ($P = 0.02$). One tracking tunnel (line 5, 150 m station) recorded mouse prints on the last night of trapping. The tunnel was 4 m from a wind-thrown rimu (*Dacrydium cupressinum*) tree that provided dense ground cover and litter.

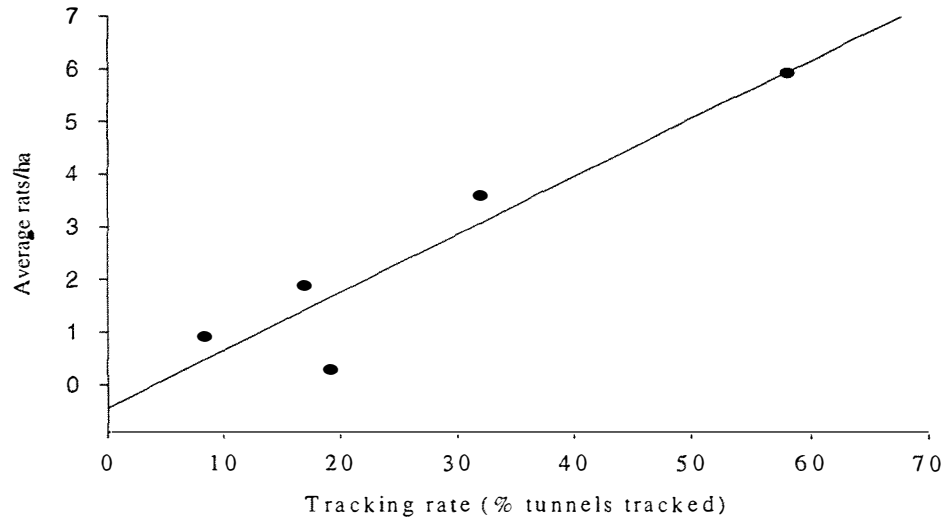

Figure 2.1 Nightly tracking rate (% of tunnels tracked) plotted against the corrected density of rats remaining on the trapping grid, over the five nights of the removal trapping experiment in June 1998. For details of the regression equation, see text.

2.3.2 Trapping line

From January to December 1997, 75 ship rats and 7 house mice were caught on the trap-line. Of the rat captures, 55 (73%) were caught under tawa canopy, 14 (18%) were caught under tree-fern canopy, and 6 (8%) were caught in coastline traps (X^2 = 10.767, df = 2, $P < 0.01$). The overall male:female sex ratio was 1.28:1, and did not differ significantly over the trapping period (X^2 = 1.213, df = 4, $P > 0.05$). More juvenile rats were caught in autumn and winter (28% and 45% respectively) than in spring and summer (23% and 0%), but the differences were not significant (X^2 = 6.31, df = 3, $P > 0.05$).

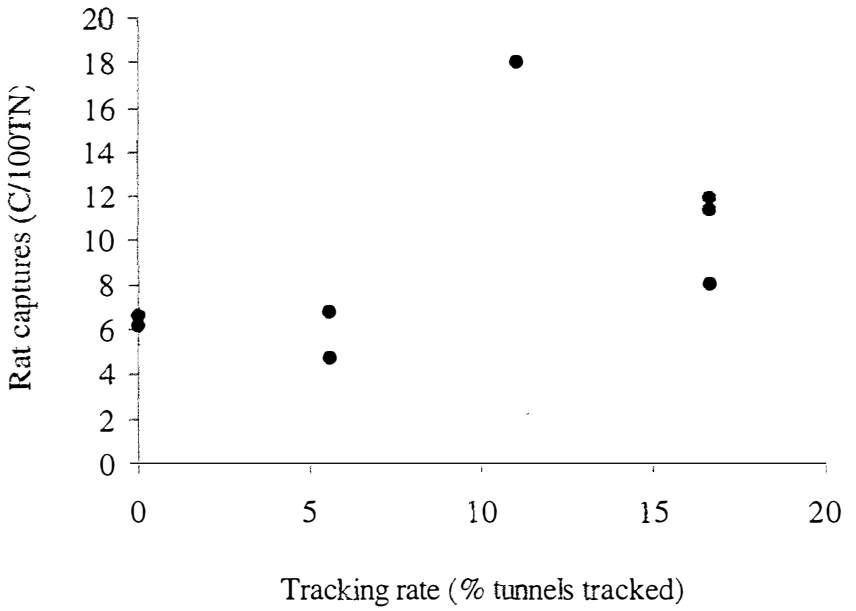

Figure 2.2 Tracking rate (% of tunnels tracked) plotted against rat captures per hundred trap nights (C100/TN), for rats caught on the rodent trapping line, between January and December 1997. A linear regression explained 31% of the variance, and was not significant.

The relationship between percentage tracking rate and snap trap C100/TN is shown in Figure 2.2. There was a significant relationship between the number of rats caught and the tracking rate ($r_8 = 57\%$, $P = 0.03$), but not between tracking rate and C/100 TN ($r_8 = 31\%$, $P = 0.15$).

2.3.3 Relationship between tracking tunnels and Fenn traps

The average number of trap nights per month (± 1 SE) on the Fenn trap-lines in tawa-podocarp forest (all traps) was 1232 ± 156 in 1996 and 1476 ± 166 in 1997, and did not differ significantly between years ($F_{1,22} = 2.58$, $P > 0.05$). The monthly tracking rates and monthly rat captures per 100 trap-nights in Fenn traps on the Halfline and all tawa-podocarp forest Fenn trap-lines are shown in Figure 2.3a. The two density

indices obtained from the Fenn traps were very similar, and only differ in their estimation of relative population trends in October 1997.

The relationship between the tracking tunnels and the Fenn traps was not as tight as that between the two Fenn trap density estimates. The tracking tunnels showed greater amplitude in fluctuations and a smaller increase in population size between Jan-Feb 1996 and Aug-Sept 1996. The tracking tunnel index stayed high longer in 1996, relative to the Fenn trap density estimates. The difference in mean density between 1996 and 1997 was significant for the tracking tunnel indices ($X^2 = 28.67$, $df = 1$, $P < 0.01$), and for the Fenn trap indices ($X^2 = 77.63$, $df = 1$, $P < 0.01$).

The co-integration analysis showed that the time-series from the tawa-podocarp forest were stationary for the tracking tunnels (Unit-root t-test = -3.69, $P < 0.001$), all podocarp Fenn traps (Unit-root t-test = -2.26, $P < 0.05$), and the Halfline Fenn traps (Unit-root t-test = -4.83, $P < 0.01$). The regression of tawa-podocarp forest tracking tunnel tracking rates on Fenn trap C/100TN was significant for all Fenn traps (regression equation: Tracking rate = 63.45 x Fenn C/100TN, SE of regression coefficient = 11.94, auto-correlation coefficient = 0.43, $P < 0.001$) and for the Halfline traps (regression equation: Tracking rate = 27.24 x Fenn C/100TN, SE of regression coefficient = 7.46, auto-correlation coefficient = 0.53, $P < 0.01$; Figure 2.3b).

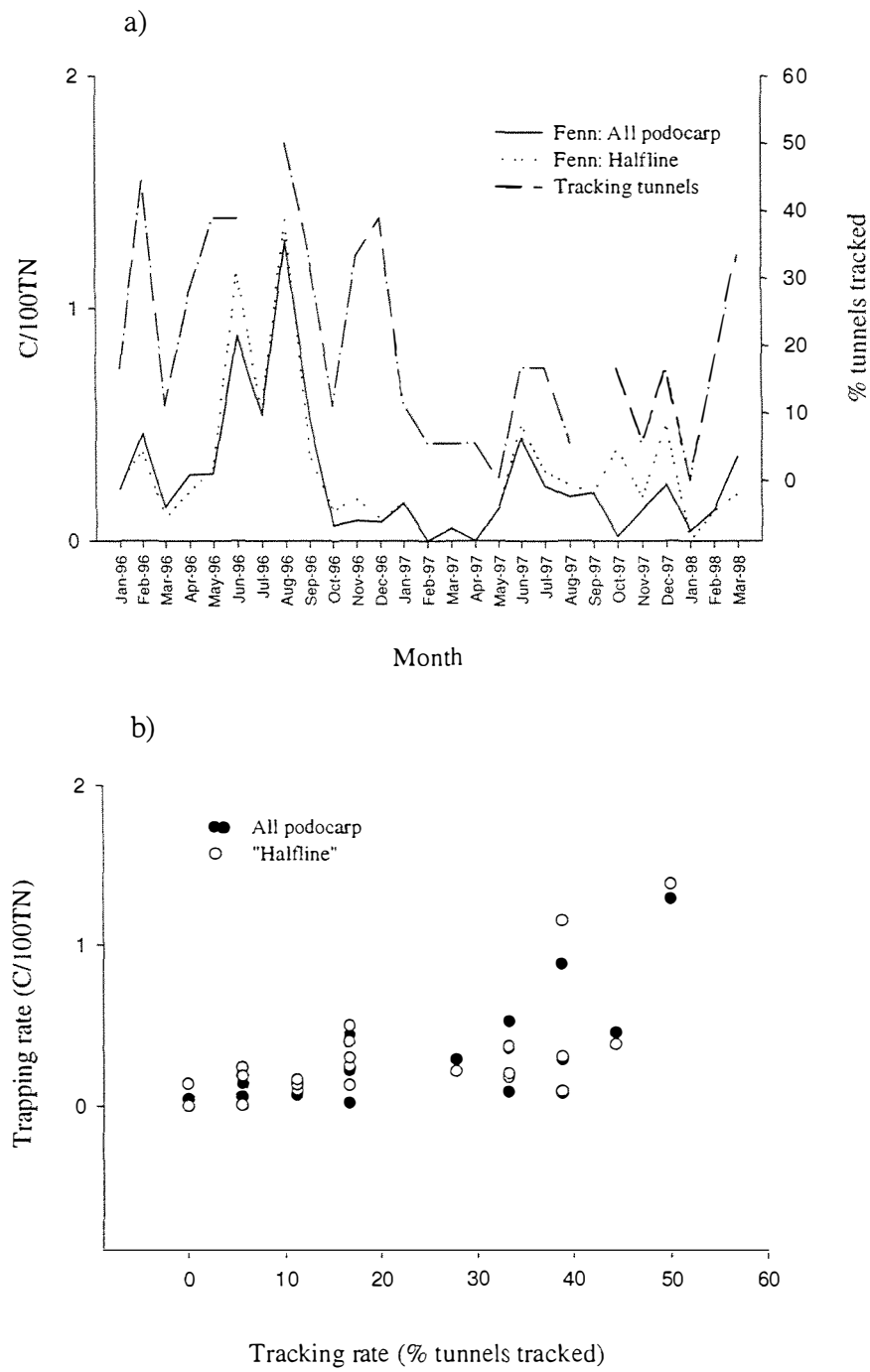

Figure 2.3 a) Monthly density indices obtained from tracking tunnels and Fenn traps run from January 1996 to March 1998 in tawa-podocarp forest at Lake Waikaremoana. For an explanation of the protocols, see text. b) The relationship between density estimates obtained from tracking tunnels and Fenn trapping lines.

The average number of trap nights per month (± 1 SE) on the Fenn trap lines in beech forest was 558 ± 42 in 1996 and 407 ± 52 in 1997, and did not differ significantly between years ($F_{1,22} = 0.26$, $P > 0.05$). The number of trap nights per month was significantly higher in tawa-podocarp forest (all traps) than in beech forest both in 1996 ($F_{1,22} = 17.45$, $P < 0.001$) and in 1997 ($F_{1,22} = 36.41$, $P < 0.001$). The monthly density estimates for rats in beech forest obtained from tracking tunnels and Fenn traps, and the relationship between the two indices, are shown in Figure 2.4. The tracking tunnels showed a peak in rat density in March-May 1996, followed by a gradual decline over 1996 to a low level in March-April 1997. This was followed by a gradual increase in density over 1997, to a peak level in March 1998 that was comparable to the March-May 1996 peak. In comparison, rat captures per 100 trap-nights from the Fenn traps showed a different trend. There was no large peak in captures in March-May 1996, and numbers remain low throughout 1996 and early 1997. Capture rates increased from June 1997, but the capture rates varied from month to month. There was no significant difference in mean density between 1996 and 1997 from either the tracking tunnels ($X^2 = 2.69$, $df = 1$, $P > 0.05$) or the Fenn traps ($X^2 = 1.86$, $df = 1$, $P > 0.05$).

The co-integration analysis for the beech forest area suggested that the tracking tunnel time-series was non-stationary (Unit-root t-test = -1.72, $P > 0.05$), while the Fenn trap data series was stationary (Unit-root t-test = -3.22, $P < 0.01$). There was no evidence of co-integration between the two series (Unit-root t-test = -1.35, $P > 0.05$). The regression of beech tracking tunnel tracking rates and Fenn trap C/100TN gave a negative relationship, and approached significance (regression equation: Tracking rate = -18.09 x Fenn C/100TN, SE of regression coefficient = 9.75, auto-correlation coefficient = 1.00, $P < 0.08$; Figure 2.4b).

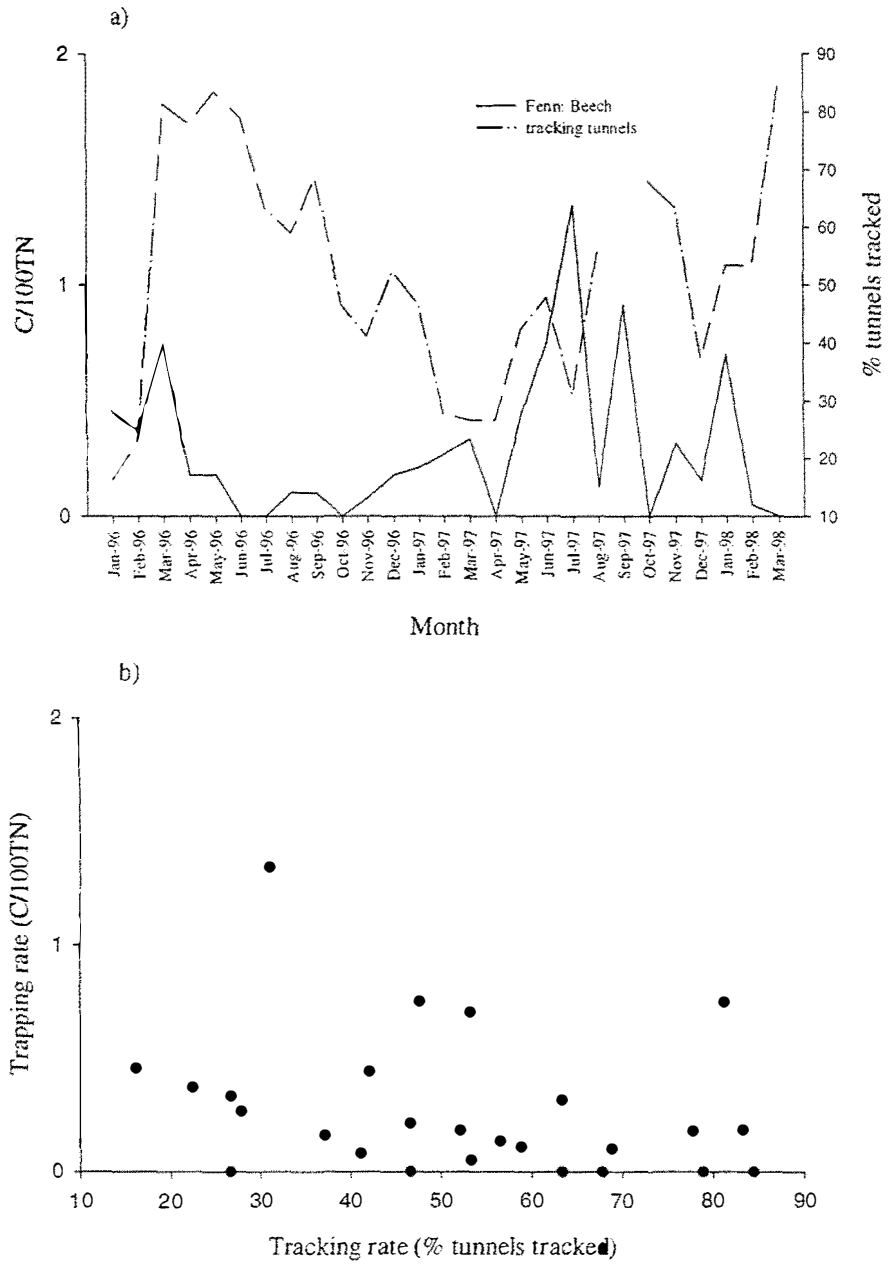

Figure 2.4 a) Monthly density indices obtained from tracking tunnels and Fenn traps run from January 1996 to March 1998 in beech forest at Lake Waikaremoana. For an explanation of the indexing protocols, see text. b) The relationship between density estimates obtained from tracking tunnels and Fenn trapping lines.

2.3.4 Comparison between density estimates from different forest types

Comparisons of relative density between the tawa-podocarp and beech forest sites show that the estimation of rat density is greatly influence by the density index used (Table 2.1). Tracking tunnels indicated significantly higher rat numbers in beech forest than in tawa-podocarp forest in both 1996 and 1997 (Figure 2.3a, 2.4a; Table 2.1). In comparison, numbers of rats caught per month were significantly higher in tawa-podocarp forest than in beech forest in both 1996 and 1997 (Figure 2.5; Table 2.1). Rat captures per 100 trap-nights were higher in tawa-podocarp forest than in beech forest in 1996, but were significantly higher in beech forest than in tawa-podocarp forest in 1997 (Table 2.1).

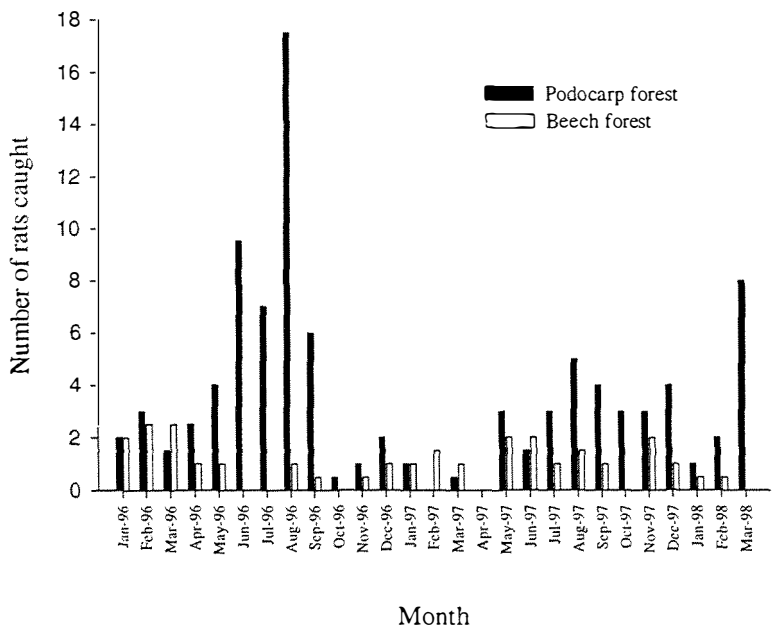

Figure 2.5 Average number of rats caught each month from January 1996 to March 1998 in tawa-podocarp forest and in beech forest at Lake Waikaremoana. Tawa-podocarp forest rat captures are for all trap-lines in that forest type, and beech forest rat captures are for Fenn line 3 and Fenn line 31.

Table 2.1 Numbers of months per year with density index of rats higher in beech or podocarp forest at Lake Waikaremoana. Density indices are estimated from tracking tunnels, numbers of rats caught and rat C/100TN. Differences between forest types are tested using the Wilcoxon Signed Ranks Test for small sample size. For an explanation of the test, see text. ns = not significant, * $P < 0.05$.

	1996				1997			
Variable	Beech	Podocarp	T	T_{crit}	Beech	Podocarp	T	T_{crit}
Tracking rate	6	3	10^{ns}	5	12	0	0^{*}	13
Rat number	2	8	9^{ns}	12	1	8	4.5^{*}	5
Rat C/100TN	4	8	25^{ns}	13	10	1	3^{*}	10

2.4 Discussion

The ship rat population density estimates obtained from the different indices used varied considerably with the index type, and with the experimental protocol used. This variation clearly warrants further investigation if research and management decisions are to be based upon information gained from these indices. Specifically, the reliability, repeatability and applicability of density estimates obtained from tracking tunnels require further examination, given their widespread and frequent use in rodent ecology in New Zealand.

2.4.1 Tracking tunnels and snap traps on a trapping grid

A significant correlation was found between footprint tracking rates and rat captures over the course of the trapping grid experiment. However, the relationship was not as tight as that found by Brown *et al.* (1996), due to the high tracking rate recorded on the last night of trapping. I believe these tracks to be those of immigrant rats because:

1) all the tracking tunnel records were located on the two end transect lines, adjacent to un-trapped areas of forest; and 2) eight of the nine rats caught on the last night were trapped within 25 m of the edge of the grid. This violates one of the assumptions of Zippin (1958) that there is no immigration during the experiment. However, given the short time frame of the trapping, it is unlikely that births, deaths or emigration affected the results. No differences were found between capture rates of males and females, or in the proportion of adults to juveniles captured during the experiment, suggesting that all age classes were equally trappable. As a result, the estimated density is probably fairly close to the true density, although the variation found between the two indices highlights the noise naturally inherent in measuring animal density.

No mice were caught during the experiment, although mouse prints were recorded in one of the tracking tunnels in the centre of the grid on the last night of trapping. The nearest dense cover was approximately 600 m away at the lake edge, and it is unlikely this mouse, or mice, had moved into the grid from that location. It is probable that mice were present in the area at very low density, but avoided or were excluded from the tracking tunnels while rats were present. Other studies have reported increases in mice following rat removal (Innes *et al.* 1995; Miller and Miller 1995; Brown *et al.* 1996), although little can be concluded from one record in this study.

2.4.2 Tracking tunnels and snap traps on a trapping line

The lack of a significant correlation between footprint tracking rates and snap-trap indices along the same trapping line is interesting. If two indices sampling the same population fail to show the same trend, the validity of both needs to be investigated. However, a number of points may mitigate against this result. Both tracking tunnels and snap traps record activity as well as abundance (Sheppe 1965; Sarrazin and Bider 1973; King and Edgar 1977). Thus, a single night index from tracking tunnels and a three night trapping session from snap traps, run on different nights, will both be influenced by activity as much as abundance.

With small numbers of traps, C/100 TN become sensitive to the numbers of sprung traps recorded (Caughley 1977), which can be influenced by the condition of the traps, the experience of the trapper, and the densities of other non-target animals, such as possums. There were also a small number of tracking tunnels (n = 18) running in each trapping period in this experiment. As a result, small differences in tracking rates recorded, either through changes in density or activity, can have disproportionate effects on the overall tracking rate calculated.

In summary, tracking tunnels and snap trapping were correlated closely, giving similar results over the short term during removal trapping. I did not find a significant relationship between footprint tracking rates and snap-trapping indices from a trap-line, highlighting the importance of activity, sampling effort, and the underlying population size when using either of these population indices.

2.4.3 Tracking tunnels and Fenn trap captures

Tracking tunnel and Fenn trap density indices were strongly correlated in tawa-podocarp forest areas, where the underlying rat population size was high. In these areas, the rat by-catch in the predator traps showed similar timing and amplitude of population peaks and declines, as shown in the tracking rates on the tracking tunnel line. With medium to high rat population density, changes in tracking rate appear to follow changes in population density.

Previous studies in New Zealand have highlighted higher rat capture rates in podocarp forest than in beech forest (Daniel 1972; 1978; Innes 1990; Innes *et al.* 1995; King *et al.* 1996), which is mirrored by capture rates in Fenn traps in this study. At the very low capture rates recorded in beech forest, there was no significant correlation between rat density estimates from the tracking tunnels and Fenn traps. In these areas, both tracking tunnels and Fenn traps showed no significant difference in rat density between the two years of the study. In comparison, the tracking tunnels, the total numbers of rats caught, and the corrected captures per hundred trap nights all showed significant differences in estimated population size between 1996 and 1997 in the

tawa-podocarp forest. It appears that Fenn traps in beech forest are recording the same population trends as the tracking tunnels, but with reduced sensitivity.

The weak relationship between the tracking tunnel and Fenn trap rat density estimates in the beech forest site highlights the influence of behaviour on tracking tunnel density estimates. No information has been published to date on ship rat territory size and activity in beech forest. However, home range size and use in this species is know to be variable and adaptive (Ewer 1971; Daniel 1972; Innes and Skipworth 1983; Hooker and Innes 1995; Innes *et al.* 1995). The effect of rodent behaviour must therefore be implicitly considered when tracking tunnels are used as an indexing method.

2.4.4 Reliability of indices and implications for use

The problems highlighted with the various rodent density indices tested suggest that caution must be taken when choosing an appropriate density index. The research or management questions posed will have a large influence on the type of index selected. While there are a number of advantages in using tracking tunnels (they are easy to set and service, they do not remove individuals from the population, and they can cover large areas quickly; King and Edgar 1977) they are susceptible to changes in activity and rodent abundance. Consideration of these limitations on tracking tunnel use will greatly increase the accuracy and reliability of the index. The effect of activity on the index can be countered in a number of ways:

1) Tracking tunnels should be used to directly compare populations in the same area, or in the same habitat type only. By running tracking tunnels with a consistent protocol, by running tracking tunnels in treatment and non-treatment areas on the same night(s) to account for activity, and by only comparing the same habitat types, the density index will more closely reflect abundance, rather than activity.

2) Sufficient numbers of tunnels should be run to allow detection of treatment effects. If individual animals are not marked, tracking tunnels can only be scored as tracked or untracked. If, for example, ten tracking tunnels are used, then a difference of

one tracking event will alter the index by 10%, which may mask small, but significant, treatment effects.

3) The underlying behaviour of the study animals should be considered. A variety of tracking tunnel protocols have been presented that use different trap layouts and spacing (King and Edgar 1977; Innes *et al.* 1995; Brown *et al.* 1996). Studies of ship rat home range use in broadleaf-podocarp forest in New Zealand have highlighted average home ranges of around 1 ha for males, and smaller for females (Hooker and Innes 1995). A tracking tunnel spacing of 50 m will therefore be susceptible to contagion of the index, through multiple tracking of tunnels by the same individual. In this case, a tracking tunnel spacing of 100 m would lower the number of tunnels, but increase the reliability of the index.

4) The tracking tunnel index should always be complemented by a second density measure. The first experiment presented here showed that tracking tunnels and snap traps were highly correlated on a trapping grid, while tracking tunnels and Fenn traps were significantly correlated on the tawa-podocarp forest trap-lines. The use of more than one index allows the calibration of the density index and increases the confidence in observed population trends. The use of a second, separate index will also increase the quality of information gained. For example, the use of a kill-trapping index can allow the collection of morphometric and bionomic information from the population, greatly increasing the understanding of the population under observation.

In conclusion, tracking tunnels are an efficient and generally reliable small-mammal index. They can be used to record relative changes in population density and variations both within and between areas. Confidence in the accuracy of the index can be increased by comparing population dynamics within similar habitat types, by paying attention to the influence of sampling effort and target species behaviour, and by calibrating density estimates obtained from tracking tunnels with those of a second index.

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Chapter 3: The diet and dietary selection of the introduced ship rat (*Rattus rattus* L.) in New Zealand mixed forest

3.0 Abstract

The diet of introduced ship rats (*Rattus rattus* L.) in mixed forest in New Zealand was compared with estimates of food availability. Levels of stomach parasite infection were also investigated, and compared to consumption rates of potential intermediate hosts. A total of 170 stomachs of rats caught on a trap-line and trapping grid were analysed. Invertebrates were important in the diet with Orthoptera, Coleoptera, and Phasmatidae eaten throughout the year, while larviforms were eaten in all seasons except summer. None of the seasonal trends were significant. Seeds were eaten more frequently by females than by males on both the trapping line and the trapping grid, while larviforms were eaten more frequently by female rats on the trapping line. Seeds were eaten more frequently by adult rats than by juvenile rats. Overall, there was little correlation between the frequency of occurrence of items in the diet and estimates of environmental availability of those items. In total, 51% of stomachs were infected with the New Zealand endemic nematodes *Mastophoris muris* and *Physaloptera muris*. Infection rates were highest in spring and summer (72% and 79% of rats infected respectively) and lowest in autumn and winter (61% and 50 % respectively). The numbers of nematodes per rat was highly skewed to the right. The geometric mean number of nematodes per rat was 6.36 (range 0 to 80), and was significantly highest in summer. The number of nematodes per rat was significantly related to rat age, but not to an estimate of rat condition. Overall, rats caught in the study exhibited a opportunistic, omnivorous diet, and showed no measurable detrimental effects of parasite infection. The rats' diet and diet flexibility is important in explaining the widespread success of this introduced species in a range of New Zealand habitats.

3.1 Introduction

The feeding strategies employed by rodents to meet their dietary requirements can be classified as herbivorous, grainivorous, insectivorous, or omnivorous (Landry 1970; Watts and Aslin 1981), with resulting degrees of habitat and dietary specialization. The range and type of foods consumed can range from a very small number in grainivorous species (Jensen 1982) to a wide choice in omnivores such as the ship rat (*Rattus rattus* L.) (Clark 1982; Innes 1990). Rodent diet can be influenced by a number of factors, including food availability (Churchfield 1982; Clark 1982; Jensen 1982; Cheal 1987; Luo and Fox 1994), food quality (Jung and Batzli 1981; Bomford 1987a; Bomford 1987b; Bunn and Craig 1989), breeding requirements (Bomford 1987c; Bomford 1987a; Hansson 1987), and learning (Terkel 1996).

For an omnivorous species, the food items consumed can be chosen from a broad range of available foods (Clark 1982). A number of small mammal studies have highlighted a frequent lack of correlation between the invertebrates present in the environment, and those consumed by the animal (Pernetta 1976; Churchfield 1982; Green 1989). In such situations, individual differences in diet choice may be more important in structuring diet composition than prey abundance *per se*.

The ship rat is one of the most common rodent species on the planet, having been carried to and established on all major continents (with the exception of Antarctica) and landmasses by human travellers (Innes 1990). Flexible diet choice is one of the key components of this species' success in colonising new habitats, and the diverse range of food selected, and the feeding strategies employed, can provide valuable insights into the factors affecting the ecology of rodent species.

In New Zealand, ship rats, Norway rats (*R. norvegicus* Berkenhout) and house mice (*Mus musculus* L.) were introduced by European settlers in the 18th and 19th centuries, into an environment devoid of native terrestrial mammals (Taylor 1984; Innes 1990). The ship rat and house mouse are present as the only two rodents common in native forests on mainland New Zealand. Along with the introduced predator, the stoat (*Mustela erminea* L.), they form part of a relatively simple predator/prey association, yet one that is highly damaging to endemic flora and fauna.

The ship rat is notorious as a destructive pest, but the exact impacts the species is currently having in the New Zealand environment remains unclear (Innes 1990).

A number of studies have investigated the diet of ship rats in New Zealand, and all have reported the importance of arthropod species, especially native Orthoptera and Phasmatidae in the summer, and native seeds and fruit in the winter (Daniel 1973; Innes 1979; Clout 1980; Miller and Miller 1995). The extent to which the observed diet is selected from available food has been poorly studied in New Zealand, and most studies have examined the food items consumed by the rats in isolation from the food available in the environment. Such an approach overlooks important aspects of food choice, and makes quantification of the impact consumption by rats is having on native flora and fauna extremely difficult.

Previous diet studies have frequently recorded high levels of parasite infestation in ship rats (Fall *et al.* 1971; Daniel 1973; Charleston and Innes 1980; Miller and Miller 1995). Several authors have suggested that invertebrates may act as intermediate hosts for nematodes, and that levels of infestation are correlated with the quantities of invertebrates consumed (Charleston and Innes 1980), although this trend is not always consistent (McPhee 1988). In most cases, the effect of rat population demography on the levels of infestation, and any measurable effects of infestation on condition, have not been investigated.

This study was a component of a larger project investigating the ecology and population regulation of ship rats in mixed forest in New Zealand, and had three aims:

1. To determine the diet of ship rats in mixed forest in New Zealand, and to investigate any sex- or age-related differences in diet.

2. To investigate the flexibility of the ship rat's diet, by comparing the diet composition of rats with the abundance of food items in the environment, as estimated by pitfall trapping and seed and fruit collection.

3. To investigate the factors determining levels of parasite infestation, and examine the potential impacts of parasite loadings on rat body condition.

3.2 Methods

The study was carried out at Lake Waikaremoana (38°47′S 177°05′E), situated in the south-eastern corner of Te Urewera National Park, North Island, New Zealand. The lake catchment is steep and almost entirely forested. There is a mosaic of forest types: 1) tawa-podocarp forest; with a canopy of tawa (*Beilschmiedia tawa*) and mahoe (*Melicytus ramiflorus*), an emergent layer of rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*), and miro (*P. ferruginea*), and a sparse understorey; and 2) beech forest; a canopy dominated by hinau (*Elaeocarpus dentatus*), tawari (*Ixerba brexiodes*), kamahi (*Weinmannia racemosa*) and mahoe, with emergent red, hard, black and silver beech (*Nothofagus* spp.), and a ground cover of crown fern (*Blechnum discolour*).

3.2.1 Rodent collection

A rodent trap line was established in tawa-podocarp forest in December 1996. Forty Ezeset Supreme™ rat traps were placed at 50 m intervals along the transect line, giving a total length of 2 km. Each trap was placed under a protective cover to prevent capture of non-target animals, and the traps were run for three consecutive nights at approximately six-weekly intervals between January and December 1997.

In each trapping session, traps were set on the evening of the first night, and were baited with peanut butter. Traps were checked between 0800 and 1000 h the following morning, and the species, location, sex, and date of capture of any animals caught were recorded. All specimens caught were taken to the laboratory and frozen for later autopsy. Any sprung traps were rebaited if required, and reset. All traps were sprung at the end of the trapping session, and left in place between trapping periods.

In June 1998, a 300 x 300 m grid was established in an area of tawa-podocarp forest bisected by the snap-trapping line. The grid was approximately 600 m from the edge of the lake, at an altitude of 80-100 m above Lake Level. Single Ezeset Supreme™ rat traps were placed at 25 m intervals across the grid.

Traps were placed on the lines on 21 June 1998, and run for five consecutive nights from the 23-27 June 1998. Traps were set on the afternoon of the 23 June, and subsequently checked between 0800 and 1200 h each morning. The location, species, colour morph (for *Rattus rattus*) and sex of any animals caught were recorded. Any sprung traps were recorded, rebaited with peanut butter if required, and reset.

3.2.2 Stomach analysis

In the laboratory, each specimen was weighed and measured, as per Cunningham and Moors (1983), and the age of individuals was determined using reproductive indices (Daniel 1972) and tooth wear criteria developed for *R. rattus* (Karnoukhova 1971; Innes 1990) and for *Mus musculus* (Lidicker 1966). Stomachs were removed for dietary analysis. Each stomach was towelled dry and weighed. An incision was made around the outside margin of the stomach, and the contents emptied into a petri dish. The stomach lining was re-weighed to determine the wet weight of the contents. The percentage volume of any bait or parasites present was estimated by eye and the bait was then discarded. Any stomach parasites were counted and weighed and kept for later identification. The contents were washed through 2 mm and 0.5 mm sieves, and then washed into a petri dish and examined microscopically.

Individual prey items were identified using invertebrate and plant material reference collections from the same habitat. Invertebrates could usually be identified to Family, and often to Genus using distinctive features such as head cases, tarsus and femur structure, and body markings. The percentage volume (to the nearest 10%) occupied by the food items in each stomach was estimated visually.

3.2.3 Food availability

The abundance of ground dwelling invertebrates was estimated using pitfall trapping. Two groups of ten pitfall traps were established adjacent to the trap line, and the groups were separated by approximately 900 m. In each of the groups, the traps were arranged in five pairs on a 25 x 5 m grid. Each trap was made from a plastic food

container (10 cm deep x 10 cm diameter), and was dug into the ground with the top flush with the surface. The traps were half filled with commercial anti-freeze (90 % ethylene glycol), and covered with a 25 x 25 cm metal cover to prevent capture on non-target animals. Traps were cleared monthly, and the species present were identified to Family or Genus, and counted. Only individuals with body lengths greater than 5 mm were counted, as this is smaller than the minimum prey size known to be consumed by ship rats in New Zealand (Innes 1990). No invertebrate collection was carried out during the short trapping grid experiment in June 1998.

3.2.4 Seed traps

Eight seed traps were placed at 100 m intervals adjacent to the trapping line. Each trap consisted of a metal funnel, with a catching area of 0.2 m^2, supported on a metal tripod. Seed and litterfall was collected in a metal can attached to the bottom of the funnel. Cans had holes drilled in the bottom to allow water to escape, and a wire mesh disc was placed in each can to prevent material falling through the drainage holes.

Seed traps were cleared monthly and returned to the laboratory for sorting. Each sample was oven dried for 24 h at 75° C, and then weighed. The contents of each sample were sorted into fruit, seeds, flowers, leaves, wood and twigs, and litter. Fruit, seed and flowers were identified and weighed. Leaves were identified and the percentage composition of each species was estimated, and all the separate fractions weighed.

3.2.5 Statistical analysis

Differences in proportional capture rates of rats of different ages and sexes were tested using the chi-square (X^2) goodness of fit test. The chi-square test is sensitive to small sample sizes (Sokal and Rohlf 1981); in such cases the non-parametric Fisher's exact test was used to test for differences in the frequency of occurrence of individual food items between different ages, sexes, and seasons. Fisher's test calculates the

probability of obtaining as bad a fit (or worse) to expectation as shown in the data (Sokal and Rohlf 1981). Significance levels of individual tests should be treated with caution due to possible Bonferroni correlations (Rice 1989).

Seasonal differences in the diet of rats caught on the trap line were examined using multivariate techniques. Food items in the diet were assigned to eight categories: adult Orthoptera; spiders; Coleoptera/Blattidae; arboreal insects; larval insects; seeds; wood/bark; and other plant material. Each category contained either distinct, common foods, such as orthopterans and spiders, or similar food items, such as arboreal insects, that included Hemiptera, Phasmatidae and Diptera. A Principal Components Analysis was performed in PC-ORD (McCune and Mefford 1997), using a correlation matrix, which gives greater weighting to rarer categories. The significance of any seasonal differences was tested using the Multiple Regression Permutation Procedure (MRPP) in PC-ORD. MRPP compares the association between members of *a priori* groups with a randomised distribution taken from the entire data set (Zimmerman *et al.* 1985), and does not rely on the assumption that the data are normally distributed. The test statistic is calculated as

$$T = \frac{O\Delta - E\Delta}{\sqrt{\text{var}\,\Delta}}$$

Where $O\Delta$ = observed average distance between members of a group; $E\Delta$ = average distance between randomised groups; varΔ = variance of the estimated expected Δ, and describes the separation between the groups.

The frequency of occurrence of major food items in the stomachs of trap-line rats was compared with environmental availability of those food items for each trapping session. For each trapping period, the occurrence of Orthoptera, Coleoptera/Blattidae, larvae, and spiders in stomachs was compared with mean numbers per pitfall trap of each category, and the occurrence of seeds in stomachs was compared with mean weights of seed/trap. Pearson's correlation coefficients were used to test the significance of any relationships (SYSTAT 8.0, SPSS 1998).

Numbers of nematodes per stomach were highly skewed to the right and were log transformed to normalise the data. As a result, infection rates were compared using geometric means (Charleston and Innes 1980). The effect of nematodes on body weight of rats was examined using a PCA (McCune and Mefford 1997). Rats caught on the trap line and trapping grid were pooled for the analysis of parasite investigation. For each rat, measurements taken included the head-body length, tail length, right hind foot length, and right-ear length, and these were used to calculate axis scores from the morphometric measurements from each rat. The Axis 1 scores gave a multivariate measure of size for each rat, which was regressed against the square root of weight of each rat. The residuals from the regression gave a "fatness index", where rats with positive residuals were fatter than expected for a given size, while negative residuals indicated a lighter than expected value. Multiple regression was then performed to test the influence of rat age and "fatness" on parasite loadings.

The relationship between prey item frequency and nematode loading was compared for each stomach using Pearson's correlation coefficient in SYSTAT 8.0 (SPSS 1998).

3.3 Results

From January to December 1997, a total of 75 ship rats and 7 house mice were caught on the trap line. A total of 121 ship rats were caught on the trapping grid in June 1998. Details of the age structure and sex ratios of the specimens caught have been listed elsewhere (Chapter 2), and are not repeated here.

3.3.1 Occurrence of food categories in trap-line rats

The contents of 49 stomachs were analysed from rats caught on the trap-line in 1997; 12 of which were trapped in summer, 11 in autumn, 9 in winter, and 17 of which were

caught in spring. The seasonal frequencies of occurrence of the eight food categories are shown in Figure 3.1 (the total number of rats examined in each category and the number of occurrences of each food category in the 1997 trap-line sample are shown in Appendix 3.1). Invertebrates were the most common food items throughout the year, especially orthopterans, arboreal insects, and coleopteran and lepidopteran larvae (Figure 3.1) although none of the trends were significant.

The seasonal data from the 1997 trap-line sample were pooled to look for sex- or age-related differences (Figure 3.2a, b; Appendix 3.1). The frequency of occurrence of food items was not significantly different between males and females. Seeds occurred in 32% of female stomachs, as compared to 10% of male stomachs (Fisher exact test; $P = 0.12$), and larvae were recorded in 42% of female stomachs, compared to 19% of male stomachs (Fisher exact test; $P = 0.17$). The frequency of occurrence of food items between juvenile and adult were not significantly different (Figure 3.2b).

3.3.2 Occurrence of food categories in trapping grid rats

The frequency of occurrence of food categories between ages and sexes for the large winter 1998 trapping-grid sample are shown in Figure 3.3a and b. The total number of rats examined in each category and the number of occurrences of each food category in the 1998 trapping grid sample are shown in Appendix 3.2. Seeds were eaten significantly more often by female than by male rats (30% and 15% for females and males respectively; $X^2 = 4.026$, $df = 1$, $P = 0.05$), and were eaten significantly more often by adults than by juvenile rats (39% and 17% respectively; $X^2 = 7.146$, $df = 1$, $P < 0.01$). Coleoptera and Blattidae were present in 10% of male stomachs compared to 2 % of female stomachs ($X^2 = 4.061$, $df = 1$, $P = 0.04$). None of the other food categories differed significantly between ages or sexes. Bird feathers were found in 5% of stomachs. Five pregnant females were caught over the course of the study, too few to allow for an analysis of the effects of pregnancy on diet.

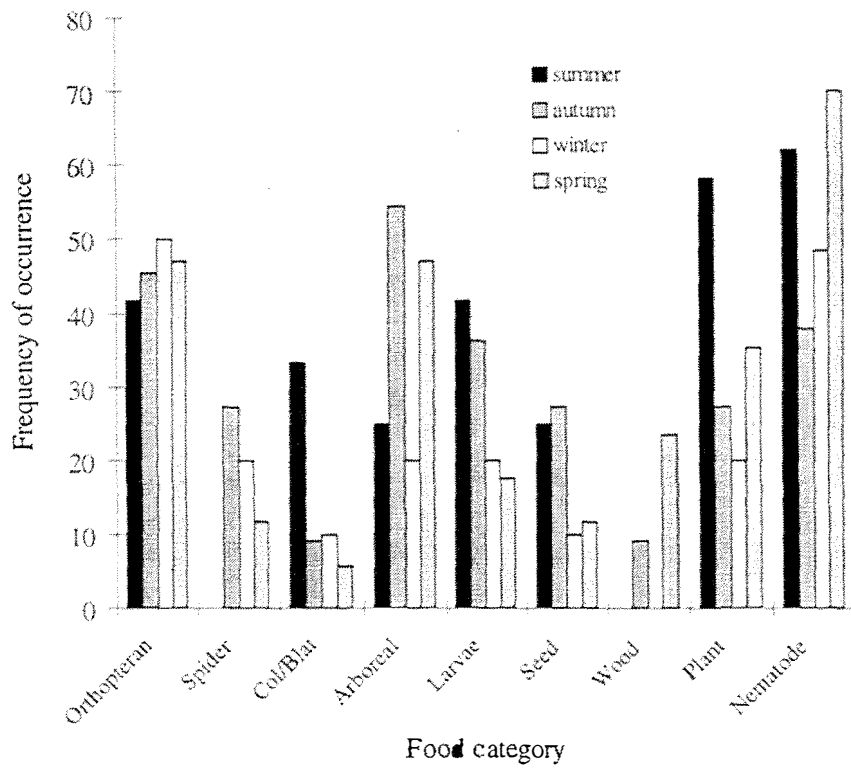

Figure 3.1 Seasonal frequency of occurrence of food categories in stomachs of rats caught on the 1997 trap line at Lake Waikaremoana, New Zealand. Frequencies were calculated as the number of stomachs containing a particular food item divided by the total number of stomachs containing food in that season. Full descriptions of category composition are given in the text.

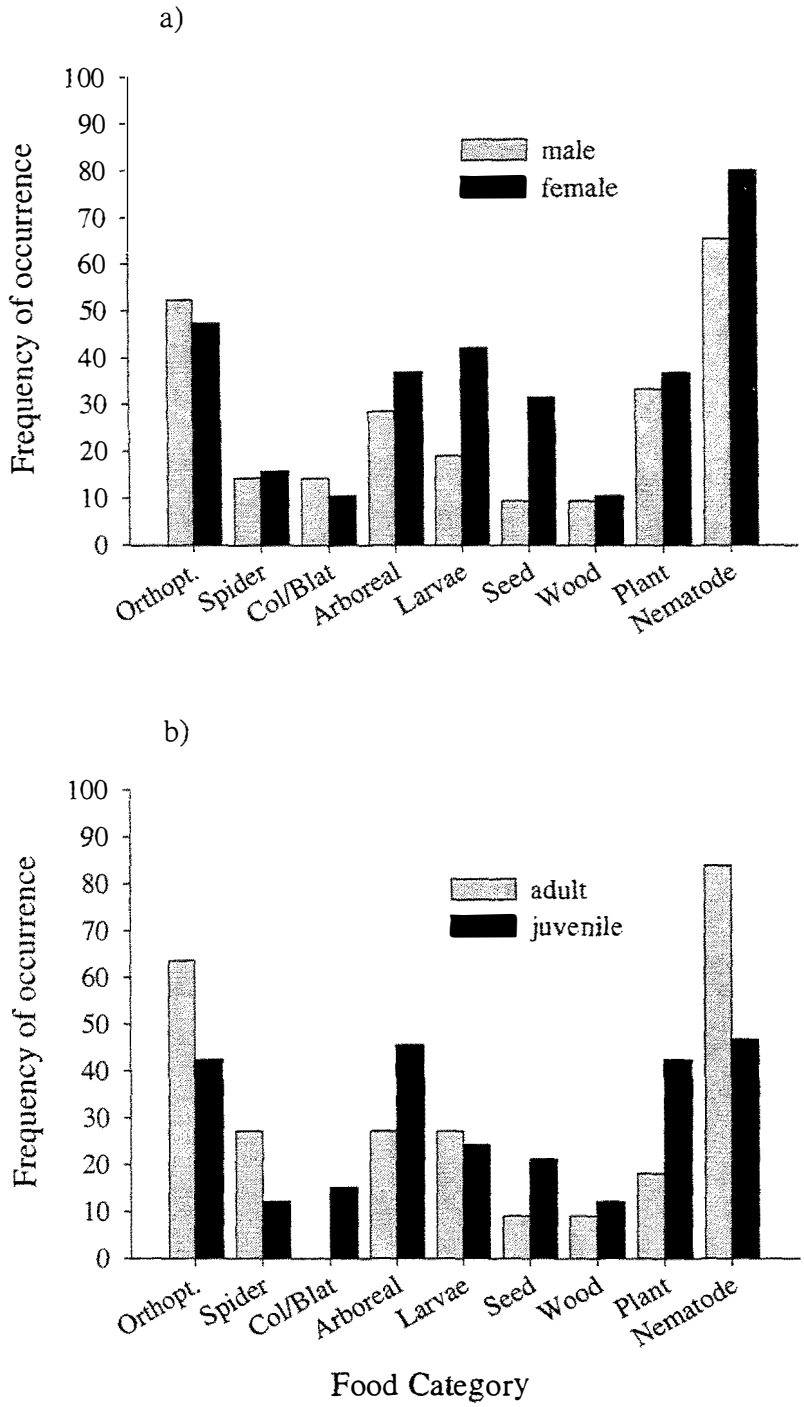

Figure 3.2 Frequency of occurrence of food categories and nematodes in stomachs of rats caught on the 1997 trapping line at Lake Waikaremoana, New Zealand. Frequencies are shown for a) males and females, and b) adults and juveniles. For an explanation of the categories, see text.

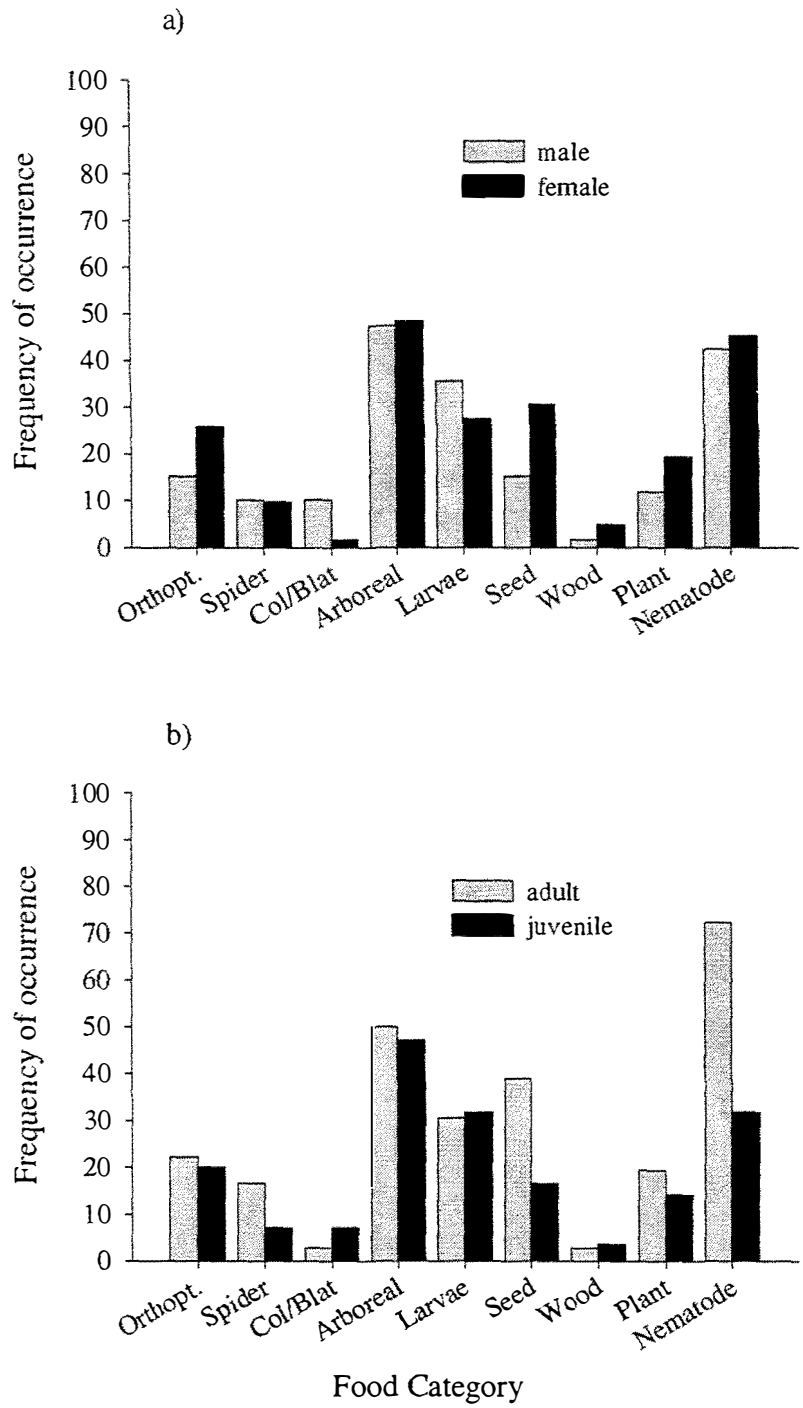

Figure 3.3 Frequency of occurrence of food categories and nematodes in stomachs of rats caught on the 1998 trapping grid at Lake Waikaremoana, New Zealand. Frequencies are shown for a) males and females, and b) adults and juveniles. For an explanation of the categories, see text.

3.3.3 Seasonal differences

The multivariate analysis of the overall diet composition of trap-line rats is shown in Figure 3.4. There were no consistent trends in diet composition, either between individuals, or throughout the year. No significant seasonal trends were found in the diet structure (Table 3.1).

Table 3.1 Average distances in multivariate space between the stomach contents of rats caught in each of the four seasons at Lake Waikaremoana (n = 49). The observed delta is calculated as a weighted average of the *a priori* categories, and is compared to an expected delta value, calculated from 1000 Monte Carlo randomisations of the data set.

Variable	Observed delta	Expected delta	Test statistic	*P*
Season	0.829	0.844	-1.451	0.083^{ns}
Sex	0.842	0.846	-0.668	0.224^{ns}
Age	0.858	0.844	1.662	0.982^{ns}

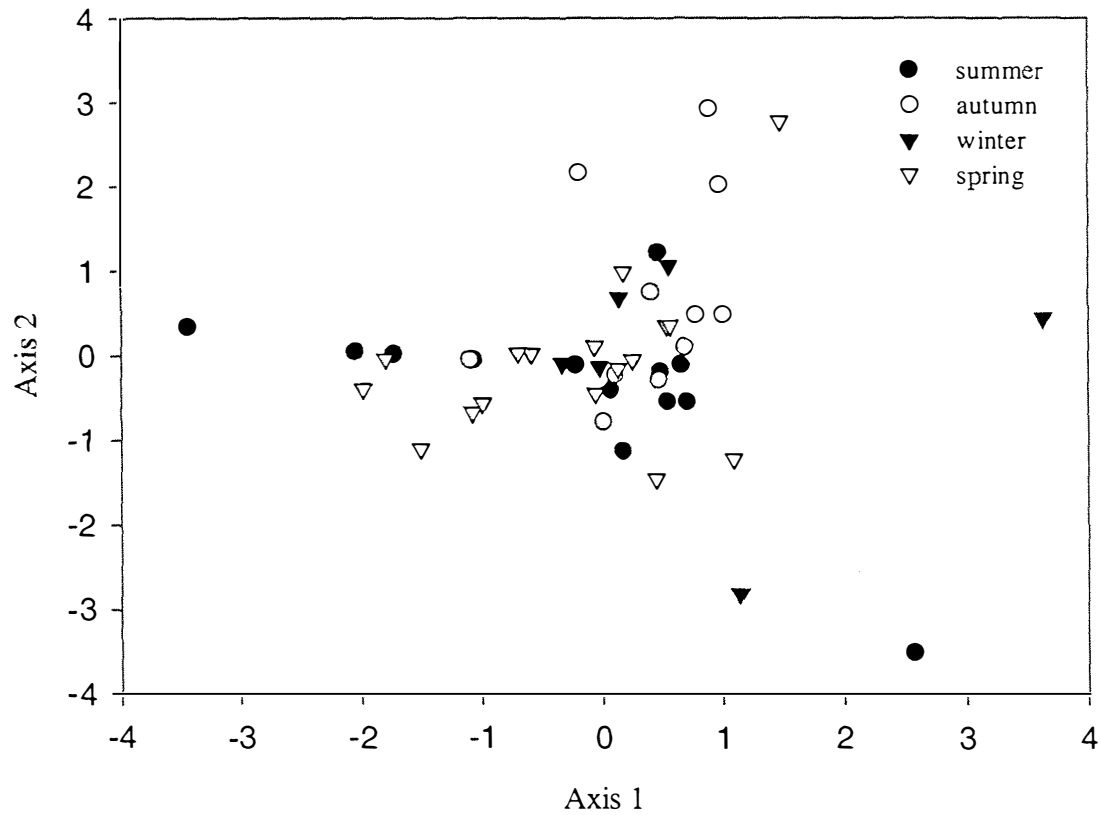

Figure 3.4 Principal Components Analysis of stomach contents of ship rats caught at Lake Waikaremoana, New Zealand. Food items were grouped into eight categories; Orthoptera, spiders, Coleoptera/Blattidae, arboreal insects, larviforms, seeds, wood/bark, and other plant material. Rats caught were assigned to summer, autumn, winter or spring trapping sessions. A correlation coefficient matrix was used in the analysis.

3.3.4 Utilization of available foods

The frequency of occurrence of the most common invertebrates in the rat diet was compared with that of food item abundance in the environment as assessed by pitfall trapping for trap-line rats (1997). There was a positive relationship between environmental availability and the amount of seeds and fruit eaten (Table 3.2), while there was an inverse relationship between consumption and availability for Coleoptera/Blattidae. For the other prey items, representation in the diet and in the pitfall traps was quite variable. Othopterans were frequently recorded at similar times in both the diet and in the environment, as were larviforms. In comparison, dipterans were recorded in the diet relatively infrequently, and their occurrence in the diet did not significantly correlate with environmental availability. Numbers of nematodes per stomach were compared with the environmental availability of the common invertebrate food items, but none of the relationships were significant.

Table 3.2 Pearson correlation coefficients calculated between frequency of occurrence of food items in rat stomachs and abundance in the environment of food items as assessed by pitfall trapping for invertebrates, and seed traps for seeds and fruit, for rats caught in the 1997 trapping period. Also shown are correlation coefficients for the relationships between prey item frequency and the number of nematodes found in each stomach. ns = not significant, * = $P < 0.05$, $^{\phi}$ $0.05 < P < 0.10$.

	Orthoptera	Coleoptera/ Blattodea	Larvae	Aranae	Seeds
Environmental availability	-0.204^{ns}	-0.713^{*}	0.427^{ns}	0.295^{ns}	0.794^{ϕ}
Nematode loading	0.047^{ns}	0.576^{ns}	0.069^{ns}	0.749^{ϕ}	0.016^{ns}
n	7	7	7	7	6

3.3.5 Levels of parasite infection

Rats from 1997 and 1998 were pooled to look at the effects of parasite infestation. Specimens were identified as the stomach nematodes *Mastophoris muris* and *Physaloptera muris* (W. A. G. Charleston, pers. comm.), but the relative frequencies of each species were not recorded. Overall, 86 of 168 stomachs (51%) examined had nematodes in them. Stomach nematodes occurred more frequently in stomachs in spring and summer (72% and 79% of stomachs respectively) than in autumn or winter (61% and 50% respectively; Figure 3.1), although the difference was not significant. The geometric mean number of nematodes in each stomach was 6.36 (range 0 to 80), but this number varied seasonally with significantly more in summer (geometric mean ± SE, 20.9 ± 1.08 nematodes rat^{-1}) than throughout the rest of the year (pooled mean ± SE, 6.36 ± 1.01 nematodes rat^{-1}; $F_{3,106} = 4.61$, $P < 0.01$). Rats with stomach nematodes were significantly older than those without nematodes (mean age class ± SE: infected rats, 4.50 ± 0.13; uninfected rats, 3.33 ± 0.13; $F_{1,183} = 38.89$, $P < 0.001$), although nematode infected rats were not significantly fatter than uninfected rats. Within the infected rats, numbers of nematodes were significantly correlated with rat age ($F_{5,101} = 11.535$, $P < 0.001$; Figure 3.5a) and with the PCA axis scores for rat size ($F_{1,88} = 7.015$, $P < 0.01$), but not with the "fatness index" ($F_{1,88} = 0.246$, $P = 0.62$; Figure 3.5b).

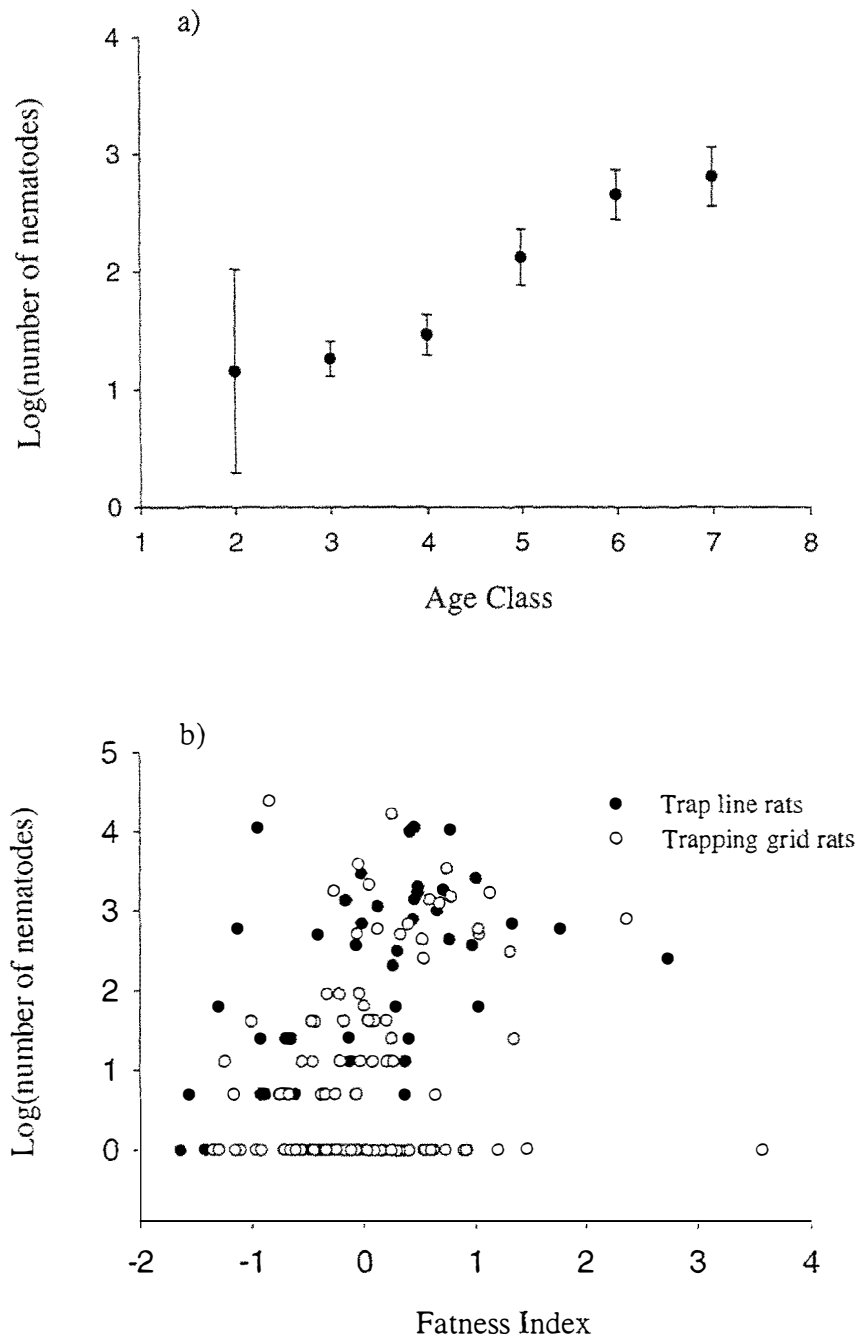

Figure 3.5 Relationship between the number of nematodes per rat and the a) age (mean ± SE) and b) fatness of rats caught at Lake Waikaremoana, New Zealand. Age classes were calculated for tooth-wear indices developed for the ship rat. Fatness was calculated as the residuals of the regression of individual rat weight against a multivariate estimate of rat size for that rat.

3.4 Discussion

Ship rats caught in this study ate a wide range of foods throughout the year, and exhibited flexible diet choice. Adult orthopterans (Raphidophoridae and Stenopelmatidae), stick insects (Phasmatidae) and spiders were common throughout the year, while coleopteran larvae, and seeds and fruit showed slight increases in summer and autumn. In separate studies, Daniel (1973) and Innes (1979) found arthropods, especially orthopterans, to be important foods in the diet of ship rats caught in lowland forest. Only Daniel (1973) reported significant consumption of plant material. Birds were an unimportant food in the diet in both studies.. In the current study, no bird remains were found in rats caught on the trap line, although feathers were present in 5% of 121 rats caught on the trapping grid.

Any study of diet and feeding ecology will be influenced by the methods used. Stomach content analysis may give a better picture of diet composition than faecal analysis (Kunz and Whitikar 1983; Dickman and Huang 1988; Kronfeld and Dayan 1998). However, the accuracy of stomach contents analysis can be influenced by a number of factors, including the degree of opportunistic feeding by the species in question, the seasonal availability of food, differing degrees of digestibility, the habitat exploited, the presence of other species, and the physiological and developmental stage of the individual (McPhee 1988). Stomach analysis also has the added disadvantage of only providing one sample per individual. Dickman and Huang (1988) demonstrated that the use of stomach pumping in a study of shrew diet gave very similar results to established stomach-content analysis techniques, and overcame a number of problems associated with standard stomach content or faecal pellet analysis.

3.4.1 Variation in diet composition

The current study found some evidence for sex related differences in diet structure, with female rats eating more seeds and larvae than males, although these results were not Bonferroni corrected. No significant differences in the diet of adults and juveniles

were found. Significant sex- and age-related differences in the diets of small mammals have been reported elsewhere. In a study of ship rats on Stewart Island, Gales (1982) found that females ate more orthopteran invertebrates, while males consumed more seeds and fruit than females. In a study of the diet of four small terrestrial mammals in rain forest in French Guyana, males were predominantly frugivorous, while pregnant females ate significantly more seeds and animal matter (Henry 1997). Both Gales (1982) and Henry (1997) attribute the more protein rich diet consumed by females to the greater energy demands of pregnancy and lactation, a finding supported by other studies. Interestingly, Gales (1982) suggests that non-consumption of orthopterans by adult ship rats would increase the availability of this food for females and juveniles, thus enhancing the fitness of the population. The non-consumption of orthopterans by adult males can be more parsimoniously explained without reference to group selection, by the relatively lower costs of gamete production in male than in female mammals (Randall *et al.* 1997), and subsequently, a lower requirement for hard to catch, protein-rich foods.

3.4.2 Diet composition and environmental availability

Although ship rats in this study ate a wide range of food items, little agreement was found between frequency of occurrence of food items in the diet, and invertebrate abundance as assessed by pitfall trapping. A number of studies have highlighted the problems with the use of pitfall traps to estimate dietary prey availability. In a study of the diet of the common shrew, *Sorex araneus*, Churchfield (1982) found a significant relationship between dietary occurrence and environmental availability for adult Coleoptera only, while in a study of *Antichinus* feeding ecology in Australia, Green (1989) found a significant relationship for Lepidoptera only. In their study of a small mammal assemblage along an elevational transect in the Philippines, Richart *et al.* (1991) found a correlation between vermivorous rodent numbers and oligochaete abundance, but no correlation between species abundance and food availability for a number of the omnivorous, insectivorous or frugivorous species.

In this study, the only correlations found between consumption and environmental availability were a positive relationship for seeds and a negative relationship for Coleoptera and Blattidae. Coleopterans were only consumed in substantial numbers in summer, and rarely in the other seasons, so the reason for this negative relationship remains unclear.

The relationships between availability and consumption for the other food items were variable. Orthopterans were recorded year round in pitfall traps. Although they were among the most common items in the stomachs examined, there was no significant relationship found between frequency of occurrence in the diet, and abundance in pitfall traps. Orthopterans have been frequently recorded in the diet of ship rats in New Zealand studies (Daniel 1973; Innes 1979; Clout 1980). Given their flightlessness, nocturnal behaviour and lack of effective defences, orthopterans may be profitable, easily caught prey for rats.

Stick insects (Phasmatidae) were also a significant component of the rat diet in this study, and yet only one stick insect was caught in the pitfall traps. Stick insects are largely arboreal, being found on the trunks and branches of canopy trees. Ship rats have been shown to spend between 40 and 96% of their time in the canopy (Innes 1977), so will frequently encounter this prey item. I have no information on stick insect abundance in the study area, but their large bodies, and apparent lack of effective defenses, appear to make them a preferred food item.

Conversely, Carabidae were extremely abundant in the pitfall traps throughout the study, and yet were never positively identified in rat stomach contents. The tough chitinous exoskeleton of carabids may make them unpalatable to ship rats, although a study of carabid beetle ecology in the Manawatu region, New Zealand, found evidence of rat predation of carabids (M. Hutchinson, pers comm.). Ship rats on Big Green Island, off the coast of Tasmania, selectively ate the soft parts of their main scarabaeid prey, leaving the hard exoskeleton (Norman 1970). Therefore, consumption of carabids by rats in this study cannot be ruled out.

The overall lack of correlation between diet composition and environmental abundance in this study and in others highlights the importance of individual choice

and behaviour in diet composition. Clark (1982) showed the importance of trace foods in the diet of ship rats in the Galápagos Islands, and suggested that ship rats may eat a range of foods to balance nutrient intake, avoid acute effects from toxic substances, and monitor the food supply (Clark 1982). Other factors may be as important as prey abundance in determining diet structure (McPhee 1988).

3.4.3 Levels of parasite infestation

Levels of nematode infestation were found to be positively correlated with both age and rat size, with the oldest, largest rats have significantly more nematodes in their stomach than young rats. Charleston and Innes (1980) suggested that orthopterans may be the intermediate host in the parasite's life cycle, and ship rats in this study consumed large numbers of orthopterans. Levels of infestation were not significantly correlated with the frequency of occurrence of any of the food categories, although the summer peak in infection rates did coincide with the highest consumption rates of Coloeptera and Blattidae, so the method of infestation remains unclear. Higher levels of infestation in older rats presumably reflect longer exposure to parasite infection. Fall *et al.* (1971) found both higher levels of invertebrate consumption and parasite infection in ship rats than in the pacific rat *R. exulans*, in the Marshall Islands. In comparison, in Papua New Guinea, *R. exulans* with a vegetation-only diet had higher levels of infestation by nematodes than those that ate vegetation and invertebrates (McPhee 1988), although no explanation is given for this.

3.4.4 Conclusion

Ship rats caught in this study ate a wide range of foods, and exhibited an opportunistic, omnivorous diet. There was no relationship between the frequency of occurrence of food items in the stomach, and estimates of environmental availability. This makes estimation of the impacts of rat predation on invertebrate species difficult, and lends support to the argument for using repeated, non-lethal sampling methods for estimating diet composition. Parasite infestation was found to be common in the

study population, and was significantly correlated with age, but not with an estimate of condition.

Coupled with a *r*-selected reproductive strategy, the opportunistic diet consumed by rats caught in this study helps to explain the widespread success of ship rats in New Zealand forests. This diet flexibility also helps explain the rapid responses in rat populations to temporally abundant food during synchronous southern beech seeding.

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Appendix 3.1 Number of occurrences (and percentage of total) of food categories in stomachs of rats caught on the 1997 rodent-trapping line at Lake Waikaremoana. Stomachs were analysed for differences between male and female rats, and between adult and juvenile individuals. Rats were aged based on tooth wear indices (see Innes 1990), with rats with tooth wear classes of 3 or less classified as juveniles. Differences in diet between seasons were also examined. Significance tests only apply within paired categories. * = $P < 0.05$, ** = $P < 0.01$, $^{+}$ = $0.06 < P < 0.1$. † = Two individuals could not be sexed. ‡ = Three individuals could not be aged.

Category	n	Orthopteran	Spiders	Coleopteran/ Blattidae	Arboreal insects	Larval insects	Seeds	Wood/Bark	Other Plant material
1997 Trapline									
male	21	11 (52)	3 (14)	3 (14)	6 (29)	4 (19)**	2 (4)$^{+}$	2 (10)	7 (33)
Female	19	9 (47)	3 (16)	2 (11)	7 (37)	8 (42)	6 (32	2 (11)	7 (27)
Total	40†								
Adult	33	14 (42)	4 (12)	5 (15)	15 (45)	8 (24)	7 (21	4 (12	14 (42)
Juvenile	11	7 (64)	3 (27)	0 (0)	3 (27)	3 (27)	1 (9)	1 (9)	2 (18)
Total	44								
Seasonal rates									
Summer	12	5 (42)	1 (8)	4 (33)	3 (25)	5 (42)	3 (25)	0 (0)	7 (58)
Autumn	11	5 (45)	3 (27)	1 (9)	6 (54)	4 (36)	3 (27)	1 (9)	3 (27)
Winter	9	5 (56)	2 (22)	0 (0)	2 (22)	2 (22)	1 (11)	0 (0)	1 (11)
Spring	17	8 (47)	2 (12)	1 (6)	8 (47)	3 (18)	2 (12)	4 (23)	6 (35)
Total	49								

Appendix 3.2 Number of occurrences (and percentage of total) of food categories in stomachs of rats caught on the 1998 rodent-trapping grid at Lake Waikaremoana. Stomachs were analysed for differences between male and female rats, and between adult and juvenile individuals. Rats were aged based on tooth wear indices (see Innes 1990), with rats with tooth wear classes of 3 or less classified as juveniles. Significance tests only apply within paired categories. * = $P < 0.05$.

Category	n	Orthopteran	Spiders	Coleopteran/ Blattidae	Arboreal insects	Larval insects	Seeds	Wood/Bark	Other Plant material
1998 Trapping grid									
male	59	9 (15)	6 (10)	6 (10)*	28 (47)	21 (36)	9 (15)*	1 (2)	7 (12)
female	62	16 (26)	6 (10)	1 (2)	30 (48)	17 (27)	19 (31)	3 (5)	12 (19)
Total	121								
adult	36	8 (22)	6 (17)	1 (3)	18 (50)	11 (31)	14 (39)*	1 (3)	7 (19)
juvenile	85	17 (20)	6 (7)	6 (7)	40 (47)	27 (32)	14 (16)	3 (4)	12 (14)
Total	121								

Chapter 4: Habitat use of house mice and ship rats in a mixed forest mosaic at Lake Waikaremoana, New Zealand.

4.0 Abstract

The patterns of habitat use of sympatric populations of house mice (*Mus musculus* L.) and ship rats (*Rattus rattus* L.) were compared in a mosaic of tawa-podocarp (Podocarpacae) and southern beech (*Nothofagus* spp.) forest in the North Island, New Zealand. Predator trapping to reduce stoat (*Mustela erminea* L.) numbers was conducted in both forest types, allowing the habitat use of *M. musculus* and *R. rattus* to be examined in areas with and without predators present. Populations of both species erupted to high density in 1996 following synchronous seeding of southern beech species, and were present at low density in most of the study area in 1997 and 1998. In low-density years ship rats showed macro-habitat selection for the more structurally diverse tawa-podocarp forest than for the more uniform beech forest. Tawa-podocarp forest had significantly higher levels of rat-palatable fruiting tree species and had significantly higher levels of ground-dwelling invertebrates in low rat-density years. In the high-density year, food availability was similar in both forest types, and ship rats showed variable habitat preferences. House mice were more strongly associated with microhabitat variables that indicated dense ground cover and characterized beech forest in the high-density year. Mice were too scarce in the low-density years to determine habitat preferences. Predator reduction was more successful in beech forest. This resulted in increased density of ship rats in these areas relative to non-treatment beech forest, and indicates that food availability and distribution, and predator pressure, both influence habitat use by ship rats in New Zealand forests. Mice were too scarce in low-density years to determine the effect of predation risk on mouse habitat use.

4.1 Introduction

Food availability (either quantity or quality) is often considered to be the primary factor influencing the distribution of small mammals (Braithwaite and Gullan 1978; Cockburn 1978; Stoddart and Braithwaite 1979; Moro 1991). Such studies are based on the assumed close relationships between habitat type, composition, and structure, abiotic conditions, and the availability of rodent food (Moro 1991).

A range of factors other than food availability has also been shown to influence spatial and temporal rodent distributions. These include disturbance regimes (Cockburn 1978), suitable nest or burrow sites (Malizia 1998), interactions with competitors (Dooley and Deuser 1990; Monamy 1995a; Monamy 1995b; Dooley and Deuser 1996), the presence of predators (Pearson 1966; 1971; Hansson 1997), and for males, the distribution of females (Ostfeld *et al.* 1985; Bergeron *et al.* 1990; Hooker and Innes 1995).

Seamon and Adler (1996) suggested that habitat-generalist and habitat-specialist rodents would respond to distribution determinants in different ways. Habitat generalists can successfully occupy a range of macrohabitats, and may not show close correlations with measured site attributes, while habitat specialists may be expected to be more closely linked to microhabitat variation (Rosenzweig 1981). Different scales of investigation are often required when studying rodent species that differ in their degree of habitat specialisation.

In New Zealand, the two most common rodents in both agricultural and native ecosystems are the ship rat, *Rattus rattus* L., and the house mouse, *Mus musculus* L. Previous studies have reported broad-scale habitat preferences for both these species, with ship rats being most common in broadleaf-podocarp forests, and scarce in southern beech (*Nothofagus* spp.) forests (Innes 1990), while the reverse is true for house mice (Murphy and Pickard 1990). Both species show periodic population eruptions to high density following synchronous seeding in southern beech forest, which causes large changes in both population density (King 1983; Murphy and Pickard 1990; Fitzgerald *et al.* 1996) and broad-scale habitat use (Blackwell *et al.* 1998). Following mast seeding several species of introduced mammalian predator, in

particular the stoat (*Mustela erminea* L.) and the weasel (*M. nivalis* Erxleben), subsequently increase greatly in number, apparently in response to increased rodent densities (King 1982; 1983).

While these population eruptions have been frequently reported, very little is know about the habitat use and preferences of individual rodents that lead to the observed population dynamics. Ship rat distributions in New Zealand have been linked to increasing forest complexity in broadleaf-podocarp forests (Daniel 1972). House mouse distributions have been shown to be associated with disturbed habitats and dense ground cover (Murphy and Pickard 1990; King *et al.* 1996), and may be influenced by the presence of other rodents (Taylor 1978; King *et al.* 1996; Blackwell *et al.* 1998). The distributions of ship rats and mice in New Zealand may also be influenced by the presence of predators, especially the stoat, a phenomenon that has been shown elsewhere (Hansson 1997).

New Zealand studies have been limited in their ability to distinguish the mechanisms underlying observed rodent distributions. They have been confined to one major habitat type (Fitzgerald *et al.* 1981; Innes and Skipworth 1983; Taylor 1984), or have not investigated the environmental and biological factors leading to the observed distribution (Innes 1979; Dowding and Murphy 1994; Hooker and Innes 1995), or have studied populations in exotic habitats (Clout 1980; King *et al.* 1996).

The only published study that investigates micro- and macro-habitat use in New Zealand (King *et al.* 1996) was conducted in mixed tawa (*Beilschmeidia tawa*) podocarp forest and exotic *Pinus* plantations, where populations do not generally exhibit eruptive population dynamics (Daniel 1972). King *et al.* (1996) found highest ship rat densities in mature native forests, while mice were most abundant in seral habitats.

In this chapter I examine habitat utilisation by house mice and ship rats along gradients of habitat type, structure and complexity, in an area of mixed old-growth forest, in the North Island, New Zealand. The study had three aims.

1). To investigate the distribution of ship rats and house mice in a heterogeneous forest habitat, to identify the factors leading to this distribution, and to determine the degree of habitat specialisation exhibited by ship rats and house mice.

2). To determine the role of periodic energy inputs, following synchronous southern beech masting, in modifying the dynamics and distribution of the small mammal assemblage.

3). To investigate the role of predators in determining habitat use patterns, through the use of large-scale (750 ha) predator removal across a mosaic of forest types.

4.2 Methods

4.2.1 Study area

The study was conducted at Lake Waikaremoana (38° 47′ S 177° 05′ E,), situated at the south-eastern corner of Te Urewera National Park (212,000 ha), in the North Island of New Zealand (Figure 1.1, Chapter 1). This study was part of a larger project investigating the dynamics of the rodent and mustelid predator/prey system, and the implications this has for the threatened northern brown kiwi (*Apteryx australis mantelli* Bartlett).

The lake covers 5,170 ha and lies at an altitude of 582 m a.s.l. The catchment is steep and forested, and has not been logged. There is a mosaic of forest types: 1) tawa-podocarp forest, with a canopy of tawa and mahoe (*Melicytus ramiflorus*), with emergent rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*), and miro (*P. ferruginea*), and a sparse understorey, and 2) beech forest; a canopy dominated by hinau (*Elaeocarpus dentatus*), tawari (*Ixerba brexiodes*), kamahi (*Weinmannia racemosa*) and mahoe, with emergent red, hard, black and silver beech (*Nothofagus* spp.), and ground cover of crown fern (*Blechnum discolour*).

4.2.2 Rodent indexing

In October 1995 footprint tracking tunnel lines (King and Edgar 1977) were established in areas of tawa-podocarp and beech dominated forest on two peninsulas at Lake Waikaremoana. Indexing lines generally ran up into the bush from the lake edge, and were 1300-1800 m in length. Three lines were placed in tawa-podocarp forest, and three in beech forest. Three lines were in areas with intensive predator trapping, and were designated treatment areas (Treatment 1, tawa-podocarp forest; Treatment 2, beech forest; and Treatment 3, tawa-podocarp forest), and three lines were in areas with no predator reduction and were run as non-treatment areas (Non-treatment 1, tawa-podocarp forest; Non-treatment 2, beech forest; and Non-treatment 3, beech forest).

Studies have shown that the average home range diameter for ship rats in tawa-podocarp forest is 80-150 m (Hooker and Innes 1995). A tracking tunnel spacing of 100 m was therefore chosen to permit the best compromise between having a high probability of all animals encountering the indexing method, and preventing a contagion effect due to individual animals tracking multiple tunnels. Tunnels were baited with peanut butter, and run for a single-night index each month between January 1996 and March 1998 (Non-Treatment 1, 2; and Treatment 1, 2), or between April 1996 to March 1998 (Non-Treatment 3), or from December 1996 to December 1998 (Treatment 3). Tracking tunnels in the same forest type in the two treatment regimes were run on the same night, to minimise the effect of activity on the index (Sheppe 1965; Sarrazin and Bider 1973; King and Edgar 1977). For each area, tracking rates of ship rats and mice were calculated as the proportion of tunnels tracked by each species in each tracking session.

Over the course of the experiment, a concurrent predator kill-trapping program was conducted in the treatment area. In September 1994, Mk 4 and Mk 6 Fenn kill traps (FHT Works, Redditch, England) were placed at 150 m intervals along each of the transect lines on Puketukutuku peninsula, and on several additional ridges between transects. Traps were placed at 25 m intervals across the neck of the peninsula in an

attempt to intercept any predators moving onto the trapped areas. Fenn traps were also placed at each of the coastline stations on Puketukutuku peninsula. All traps were placed under wooden covers to prevent capture of non-target animals, and were baited with either hens' eggs or rabbit meat. Traps were run continuously from May 1995, and are checked every 7-10 days on the main trap lines. Several of the lines were checked less frequently, with intervals between checks of 2-4 weeks. The species, sex, and capture date and location of all animals caught was recorded.

4.2.3 Vegetation surveys

Vegetation surveys were conducted at each of the tracking tunnel sites, following the methods of King *et al.* (1996). At each site a 15 m circle was used to assess the vegetation present. The species composition and percentage cover of each species present was assessed in six height tiers (20 m +, 12-20 m, 5-12 m, 2-5 m, 0.3-2 m, and <0.3 m). At each site, the height of the canopy, and percentage of the sky covered were estimated. Importance values for each site were calculated by summing the percentage cover values for each species in all tiers, but weighting the upper tiers as more important in determining overall site structure (King *et al.* 1996). At each site environmental variables were recorded: altitude, aspect, slope, site type, drainage, and the percentage of ground covered by vascular plants, non-vascular plants, litter, bare soil and exposed rock. The distance to any small mammal cover (e.g. logs, thick ground cover) was also estimated, using the method of King *et al.* (1996).

4.2.4 Food availability

The abundance of ground dwelling invertebrates in each area was estimated using pitfall trapping. Two groups of ten pitfall traps were established adjacent to the tracking tunnel line, and were separated by approximately 500-900 m in each area. In each of the groups, the traps were arranged in five pairs on a 25 x 5 m grid. Each trap consisted of a plastic food container (10 cm deep x 10 cm diameter) dug into the ground, with the top flush with the surface. The traps were half filled with

commercial anti-freeze (90% ethylene glycol), and covered with a 25 x 25 cm metal cover to prevent capture of non-target animals. Traps were cleared monthly, and the species present were identified to Family or Genus, and counted. Only individuals with body lengths greater than 5 mm were counted, as this is smaller than the minimum prey size known to be consumed by ship rats in New Zealand (Best 1969; Innes 1979; 1990). The diet of ship rats caught in the study area was determined (Chapter 3), and this was used to calculate a measure of food availability for rats.

In four of the areas (Non-treatment 1, 2, Treatment 1, 2) populations of weta (Orthoptera) were indexed using "weta galleries". Each gallery consisted of a section of 300 x 50 x 50 mm timber, with a 20 mm diameter hole drilled down the length of the gallery, and a rubber bung placed in the top of the hole. In each area, 40 galleries were placed in 12 groups of three and one of four at 100 m intervals along the tracking tunnel line, giving a total of 13 stations per area. At each station, the three galleries were placed on canopy or sub-canopy trees at a height of 1-1.5 m above the ground, and were placed within a ten-metre radius of the tracking tunnel. The galleries were checked monthly, and the number of weta (and their identity to Family) was recorded. Weta numbers were expressed as the number of weta per station per month.

4.2.5 Seed traps

Eight seed traps were placed at 100 m intervals adjacent to the trapping line in all areas except Treatment 3. Each trap consisted of a metal funnel with a catching area of 0.2 m^2, supported on a metal tripod. Seed and litter-fall was collected in a metal can attached to the bottom of the funnel. Cans had holes drilled in the bottom to allow water to escape, and a wire mesh disc was placed in each can to prevent material falling through the drainage holes.

Seed traps were cleared monthly and returned to the laboratory for sorting. Each sample was oven dried for 24 h at 75°C, and then weighed. The contents of the sample were sorted into fruit, seeds, flowers, leaves, wood and twigs, and litter. Fruit, seed and flowers were identified and weighed. Leaves were identified and the percentage composition of each species was estimated, and all separate fractions were

weighed. Average weights of seed and fruit falling in each month in each area were calculated.

4.2.6 Statistical analysis

Differences in tracking rates between seasons and between areas were analysed using the Genmod procedure in SAS (SAS Inc. 1996). An individual tunnel could be either tracked or untracked, so a binomial analysis was used. Differences between periods were analysed using a repeated measures design to investigate temporal trends in the data. The Genmod analysis produces a X^2 statistic that can be compared with the critical value from the X^2 distribution with the appropriate degrees of freedom.

Differences in capture rate between areas and years were analysed using the Genmod procedure in SAS, with a binomial approximation, and a auto-regressive model of order 1, which correlates the residual of a predicted value with the previous value only (SAS Inc. 1996).

Ordinations were performed on the rodent tracking sites using the Detrended Correspondence Analysis in the PCORD computer program (McCune and Mefford 1997). Two separate ordinations were performed on the data. The first used the weighted averages for vegetation species present at a site to construct overall gradients of forest composition, while the second used physical site variables measured at each site to construct gradients of habitat structure. This allowed the examination of rodent habitat preferences at both the microhabitat scale using the raw site variables, and at the macrohabitat scale using the site scores from the ordinations.

Gradients in habitat use were examined separately for non-treatment and treatment areas, to examine the effect of predator removal on rodent habitat use. The relationship between habitat use and site variables was examined separately for each year of the study, using average annual density indices for each tracking station. This allowed examination of the effect of a large energy input into the ecosystem following the synchronous mast seeding of *Nothofagus* spp. in March-April 1995.

For each year and treatment, the relationship between rodent density and micro- and macro-habitat gradients was examined using a stepdown multiple regression, whereby all variables are included in the analysis and then non-significant variables are subsequently eliminated, with a probability to remove of 0.15. The microhabitat and macrohabitat variables (and a description of their meanings) used in the regressions, are shown in Appendix 4.1.

Macrohabitat variables that were predicted to influence rodent distribution (invertebrate numbers per area, seed-fall rates per area) were examined for differences between areas, overall forest type, treatment regimes and years, using the General Linear Model procedure in SYSTAT (SPSS Inc, 1996).

Rat tracking rates in beech forest and tawa-podocarp forest over the course of the study were used to calculate habitat use ratios for treatment and non-treatment areas. Changes in habitat use ratios in treatment and non-treatment areas were analysed using a linear regression in SYSTAT (SPSS Inc, 1996).

4.3 Results

Rodent density was recorded continuously from November 1995 to March 1998 at a total of 87 sites (44 non-treatment, 43 treatment). House mice were present in moderate numbers at the start of the study, following the synchronous *Nothofagus* mast seeding in April 1995 (Dr C. Ward, pers. comm.). Numbers were crashing at the start of the study, and mice became scarce by spring 1996, and remained so for the rest of the study. As a result, habitat use by mice was examined for the 1996 time-period only. Ship rat tracking rates were high in January 1996, and peaked in autumn 1996, before dropping to low levels in late 1996 and throughout 1997 (Figure 4.1).

4.3.1 Habitat characteristics

Both the vegetation ordination and the physical site attribute ordination produced similar relationships between tracking tunnel sites (Figure 4.2a, b). Beech forest sites

were clumped together indicating similar floristic composition, while tawa-podocarp sites were more scattered in the vegetation ordination, reflecting the greater variability in species composition in this forest type. Beech forest was characterized by an emergent layer of *Nothofagus truncata*, *N. menziesii* and *N. fusca*, and a canopy of *Ixerba brexioides* and *Quintinia acutifolia* (Plate 4.1). *Dracophyllum pyramidale* was common in the sub-canopy, and abundant *Leucopogon fasticulatus* in the shrub layer, and a dense ground cover of *Blechnum discolour* characterized beech sites. Beech forest sites tended to be on steeper, drier, north facing slopes, and with lower species richness, and dense ground cover (Figure 4.2b).

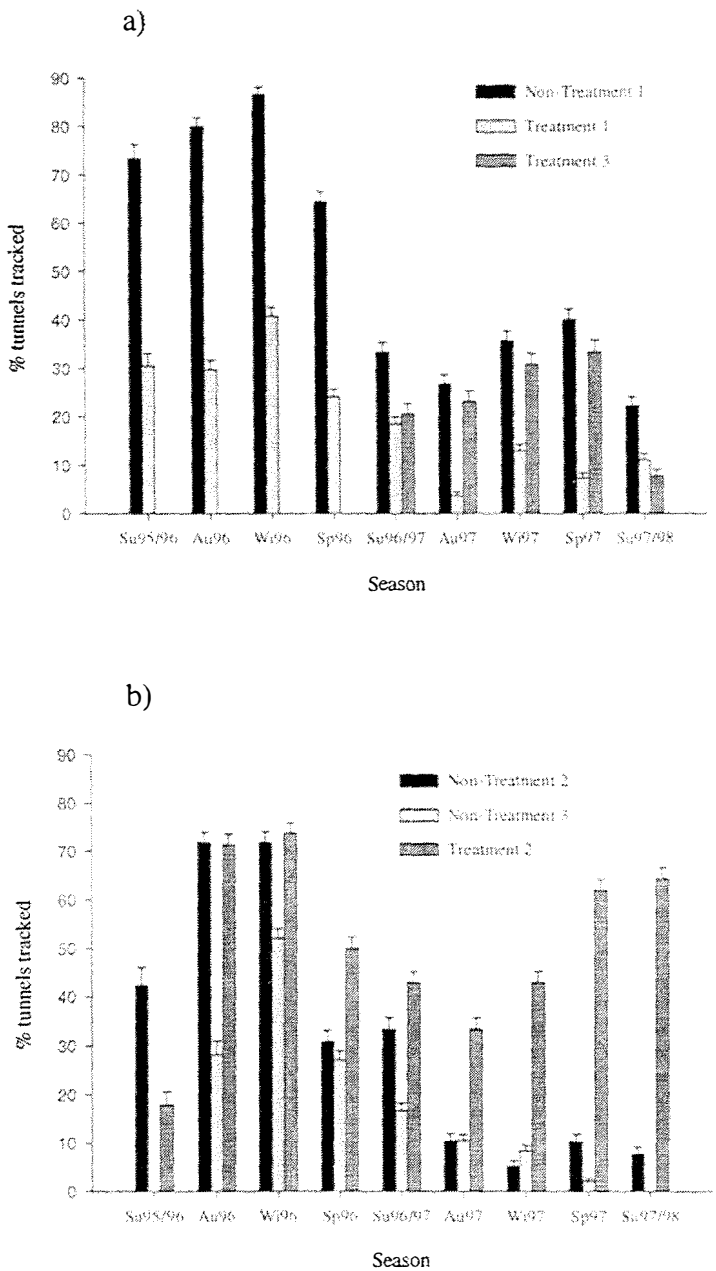

Figure 4.1 Seasonal tracking rate (% tunnels tracked) for ship rats on a) podocarp-tawa forest, and b) beech forest index lines. Error bars denote the upper 95% confidence interval of the mean. Predator trapping commenced in autumn 1995. The number of tunnels run per month in each area was Non-treatment 1 = 15; Non-treatment 2 = 12; Non-treatment 3 = 16; Treatment 1 = 18; Treatment 2 = 14; Treatment 3 = 12.

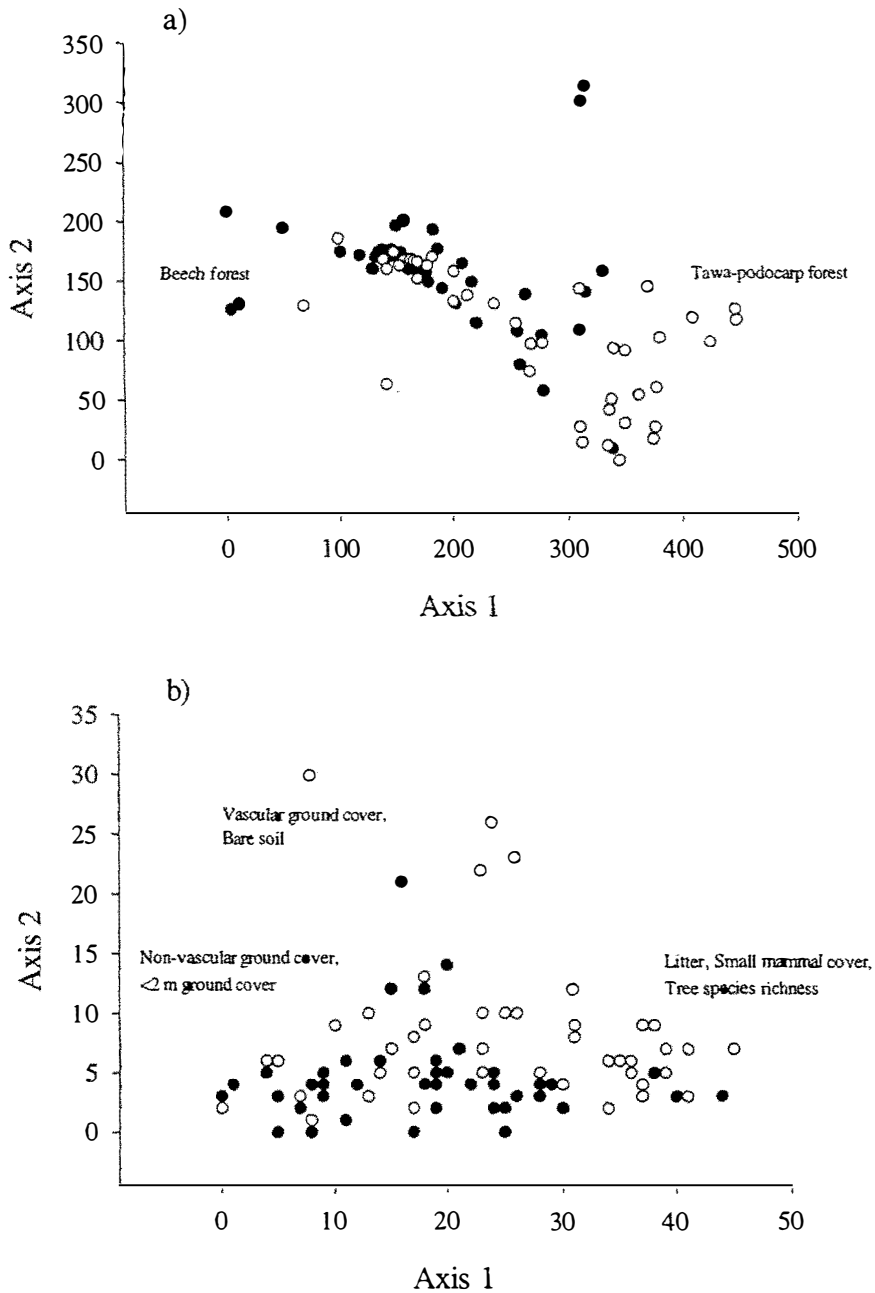

Figure 4.2 Ordinations for rodent indexing sites in Non-Treatment (open circles) and Treatment (closed circles) areas at Lake Waikaremoana, New Zealand. Detrended Correspondence Analyses were performed using a) the vegetation present at each site and b) the physical site attributes measured at each site.

Plate 4.1 Beech forest in Non-treatment area 3, Lake Waikaremoana, New Zealand. Canopy trees are tawari (*Ixerba brexioides*), with emergent red beech (*Nothofagus fusca*), and a ground cover of crown fern (*Blechnum discolour*). A seed trap is shown in the foreground, with a tracking tunnel on the far right.

Tawa-podocarp sites exhibited a much greater floristic diversity (Plate 4.2). Such sites were strongly characterized by the presence of *Beilschmeidia tawa* (correlation between species and Axis 1 score; Pearson r = 0.615, $p < 0.01$) and *Dicksonia squarosa*, both of which showed strong associations with Axis 1 of the vegetation ordination (Figure 4.2a). This suggests that Axis 1 largely separates tawa-podocarp and beech forest sites. Within the tawa-podocarp sites, a wide range of species showed significant associations with Axis 2 of the ordination, which can be interpreted as measuring the between site variation in floristic composition in the tawa-podocarp forests. Species that were significantly associated with Axis 2 of the vegetation ordination included the emergents *Dacrydium cupressinum* and *Nothofagus fusca*, the canopy species *Ixerba brexioides*, the sub-canopy species *Metrosideros colensoi*, *Pseudowintera colorata* and *Aristolelia serrata*, and the tree fern *Cyathea smithii*. The physical site attributes showed that tawa-podocarp sites tended to be positively associated with leaf litter and the presence of logs and other small mammal refugia.

Tawa-podocarp areas had greater numbers of rat-palatable fruiting tree species per site (total number of species ± SE per site: Tawa-podocarp forest, 4.05 ± 0.15; Beech forest, 2.23 ± 0.15; $F_{1,83} = 72.32$, $P < 0.001$). In all years, the amount of rat-palatable fruit and seed collected in the seed-traps was significantly higher in tawa-podocarp areas than in beech forest areas ($F_{2,115} = 3.47$, $P = 0.03$). For all years pooled, both the species richness of rat-palatable invertebrates ($F_{1,135} = 21.575$, $P < 0.001$), and the total number of individuals of edible species ($F_{1,135} = 21.804$, $P < 0.001$) were significantly higher in tawa-podocarp forest than in beech forest (Table 4.1). Numbers of weta found in weta galleries were not significantly different between tawa-podocarp and beech forest sites ($F_{1,102} = 0.977$, $P = 0.33$; Table 4.1). Tawa-podocarp forest sites were more complex (Figure 4.2), and had significantly higher levels of invertebrate and seed and fruit rodent food. (Table 4.1), irrespective of whether the site was in a treatment or non-treatment area.

Plate 4.2 Tawa-podocarp forest in Non-treatment area 1, Lake Waikaremoana, New Zealand. A fairly uniform canopy of tawa (Beilschmeidia tawa) characterized tawa-podocarp sites, with an understorey of the tree fern *Dicksonia squarosa*. Ground cover was generally sparse, with large amounts of litter present.

Table 4.1 Analysis of variance of rodent food abundance between tawa-podocarp forest and beech forest areas in each year of the study. The fruit and seed and invertebrate species used in the analysis are species known to be consumed by ship rats in New Zealand.

Test	Source	SS	*df*	MS	F	*P*
Fruit fall	Year	1.674	2	0.837	2.2145	0.114
	Habitat	6.608	1	6.608	17.478	0.0001
	Year by Habitat	2.624	2	1.312	3.471	0.034
	Error	43.479	115	0.378		
Invertebrate species richness	Year	236.194	2	118.097	14.393	0.0001
	Habitat	117.025	1	117.025	21.575	0.0001
	Year by Habitat	31.842	2	15.921	1.940	0.148
	Error	1107.694	135	8.205		
Invertebrate species number	Year	2337.009	2	1168.505	28.936	0.0001
	Habitat	880.502	1	880.502	21.804	0.0001
	Year by Habitat	347.147	2	173.573	4.298	0.015
	Error	5451.600	135	40.382		
Weta numbers	Year	0.135	2	0.067	4.064	0.020
	Habitat	0.016	1	0.016	0.977	0.323
	Year by Habitat	0.020	2	0.010	0.605	0.548
	Error	1.693	102	0.016		

4.3.2 Ship rat distribution in unperturbed areas

In low density years (1997 and 1998), ship rats were associated with both microhabitat and macrohabitat site variables (Table 4.2, 4.3). Positive associations with the vegetation ordination (Vegetation ordination axis 1 and Vegetation ordination axis 2), with physical site characteristics (Site ordination axis 1), and with the species richness of fruiting trees in the 12-20 m layer, all highlight a macrohabitat preference for tawa-podocarp forest sites over beech forest areas. There were significant associations between microhabitat variables and ship rat habitat use (Table 4.2, 4.3), and there was year to year variability in the microhabitat variables that were associated with habitat use (significant contributions from Vascular ground cover, Litter, < 2 m ground cover, 5-12 m fruiting tree species richness and 2-5 m fruiting tree species richness in 1997;and Non-vascular ground cover, Litter, Distance to small-mammal cover, North-South gradient, and East-West gradient in 1998).

4.3.3 Response of ship rats to large energy inputs

Synchronous southern beech (*Nothofagus* spp.) seeding occurred in April-May 1995. Following this large energy input, numbers of rat-palatable ground-dwelling invertebrates increased, and were significantly higher in summer 1995/96 than in the post-seeding summer 1996/97 ($F_{1,55} = 16.1$, $P < 0.001$; Table 4.4). Ship rat numbers also erupted to significantly higher levels in autumn/winter 1996, before declining back to low levels by autumn 1997 ($X^2 = 62.84$, $df = 3$, $P < 0.01$; Figure 4.1).

Table 4.2 Significant variables in stepdown multiple regression of factors determining ship rat habitat use in non-treatment and treatment areas in 1997. The probability to remove was set at 0.15, and the model statement refers to the most significant fit obtained from the regression. ** = $P < 0.01$. Positive coefficients indicate the variable is associated with tawa-podocarp forest habitat choice, negative coefficients indicate the variable is associated with beech forest habitat choice.

Category	Variable	Coefficient	*t*	*P*	Model
Non-treatment	Vascular ground cover	0.017	3.508	0.001	$F_{9,34}=11.198^{**}$
	Litter	-0.012	-2.465	0.019	
	<2-m ground cover	0.007	1.880	0.069	
	Vegetation ordination axis 1	0.001	2.062	0.047	
	Vegetation ordination axis 2	0.001	2.498	0.018	
	Site ordination axis 1	0.030	2.243	0.032	
	12-20 m fruiting tree richness	0.212	4.423	0.001	
	5-12 m fruiting tree richness	-0.067	-1.895	0.067	
	2-5 m fruiting tree richness	-0.079	-1.905	0.065	
Treatment	Vegetation ordination axis 2	-0.002	-1.891	0.067	$F_{5,37}=8.019^{**}$
	Site ordination axis 1	-0.006	-1.715	0.095	
	20-m + fruiting tree richness	-0.188	-3.302	0.002	
	5-12 m fruiting tree richness	-0.116	-3.011	0.005	
	2-5 m fruiting tree richness	-0.116	-2.819	0.008	

Table 4.3 Significant variables in backward stepwise regression of factors determining ship rat habitat use in non-treatment and treatment areas in 1998. For an explanation of the analysis, see Table 2. ** = $P < 0.01$. The probability to remove was 0.15.

Category	Variable	Coefficient	*t*	*P*	Model
Non-treatment	Non-vascular ground cover	-0.006	-1.942	0.060	$F_{8,35}=6.253^{**}$
	Litter	-0.006	-1.899	0.066	
	Distance to small-mammal cover	0.036	1.580	0.123	
	North-South gradient	0.351	2.032	0.050	
	East-West gradient	-0.148	-1.624	0.113	
	Vegetation ordination axis 1	0.001	1.559	0.128	
	Vegetation ordination axis 2	0.001	2.765	0.009	
	12-20 m fruiting tree richness	0.162	2.077	0.045	
Treatment	Vegetation ordination axis 1	-0.002	-2.489	0.020	$F_{5,25}=6.972^{**}$
	Vegetation ordination axis 2	-0.003	-1.668	0.108	
	Site ordination axis 2	-0.018	-2.215	0.036	
	20-m + fruiting tree richness	-0.191	-1.845	0.077	
	12-20 m fruiting tree richness	-0.218	-2.996	0.006	

Table 4.4 Analysis of variance of individual invertebrates in pitfall traps in summer/autumn 1995/96 and 1996/97, caught at Lake Waikaremoana. Invertebrates are species known to be eaten by rats (Chapter 3).

Source	SS	*df*	MS	F	*P*
Su/Au 96 vs Su/Au 97	145.89	1	145.89	16.51	0.0002
Treatment	44.10	1	44.10	4.99	0.029
Habitat	80.03	1	80.03	9.06	0.004
Treatment by season	15.58	1	15.58	1.76	0.190
Habitat by treatment	0.78	1	0.78	0.09	0.767
Habitat by season	18.89	1	18.89	2.13	0.149
Error	485.89	55	8.83		

During the peak year (1996), ship rat density patterns in non-treatment areas were associated with the macrohabitat variables Vegetation ordination axis 1 and Site ordination axis 2, and indicated broad scale selection of tawa-podocarp forest (Table 4.5). Only one microhabitat variable (12-20 m fruiting tree species richness) had a significant effect on rat distribution, and this variable is largely influenced by the larger scale macrohabitat gradients. In the low density years (1997 and 1998), ship rats still showed positive associations with the macrohabitat gradients (Table 4.2, 4.3), but were significantly influenced by a larger range of microhabitat variables.

In treatment areas, rats did not show clear consistent trends in habitat use during the high-density year. There was a strong negative influence of fruiting tree species richness in the 12-20 m layer on rat distribution indicating rats are more active in beech forest. However, negative effects of both Non-vascular ground cover and Litter on rat distribution indicate contradictory associations between tawa-podocarp and beech forest areas, and suggest that ship rat activity was fairly equal between the two forest types. In 1997 and 1998 there was an increasing trend for rats to be associated with beech forest, as indicated by negative associations with the Vegetation ordination axis 2, Site ordination axis 1, and the three measures of fruiting tree species richness in 1997 (Table 4.2). In 1998, rats were negatively associated with Vegetation ordination axis 1, Vegetation ordination axis 2, Site ordination axis 2, and two measures of fruiting tree species richness (Table 4.3). In both the low-density years, rats in treatment areas show little association with microhabitat variables.

Data from the rat by-catch in the predator-trapping program lends support to these conclusions (Figure 4.3). In the peak year (1996), rat captures per 100 trap-nights (C/100TN) were significantly higher in the tawa-podocarp forest than in the beech forest (X^2 = 15.90, df = 1, P < 0.001), while the reverse trend was apparent in 1997, with rat C/100TN significantly higher in the beech forest than in the tawa-podocarp forest (X^2 = 20.66, df = 1, P < 0.001), but not in 1998 (X^2 = 0.006, df = 1, P = 0.93).

4.3.4 Response of house mice to large energy inputs

House mouse tracking rates increased in spring 1995 and summer 1995/96 following the autumn 1995 beech seed-fall. In both non-treatment and treatment areas, mice showed fairly weak habitat preferences, and were associated with a range of microhabitat and macrohabitat variables. In non-treatment areas, mice were not associated with any macrohabitat gradients, and showed variable microhabitat preferences (Table 4.6). They were positively associated with the amount of leaf litter and a measure of fruiting tree species richness (5-12 m height tier), both of which are associated with tawa-podocarp forest sites. However, mice were also positively associated with non-vascular ground cover, and negatively associated with measures of fruiting tree richness in the 12-20 m, and 2-5 m height tiers (Table 4.6), indicating their presence in beech forest sites. The overall model from the regression for non-treatment rats was not significant ($F_{5,38}$ = 2.036, P = 0.09).

In treatment areas, mice showed a stronger association with beech forest at both the macrohabitat (negative association with Vegetation ordination axis 1) and microhabitat (negative associations with Litter, Distance to small-mammal cover; positive association with < 0.3 m ground cover) levels (Table 4.6).

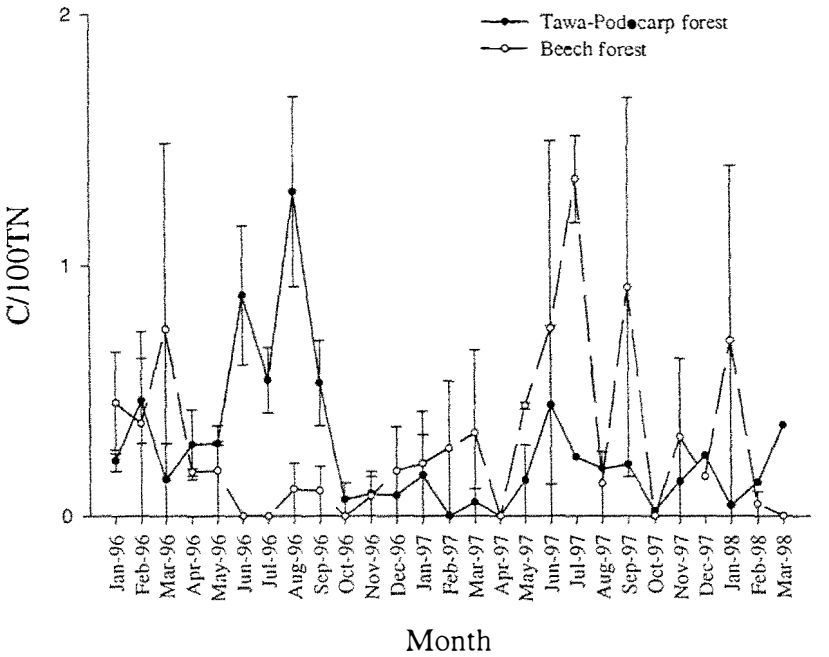

Figure 4.3 Capture rates of ship rats from January 1996 to March 1998 in Fenn traps in tawa-podocarp and beech forest on the treatment peninsula at Lake Waikaremoana. Captures are expressed as an average capture rate per 100 trap-nights (C/100TN) ± 95% confidence interval, and are corrected for sprung traps by subtracting half a trap night for any sprung traps recorded.

Table 4.5 Significant variables in stepdown multiple regression of factors determining ship rat habitat use in non-treatment and treatment areas in 1996. For an explanation of the analysis, see Table 2. ** = $P < 0.01$. The probability to remove was 0.15.

Category	Variable	Coefficient	*T*	P	Model
Non-treatment	Vegetation ordination axis 1	0.001	1.513	0.138	$F_{3,40}=6.255^{**}$
	Site ordination axis 2	0.015	1.537	0.132	
	5-12 m fruiting tree richness	0.093	1.661	0.104	
Treatment	Non-vascular ground cover	-0.005	-1.883	0.068	$F_{5,37}=6.027^{**}$
	Litter	-0.005	-2.083	0.044	
	North-South gradient	0.356	1.779	0.084	
	East-West gradient	-0.154	-1.804	0.079	
	12-20 m fruiting tree richness	-0.184	-2.863	0.007	

Table 4.6 Significant variables in stepdown multiple regression of factors determining mouse habitat use in non-treatment and treatment areas in 1996. For an explanation of the analysis, see Table 2. # = $0.10 > P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$. The probability to remove was 0.15.

Category	Variable	Coefficient	*T*	*P*	Model
Non-treatment	Non-vascular ground cover	0.004	2.75	.009	$F_{5,38}=2.036^{\#}$
	Litter	.003	2.595	0.013	
	12-20 m fruiting tree richness	-.042	-1.831	0.075	
	5-12 m fruiting tree richness	0.034	1.767	0.085	
	2-5 m fruiting tree richness	-0.033	-1.504	0.141	
Treatment	Altitude	-0.001	5.066	0.031	$F_{7,35}=3.011^{*}$
	Litter	-0.003	4.295	0.046	
	Distance to small-mammal cover	-0.012	2.780	0.104	
	< 0.3-m cover	0.008	2.929	0.096	
	Vegetation ordination axis 1	-0.001	5.917	0.020	
	Site ordination axis 1	0.006	3.395	0.074	
	2-5 m fruiting tree richness	0.026	2.172	0.149	

Mice were also associated with variables that characterize tawa-podocarp forest (Vegetation ordination axis 1, 2-5 m fruiting tree species richness). In the post-seeding years (1997,1998), mice were either scarce or absent from beech and tawa-podocarp forest in treatment and non-treatment areas, and the records were too few to allow statistical analysis.

4.3.5 The role of predation in determining rodent habitat use

Predator removal commenced in May 1995, and continued throughout the duration of the study. The reduction in predator density corresponded with large increases in rodent tracking rates in the post-seeding years in the beech forest treatment site (Figure 4.1b), which was mirrored in the Fenn trap capture rates (Figure 4.3). Concurrently, there was a reduction in rodent numbers in Treatment area 1 (tawa-podocarp forest), which may have been influenced by a large rat by-catch in Fenn traps in the area (Figure 4.1a; 4.4). In effect this resulted in reduced predation on rats in beech forest and increased (artificial) predation in Treatment area 1. Over the course of the experiment this led to a change in the broad scale habitat use of ship rats in treatment areas, relative to non-treatment areas (Figure 4.4), with rats becoming significantly more common in beech forest in treatment areas than in non-treatment areas over the low phase (Average % tunnels tracked ± 95% CI: T2; 64.3 ± 9.1%; Pooled non-treatment; 4.7 ± 2.8; $X^2 = 183.30$, $df = 2$, $P < 0.001$). In non-treatment areas, the ratio of rat density in beech forest:tawa-podocarp forest decreased fairly consistently, with the model ($F_{1,7} = 37.29$, $p < 0.001$) explaining 84 % of the variance. In comparison, the ratio of rat density in beech forest: tawa-podocarp forest in treatment areas was more variable, with the model ($F_{1,7} = 9.57$, $p = 0.02$) explaining 58 % of the variance (Figure 4.4).

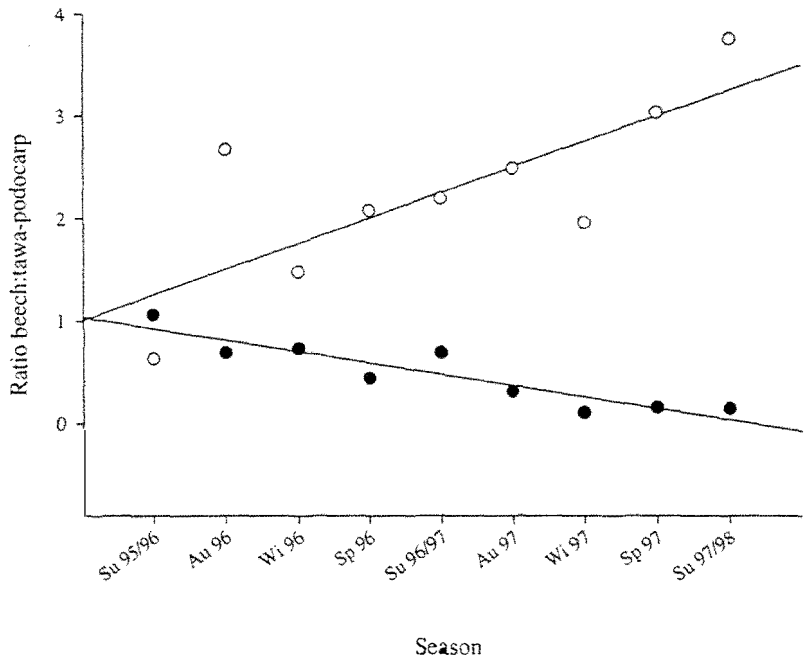

Figure 4.4 The ratio of rat tracking rate in beech forest:tawa-podocarp forest for non-treatment (filled circles) and treatment (open circles) areas from summer1995/96 to summer 1997/98). Density is estimated from the average ship rat tracking-rate in each season for each forest type. Within non-treatment areas, the seasonal tracking rate in the two beech forest lines (areas NT2, NT3) was averaged, while in treatment areas, the tracking rate was averaged for the two tawa-podocarp forest lines (T1, T3).

This trend is highlighted by the importance of the variables that characterize beech forest sites in determining rodent distribution in treatment areas in the post-masting years (Table 4.2, 4.3). In both 1997 and 1998, rats in treatment areas showed the inverse relationship to the vegetation gradients Vegetation ordination axis 1, Vegetation ordination axis 2, and to the physical site composition gradient 1 (Site ordination axis 1) to that shown by rats in non-treatment areas. Rats in non-treatment and treatment areas also showed opposite associations with fruiting-tree species richness (12-20 m fruiting tree species richness) in 1998. Rats in treatment areas showed little association with microhabitat variables in the post-mast years, in comparison to non-treatment area rats that were significantly influenced by a range of microhabitat variables.

4.4 Discussion

4.4.1 Habitat generalists vs. habitat specialists

Theory predicts that habitat specialists should be associated with single measures of microhabitat variability (Seamon and Adler 1996), and should show little temporal variation in association with microhabitat variables. Habitat generalists on the other hand should vary temporally and spatially in their distribution, depending on which microsites are the most suitable. Individual fitness is predicted to vary along micro- and macrohabitat gradients (Rosenzweig 1981; Halama and Dueser 1994; Seamon and Adler 1996). Ship rats in this study behaved in a generalist way with respect to microhabitat and macrohabitat variables. Different variables and macrohabitat gradients became important at different times during the study, and some microhabitat variables showed opposite influences on rat populations in different years. Rats also showed significant associations with the macrohabitat gradients, suggesting that broad-scale habitat choice was more important than any particular microhabitat variable. The habitat associations exhibited by ship rats in this study were highly

flexible and opportunistic, as illustrated by the ability to use the beech forest sites in the mast-seeding year, where these sites generally support negligible rat numbers in low-density years.

House mice were only present in significant numbers in the first year of the study, before dropping down to low levels in all treatment and non-treatment areas. Mice showed a range of habitat preferences. They were too scarce in the low-density years to allow a definitive classification as habitat specialists or generalists. However, house mice in New Zealand show similar plasticity in behaviour and microhabitat choice to mice elsewhere (Berry and Peters 1975; Bronson 1979; Berry 1981; Berry and Bronson 1992), and may thus be considered as habitat generalists. A number of New Zealand studies have highlighted the preference of house mice for beech forest (King 1983; Murphy and Pickard 1990; Fitzgerald *et al.* 1996) and for disturbed habitats (King *et al.* 1996). There may be sufficient food available during the beech-masting that mice can occupy a range of temporally suitable sites, before retreating to refugia when resources become scarce. Following the population crash, mice were present in low numbers, scattered throughout seral habitat around the edge of Lake Waikaremoana (Blackwell *et al.* 1998).

4.4.2 Determinants of rodent distribution

Although ship rats (and house mice) can be classified as habitat generalists, they still exhibited definite habitat preferences. In undisturbed, non-treatment areas, ship rat distribution was determined by factors that characterised tawa-podocarp forest. This included macrohabitat variables such as Axis 1 from both the vegetation ordination and physical site characteristics ordinations, and microhabitat variables such as the amount of leaf litter, the presence of logs and other refugia, and by high fruiting tree species diversity. This forest type was more structurally and floristically diverse than the beech forest, and it has been suggested that this increased complexity can support higher rat numbers in New Zealand (Daniel 1978).

The primary determinants of rodent distribution in this study were the amounts of rodent food available in the two different habitats. A number of studies have

previously highlighted this link, both for murid rodents in New Zealand (Daniel 1978; Murphy 1992; Fitzgerald *et al.* 1996; King *et al.* 1996), and for rodents elsewhere (Braithwaite and Gullan 1978; Cockburn 1978; Stoddart and Braithwaite 1979; Moro 1991).

Tawa-podocarp forest had significantly higher levels of rat-edible plant and invertebrate food, particularly during the non-masting years, and this is shown by the almost complete absence of rats in the beech forest in the non-treatment areas from autumn 1997 onwards. Rodents may face more severe food limitation in beech forest, at least during non-masting years.

4.4.3 Role of energy inputs into system

When food limitation is reduced, habitat generalists such as the ship rat may move from preferred habitats into previously marginal habitats (Halama and Dueser 1994; Seamon and Adler 1996). If all habitats are temporally suitable, then individuals may not exhibit microhabitat selection, but rather show broad scale macrohabitat selection for any site that provides sufficient food. When resources become limiting again, generalists begin to exhibit stronger preferences for preferred habitats, and become more closely associated with macrohabitat and microhabitat variables that indicate suitable habitats.

Following significant increases in rodent-palatable food during the 1995 mast seeding of *Nothofagus* species, mouse and rat tracking rates rose to significantly higher levels in all forest types, and exhibited modified habitat preferences in the presence of excess food. Rats became relatively abundant in previously marginal habitats (beech forest), and were able to reproduce and persist in this habitat throughout the period when resources were abundant. As predicted by theory, when resource levels dropped again after the seed-fall, rat numbers dropped in the marginal habitats (as seen in non-treatment beech forest) and rats retreated into preferred refuge habitats in the tawa-podocarp forest.

Individual fitness has been shown to vary with habitat type and quality in a range of taxa (Whitham 1978; Morris 1989; Halama and Dueser 1994). During low-density years in this study, individual fitness is presumably greater in tawa-podocarp forest, as shown by higher population densities (Blackwell, unpubl. data). Annual mortality in ship rats in New Zealand is around 90-98% (Daniel 1972), and is especially high in the decline phase following the beech mast-seeding, so that any differences in fitness may be short lived. Ship rats can be considered as strongly *r*-selected (MacArthur and Wilson 1967), so that differences in fitness (measured as lifetime reproductive success) may be slight, and highly variable between habitats and seasons.

4.4.4 The role of predation

Predators may modify prey habitat use by affecting habitat specific survival (Hansson 1996; 1997), especially in cyclic or eruptive predator/prey systems. If predation pressure differs between habitats, either through differing predator densities or predation rates, then prey distributions should reflect responses to this predation pressure.

The shift in habitat use by rats that followed predator reduction in treatment areas may have been a result of a combination of several factors. In the beech forest treatment area (T2), predator control was effective, and successfully reduced predator numbers to low levels. In this area there was a large increase in rat numbers from autumn 1997 onwards, so that rat densities were significantly higher than in the non-treatment beech forest sites. The tawa-podocarp treatment sites were adjacent to the high trap-density buffer lines running across the next of the treatment peninsula. A high ship rat by-catch was recorded in the traps on these lines, so that rat numbers may have been locally reduced in the areas surrounding the tracking tunnel indexing lines.

The response of rats in the treatment beech-forest line following predator reduction is consistent with the hypothesis that predators can limit prey population size. However, the rat density recorded in treatment area 2 towards the end of the study was similar to that recorded during the 1995/96 population eruption, suggesting that factors other than predation alone may have been involved. Invertebrates can constitute a

significant proportion of stoat diet (King and Moody 1982). Reduction in stoat numbers may therefore lead to both a reduction of predation pressure on rat populations, as well as a concurrent increase in the availability of invertebrate food for rats. However, over the course of the study, no increase in ground-dwelling invertebrates was recorded in treatment area 2 that would support this contention. It is also possible that rodents (mice and ship rats) make up a greater proportion of stoat diet in the structurally simpler beech forest (King and Moody 1982). As a result predator reduction may lead to a proportionally greater reduction in predator limitation of rodents in beech forest than in tawa-podocarp forest.

The shift in habitat use by rats in treatment areas is consistent with a modification of rodent density and distribution by predator-induced changes in habitat specific survival (Hansson 1997), but the response was probably influenced by concurrent changes in food availability.

4.4.5 Summary

Ship rats in New Zealand mixed forests behave in a generalist way with respect to habitat choice and utilisation. They show broad scale preferences for tawa-podocarp forest, but habitat use can change when food or predator limitation is reduced. Food limitation is more important than predator limitation in determining ship rat distribution in this system.

House mice also appear to be habitat generalists, although their occurrence was too infrequent to allow an accurate clarification of their overall habitat preferences. As with the ship rat, their distribution is influenced by food availability and predation levels with large population increases occurring as a result of periodic food additions. The rodent/predator assemblage in New Zealand forests is driven by bottom-up food limitation, with predation potentially important at key times during the eruptive cycle.

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Appendix 4.1 Variables used in backward multiple regression.

Variable		Description
Microhabitat	ALT	Site altitude, meters above seas level
	VASCGC	Percentage of ground covered by vascular vegetation
	NONVASCGC	Percentage of ground covered by non-vascular vegetation
	LITTER	Percentage of ground covered by leaf litter
	SMC	Distance (meters) to nearest small mammal cover, e.g. logs
	2MCOVER	Percentage of ground covered by vegetation < 2 meters high
	0.3MCOVER	Percentage of ground covered by vegetation < 0.3 meters high
	NSGRAD	Aspect of site along North-South gradient
	EWGRAD	Aspect of site along East-West gradient
	EAT20PL	Number of fruiting tree species eaten by rats in the 20 m+ tier
	EAT1220	Number of fruiting tree species eaten by rats in the 12-20 m tier
	EAT512	Number of fruiting tree species eaten by rats in the 5-12 m tier
	EAT25	Number of fruiting tree species eaten by rats in the 2-5 m tier
Macrohabitat	DCAAXIS1	Vegetation ordination axis 1, measuring overall site type; tawa-podocarp or beech forest
	DCAAXIS2	Vegetation axis 2, measuring tawa-podocarp forest diversity
	ENVDCA1	Site characteristics ordination axis 1
	ENVDCA2	Site characteristics ordination axis 2

Chapter 5: A computer simulation of rodent and predator population dynamics in an eruptive system.

5.0 Abstract

A computer model of the population dynamics of house mice (*Mus musculus* L.), ship rats (*Rattus rattus* L.) and stoats (*Mustela erminea* L.) in New Zealand forest was constructed, to test the relative importance of food availability and predation in shaping observed small-mammal population dynamics. A number of outputs and predictions from the model were developed. The model highlighted the overall importance of variation in food availability in determining the timing and amplitude of rodent population eruptions. The model showed that predators can not prevent a prey-species eruption, primarily due to differences in reproductive biology. However, predation can delay the start of the prey-population increase during the eruption. The role of predators in limiting the peak prey-population size will depend on the size of the energy input. In a full-scale eruption following maximal tree seeding, predators cannot significantly truncate peak prey-population size. Predators should be able to significantly hasten the rate of decline in the prey populations, although the strength of predator limitation will depend on the severity of food limitation and cold-induced mortality over the same period. Predators can limit prey populations during the post-crash low phase. As with the crash phase, the strength of predator limitation in the low phase will depend on the severity of food limitation and natural mortality. The model highlights gaps in current knowledge of predator and prey species biology and ecology, and suggests key areas of further study that have the most potential to increase understanding of the factors driving small-mammal communities in New Zealand.

5.1 Introduction

Small mammal population dynamics are generally divided into three categories, non-cyclic (stable), cyclic, or eruptive (Lidicker 1988; Batzli 1992; Krebs 1996). While some patterns are more common in some areas (for example, cyclic population dynamics in the Holartic, Boutin 1990; Krebs 1996), no one category of population dynamics is confined to any one region or habitat.

Many different hypotheses have been proposed to explain variation in observed small mammal population parameters and dynamics. Batzli (1992) breaks published hypotheses down into 22 different groups, and Krebs (1996) lists five broad classes of hypothesis that have been proposed to explain small mammal population dynamics. They stress the importance of food (Bomford 1987a; Bomford 1987b; Bomford and Redhead 1987; Craig and Bunn 1989), predation (Norrdahl and Korpimaki 1995; Reid *et al.* 1995; Korpimaki and Norrdahl 1998), food and predation (Newsome 1990; Sinclair *et al.* 1990; Pech *et al.* 1992), individual differences (Chitty 1960; Gilwicz 1990; Blackburn *et al.* 1998), and multiple factors (Sinclair 1986; Lidicker 1988). While some workers are currently suggesting a shift away from simple, single-factor explanations to multi-factorial approaches (Lidicker, 1988; Krebs, 1996; May 1999), most studies can only hope to manipulate one or two potentially important variables at a time.

Given a complex system with many extrinsic and intrinsic factors interacting with a given species, the pertinent question becomes at what time, and under what conditions does predation become important, if at all?

In Fennoscandia, populations of voles (*Clethrionomys* spp. and *Microtus* spp.) exhibit strongly cyclic population dynamics in the north, but are non-cyclic (Hanski *et al.* 1991), or weakly so (Hansson and Henttonen 1985), in the south. This pattern has been attributed to higher predation pressure, in a more complex environment, at lower latitudes. High numbers of year-round generalist predators, combined with increased habitat fragmentation at low latitudes, are hypothesized to lead to stable population dynamics. In a simpler environment, as seen in northern Fennoscandia, a smaller

number of specialist predator species (feeding almost exclusively on voles) are thought to deepen and extend the low phase of cyclic vole populations. In a recent test of this hypothesis, Korpimaki and Norrdahl (1998) removed all vertebrate predators from large (2-3.5 km^2) areas in western Finland. They found that the summer decline in cyclic vole populations was averted, thus demonstrating the role of specialist predators in this system.

In eruptive small mammal systems in Australia, Newsome *et al.* (1989) proposed the concept of Environmentally Modulated Predation to explain eruptions of European rabbit (*Oryctolagus cuniculus* Linnaeus.) populations in semi-arid areas. Red foxes (*Vulpes vulpes* Skjoldebrand) and feral cats (*Felis catus* L.) were shown to be able to suppress rabbit populations during drought conditions, but were unable to prevent rabbit population outbreaks following extensive rainfall, and the onset of favorable conditions. Pech *et al.* (1992) suggested that density dependent changes in the predator functional response could regulate low density rabbit populations, but could not prevent the large numerical response in rabbits to drought-breaking conditions, a mechanism that has also been suggested for eruptive house mouse (*Mus musculus* L.) populations preyed upon by foxes in South Australian wheatlands (Sinclair *et al.* 1990).

In New Zealand forests, introduced feral house mice and ship rats (*Rattus rattus* L.) are widespread in native forest ecosystems (Innes 1990; Murphy and Pickard 1990). Ship rats are generally more abundant in broadleaf-podocarp forest than in beech forest (Daniel 1978; Chapter 4), while mice are generally rare in most habitats (Murphy and Pickard 1990). Both ship rats and mice show periodic population eruptions from sustained low densities, following southern beech (*Nothofagus* spp.) mast seeding (Fitzgerald 1978; King 1983b; Fitzgerald *et al.* 1996), a phenomenon that occurs every 4-5 years. Following mast seeding, several species of introduced mammalian predator, especially the stoat (*Mustela erminea* L.) and weasel (*M. nivalis* Erxleben), subsequently increase greatly in number, apparently in response to increased rodent densities (King 1982b; 1983b).

The New Zealand forests present a unique system where ship rats and house mice are the only small mammalian prey species present in the environment. Similarly, their only common mammalian predator is the stoat, with weasels present seasonally in low numbers (King 1990b). This is the only known system with this relatively simple combination of small mammals/mammalian predator, and therefore provides an ideal experimental system for testing, on a large scale, the role of predators in small mammal population dynamics (May 1999).

While the basic biology of these species and the timing and amplitude of the population fluctuations of small mammals have been well studied in New Zealand, no attempt has been made to implicitly clarify the role of predators in the eruptive population dynamics of rodents in the New Zealand system. To date, there has been no concerted effort to reconcile small mammal systems in New Zealand with current ecological theory.

One way to test our understanding of the system is to construct a model of the eruptive population dynamics exhibited by these species. The modelling of a dynamic process involves the abstraction and simplification of a complex natural system, and must strike a fine balance between revealing underlying principles and processes, and over-simplifying or distorting the system to the extent that it no longer reflects the natural processes occurring (Jeffers 1982; Jørgensen 1986). These factors must be borne in mind when constructing or testing any model of a natural system or process.

There are, however, a number of valid reasons for constructing a model of population dynamics. The model construction process implicitly tests our current knowledge of the system, and highlights any deficiencies in our knowledge that may preclude a correct understanding of the processes involved (Jeffers 1982). In doing so, the model can focus attention on the key processes driving or influencing a population or system (Jørgensen 1986). A well-designed model allows the generation of predictions and hypotheses about the system, which can then be tested under field conditions, and in situations where field data are lacking. A model is especially useful in focusing research into areas that are most likely to increase understanding of the system (Costanza and Gottlieb 1998). The model output may also suggest unexpected outcomes of manipulations of the system. This is important in a number of situations

in ecology and conservation biology, where manipulation of pest species can have unpredictable outcomes for endemic or commercial species (Anastácio *et al.* 1999).

In this chapter, I present a quantitative computer model of the role of predators in the eruptive small mammal system in New Zealand forests. Using current knowledge on the biology and ecology of predator and prey species, both from published accounts, and from the current study, a model of the eruptive population dynamics of house mice, ship rats and stoats is constructed. Key parameters in the model are tested, and the output is compared with current predator-prey theory to generate a number of predictions regarding the role of predators in the eruptive system in New Zealand. The construction of the model has two main functions. It places New Zealand small-mammal communities in the context of current ecological theory and generates predictions regarding the role of predators in the New Zealand ecosystem. Additionally, the construction of the model requires a large number of parameters pertaining to the biology and ecology of the predator and prey species. Therefore, it tests current understanding of small-mammal ecology in New Zealand, and serves to highlight deficiencies in current knowledge.

5.2 Methods

5.2.1 Model overview

A three species dynamic model consisting of house mouse, ship rat and stoat populations (termed ERRPTS, Eruptive rodent/predator theoretical simulation) was constructed using the STELLA II modelling package (High Performance Systems, Inc 1990) (Figure 5.1; Appendix 5.1, 5.2, 5.3). The STELLA II programming language uses an iconographic interface to facilitate construction of dynamic system structures (Costanza and Gottlieb 1998).

In order to keep the model as parsimonious and general as possible, a number of assumptions were made in the construction of the model. Each species was separated into juvenile and adult age classes, and the same basic model structure was used for mice and rats, with the insertion of appropriate parameters. It was assumed that immigration and emigration were negligible (or equal), and mortality functions were modified so that no species went extinct in the model over the course of the simulation. Predation by species other than stoats is known to be minimal in most forest habitats in New Zealand (King 1990a, b), and was assumed to be zero in the model. The model was run for 60 months in each simulation.

5.2.2 Parameters and model construction

Parameters for the model were gained from the literature on mice, rats, and stoats in New Zealand where available (Table 5.1), and generalized functions for density dependent reproduction or mortality were used from the literature if no specific information was available. The equations used to construct the model are given in Appendix 5.2, and are presented in standard mathematical notation in the addendum at the end of the thesis.

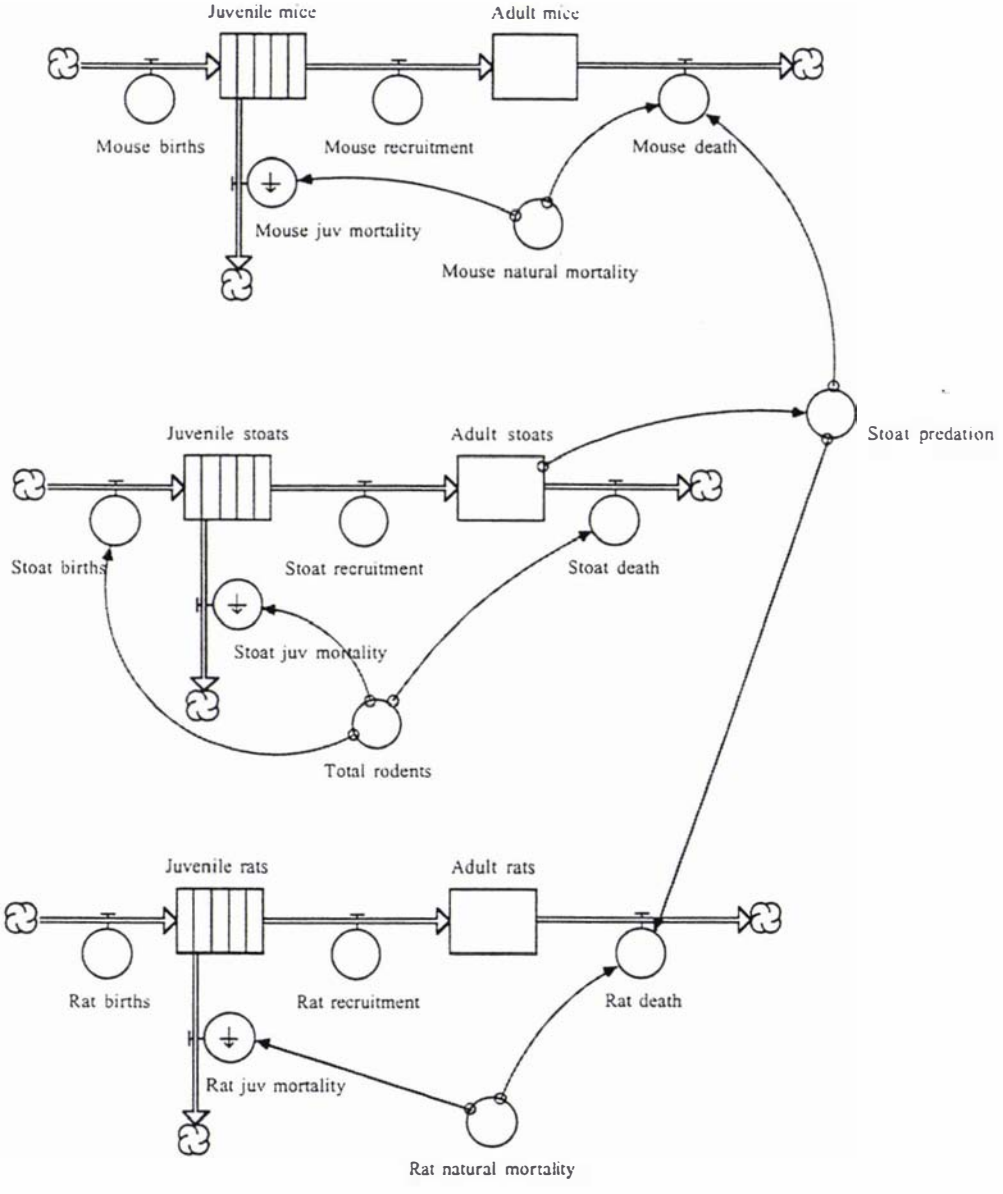

Figure 5.1 Simplified overview of ERRPTS (eruptive rodent/predator theoretical simulation) population dynamics model constructed in the STELLA II computer program. See text for details.

Table 5.1 Key parameters used in the STELLA II ERRPTS model. Sources of values used are listed in the text.

Parameter	Mice	Rats	Stoats
Breeding season			
Non-mast year	September to March	September to March	September/October
Mast year	April-January/March†	April/May-March	September/October
Breeding rate			
Non-mast year	34.2 young/female (2.4 young/mouse/month)	11.1 young/female (0.8 young/rat/month)	2.2 young/female (1.1 young/stoat/year)‡
Mast year	57.2 young/female (2.9 young/mouse/month)	28.1 young/female (1.4 young/rat/month	8.8 young/female (4.4 young/stoat/year)
Predation rate			
Non-mast year	12.1 mice/stoat/month	6.1 rats/stoat/month	
Mast year	47.3 mice/stoat/month§	23.3 mice/stoat/month§	

† Breeding in mice may cease earlier (in January) in a mast year, even though food is still available (Murphy and Pickard 1990). ‡ Stoats only breed once per year, with a single litter of young produced in late September/Early October (King and Moody 1982; King 1983a). Rats were assumed to be twice as profitable as mice for stoats (Day 1968). Predation was assumed to switch onto mice if the number of mice was more than twice that of rats. § See section 5.2.6.

5.2.3 Mouse population

Both mice and rats were divided into juvenile and adult age classes. Mice were classified as juveniles for two months (Murphy and Pickard 1990), after which time they entered the adult population and could breed. Breeding rates varied depending on whether the year was a mast year or non-mast year. In a non-mast year, mice breed between September and March (Fitzgerald 1978), and produce an estimated 34.2 young/female over that period (average litter size 5.72, 6 litters female)[1]. In a mast year, mice start breeding earlier (April-May), stop breeding in January or February (King 1982a), and produce an estimated 57.2 young/female over that period (average litter size 5.72, 10 litters/female)[1]. The breeding rate of mice ranges from 30% of females breeding in low-density populations, to 10% breeding in high-density

[1] Data from Murphy and Pickard (1990)

populations (Fitzgerald 1978; King 1982a), so the proportion of mice breeding in the population was scaled to density.

Natural mortality of mice is high in all years, and is largely controlled by food availability (Fitzgerald 1978; Fitzgerald *et al.* 1981) and environmental conditions (Bronson 1979). The carrying capacity and the resulting level of mortality were set by an arbitrary function that allowed a six-fold variation in density between mast and non-mast years. Mortality ranged from 1.5%/month at low density to 97%/month at the carrying capacity. For simplicity, it was assumed that no predation of juvenile rodents occurred. Adult natural mortality followed a similar function to that for juvenile mortality, but rose to a maximum level of 71.5%/month at the carrying capacity.

5.2.4 Rat population

Rats were classified as juveniles for three months (Innes 1990), at which time they entered the adult breeding population. Rat breeding was structured in the same way as for mice. The non-mast breeding season extended from September to March, with an estimated production of 11.1 young/female in that period (average litter size 5.6, 2 litters/female)[1]. The mast breeding season extended from June to March, with an estimated production of 28.1 young/female (litter size 5.6, 5 litters/female)[1]. The density dependent proportion of rats breeding ranged from 71.6% breeding at low density to 10.8% at high densities. This breeding proportion was required to generate population fluctuations similar to those seen in the field, given the rat breeding rates used in the model. Natural mortality of juvenile and adult rats used the same functions as for mice, but were scaled to allow a four-fold variation in the carrying capacity between mast and non-mast years.

[1] Data from Innes (1990)

5.2.5 Stoat population

In comparison to the two rodent species, stoat breeding is controlled by day-length (King 1990a), so that only one litter is produced in late September-early October (King 1982b; King and Moody 1982; King 1983b). On average, pregnant female stoats produce 8.8 embryos (King 1990a), however both the birth and recruitment rates are highly dependent on food availability, and can range from 0-2.6 young/female in a poor-food year, to 10-13 young/female in a mast year (King 1983b). Similarly, juvenile and adult mortality is closely correlated with food availability, with juvenile mortality of up to 90% recorded in non-mast years (King 1990a). Rodents occurred in 4-53% of stoat stomachs collected in a national survey of stoat diet (King and Moody 1982). Therefore, in the model, stoat fecundity, recruitment and mortality were all related to rodent (as a proxy for total food) availability, and were controlled through rodent:stoat ratios (Appendix 5.2).

5.2.6 Predation rates

In Britain, stoats are known to eat c. 23% of their body weight per day for males, and c. 14% per day for females (Day 1968), although consumption rates in New Zealand are unknown. The average size of stoats in New Zealand is 324.4 g for males, and 207.2 g for females (King 1990a). Daily food requirements equate to 75 g/food/day for male stoats, and 30 g/food/day for female stoats. Rats make up c. 30% of the diet of stoats in the study area, and mice c. 24% of the diet (King and Moody 1982). Therefore, male stoats eat approximately 22.5 g rat/day, and female stoats eat approximately 9 g rat/day. Given an average meal size for stoats of 20 g per rat and 10 g per mouse (Day 1968), this gives an average consumption rate of 1.13 rats/stoat/day for males, and 0.45 rats/stoat/day for females, giving an overall average of 0.79 rats/stoat/day, or 23.63 rats/stoat/month. The same calculation for mice, assuming an average meal size of 10 g, gives a consumption of 47.26 mice/stoat/month.

5.2.7 Prey switching

Mustelids are known to show functional shifts in feeding as preferred foods change in abundance (Tapper 1979; Hanski *et al.* 1991; Murphy and Bradfield 1992). Therefore, stoat predation was set to switch between low and high rodent consumption rates over a threshold range of 350-450 rodents per stoat, which allowed maximal predation during a mast year. It was assumed that rats are twice as profitable as mice, and that mouse numbers greatly exceed rat numbers during an eruption, so stoat predation switched entirely onto mice when the ratio of mice to rats was greater than 2:1. Early simulation runs of the program showed that this level of predation on rats would cause the extinction of the rat population. Under field conditions, rats do not become extinct over large areas, due to immigration and prey switching by predators, so a minimum number of 100 rats (1/ha) was set, below which no stoat induced rat-mortality occurred.

Variation in mast and non-mast year breeding rates of rodents (mean ± SD from published studies) was incorporated into the model to add a measure of stochasticity into the model, but the model still remained primarily deterministic.

5.3 Results

5.3.1 Calibration of the model

Data on population dynamics in pure beech forest in the South Island, New Zealand, were used to calibrate the model (King 1983b; King and Moller 1997).

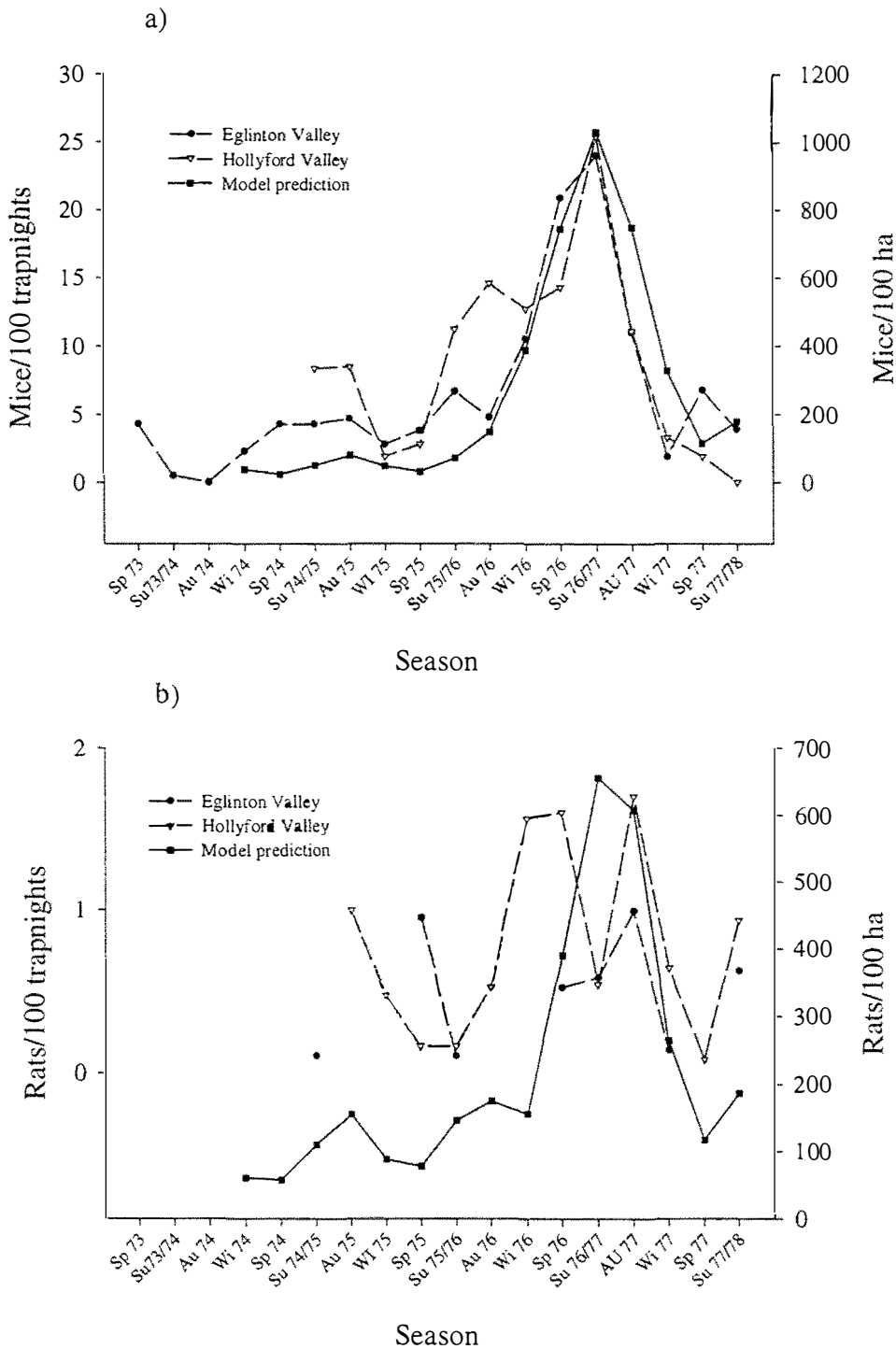

Figure 5.2 Calibration of model output with field data for a) mice, and b) rats from the Eglinton and Hollyford Valleys. Data for mice are from King (1983b) and for rats from King and Moller (1997).

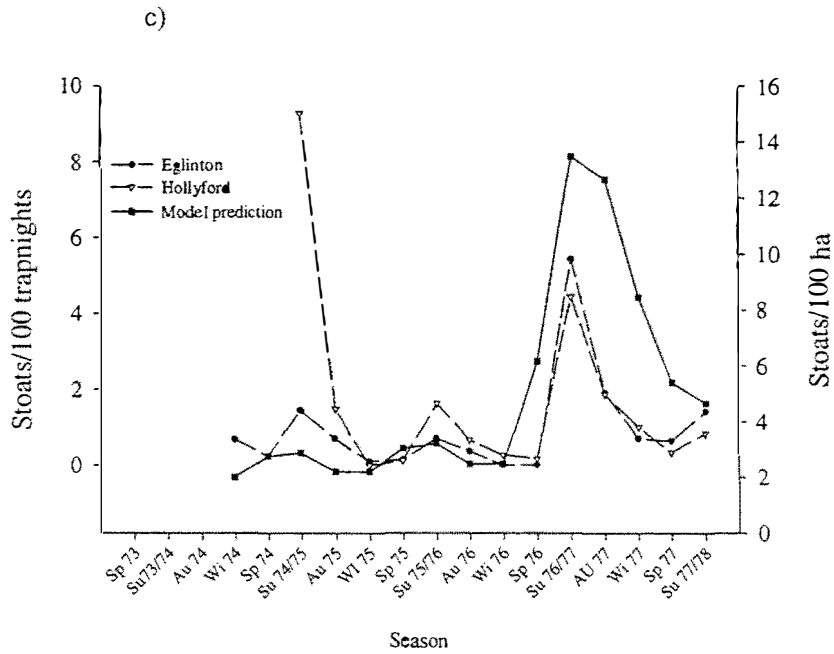

Figure 5.2 cont'd c) Comparison between simulated stoat population dynamics and field data for stoats from the Eglinton and Hollyford Valleys. Data are from King (1983b).

The population trends for mice, ship rats and stoats predicted by the model were compared to population trends from the field data sets for each species. The model correctly predicted the timing and amplitude of the species' responses to a beech masting, especially for mice (Figure 5.2a) and stoats (Figure 5.2c). The correlation for rats was not as tight (Figure 5.2b), with more variation in the field data than predicted by the model.

The amplitude of fluctuation in peak density between mast and non-mast years from the field data was approximately 6-fold for mice (c.f. 8-fold from the model); 10-fold for rats (c.f. 4-fold from the model); and 8-fold for stoats (c.f. 7-fold from the model).

5.3.2 Sensitivity analysis

The dynamic nature of the model and the program structure makes multiple tests of parameter sensitivity laborious and time-consuming. Therefore, key parameters (or key parameter pairs in the case of rodent breeding rates in mast and non-mast years) were varied by ± 10% and ± 50% to examine their effects on model performance (Jørgensen 1986).

Mouse and rat populations were more sensitive to changes in breeding rates than to changes in predation intensity (Table 5.2). Both rodent species were more sensitive to a decrease in breeding effort than an increase, and rats were much less sensitive to large changes in predation by stoats than mice, as a result of the 2:1 ratio of mouse:rat predation used in the model. An increase of 50% in the predation rate was enough to largely prevent a mouse eruption, while the same increase in predation on rats barely suppressed rat numbers. Both rats and mice were insensitive to changes in the timing of stoat breeding, and would erupt irrespective of the time at which adult stoats appeared in the system.

Table 5.2 Results of sensitivity analysis of the influence of key reproductive and predation parameters on peak eruption density in the ERRPTS population dynamics model. The range in peak densities for each set of manipulations is shown. The model was run 10 times with each set of parameter values.

		Mice			Rats		
Parameter		Density	SE	Range	Density	SE	Range
Breeding	+10%	1239.47	14.02	278.90	883.26	5.22	215.67
	-10%	960.57	9.93		667.59	7.76	
	+50%	1751.12	8.00	1677.56	1026.16	5.38	720.55
	-50%	73.56	5.27		305.61	5.36	
Predation	+10%	1047.67	16.02	84.89	766.52	5.71	44.15
	-10%	1132.56	12.60		810.67	3.84	
	+50%	583.40	16.55	1256.55	708.53	5.64	141.47
	-50%	1264.67	8.12		850.00	4.07	
Non-treatment		1020.00	0.00		790.02	7.32	

The model generated sequential increases and declines in mouse, ship rat and stoat populations known to occur during a masting event (Figure 5.3). Stoats did not increase in numbers until rodent numbers had almost peaked, and their decline followed the severe population crashes exhibited by mice and rats. The driving of stoat dynamics by rodent density affects the predator:prey ratios throughout the eruption (Figure 5.4), so that the ratio is highest in the non-mast years.

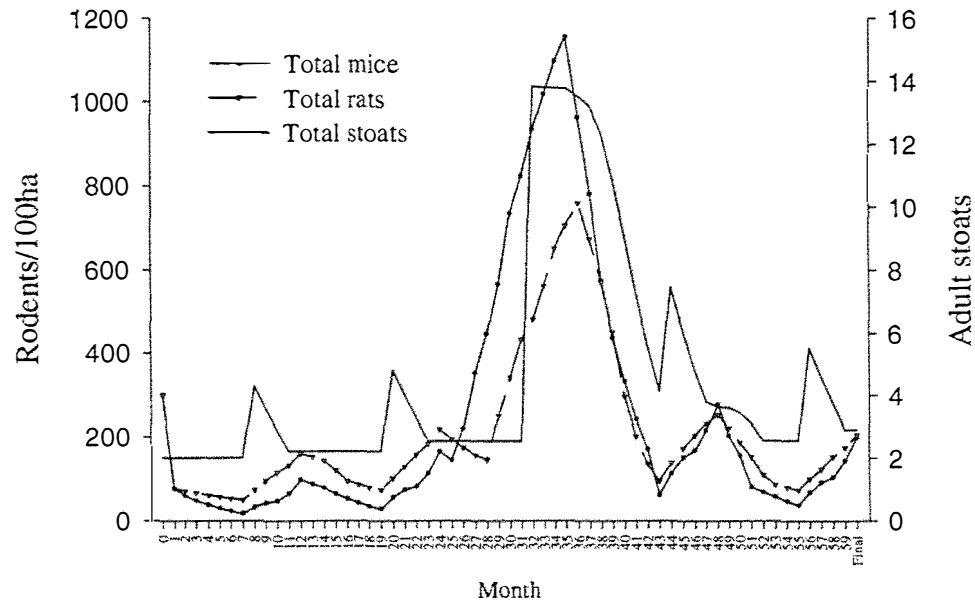

Figure 5.3 Population trends of house mice, ship rats and stoats generated in the ERRPTS dynamic model. The third year of the model was designated as a beech-mast year, and the population dynamics of the three species were simulated following a large energy input.

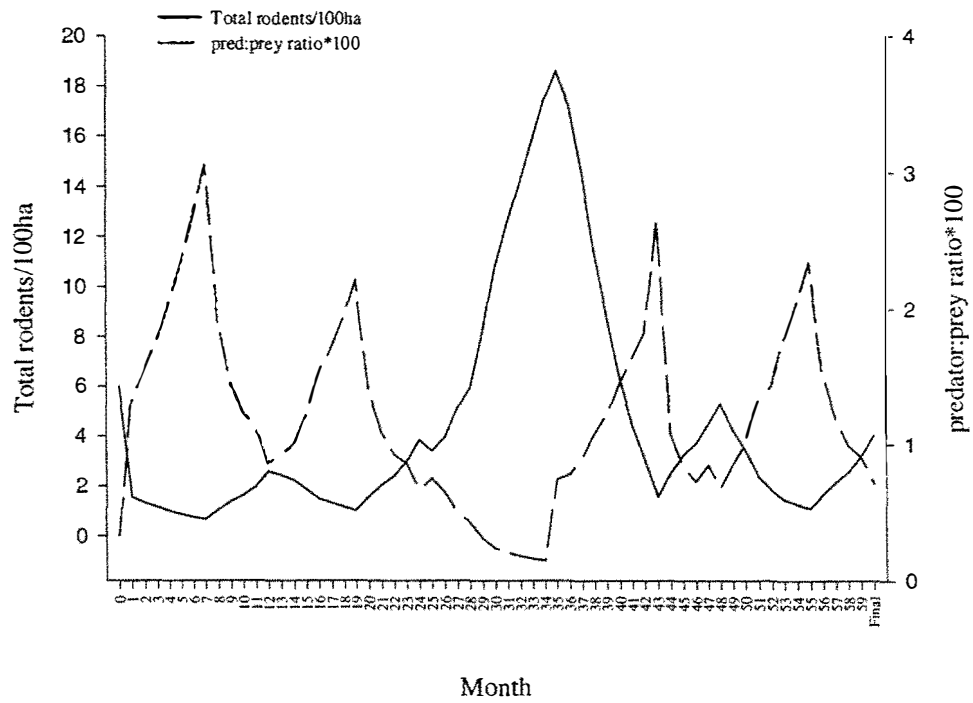

Figure 5.4 Trends in predator:prey ratios throughout the eruptive cycle, plotted against the total number of rodents present.

5.3.3 The effect of predation on rodent populations

The effect of stoat removal on mouse and rat populations was investigated by scaling the output from the rodents-eaten function (Appendix 5.1) in the model from 0 (no stoats present) to 1 (100% stoats present).

As predator:prey ratios peak and then drop following the crash (Figure 5.4), predator limitation is reduced, so that populations with and without predator present show little difference. The model predicts that stoats should have a large effect on mouse populations, and may limit their numbers throughout most of the eruptive cycle (Figure 5.5a). Stoat predation can delay and truncate the eruption of mice following a beech masting, and can potentially hasten the decline. The rate at which the carrying capacity drops, and the amount of natural mortality (Figure 5.5b) control the severity

of predator limitation in the crash and low phase. With a more gradual decline in the carrying capacity following an eruption, predator limitation becomes more important.

The response of rats to stoat reduction is similar to that of mice, but less pronounced (Figure 5.6a). Predators can limit rat populations in the low phase, and delay the increase during an eruption, but limitation at the peak is much less pronounced than that seen in the mouse population. Stoat predation can theoretically cause rat populations to crash more quickly and deeply than food limitation alone would produce (Figure 5.6b). As with the mouse population crash, the importance of predator limitation in the crash phase will depend on the severity of natural mortality over the same period.

The ability of predators to prevent an outbreak was tested by shifting stoat breeding forward, so that adult stoats were present as the rodents started to increase. Neither mouse nor rat population dynamics differed with predator breeding advanced. Both mouse and rat populations erupted to similar levels with stoat breeding advanced, suggesting it is not the lag in stoat breeding that is the primary reason for the inability of stoats to prevent or truncate a rodent eruption.

The effect of the amount of food supplied to the system was examined by varying the reproductive effort during the population eruption, as a proxy measure of energy input. The breeding rate in the mast period was varied from the non-mast level (0.794 young/rat/month; 2.44 young/mouse/month), to the maximum level used in the model (1.41 young/rat/month; 2.86 young/mouse/month; Figure 5.7a, b). Stoat predation had a proportionally greater effect on prey dynamics at low breeding rates, than at maximum rates of rodent breeding. However, even at normal (non-mast) breeding rates in a mast year (longer, earlier breeding season), predation could not prevent prey populations increasing to significantly higher levels than in non-mast years (Figure 5.7).

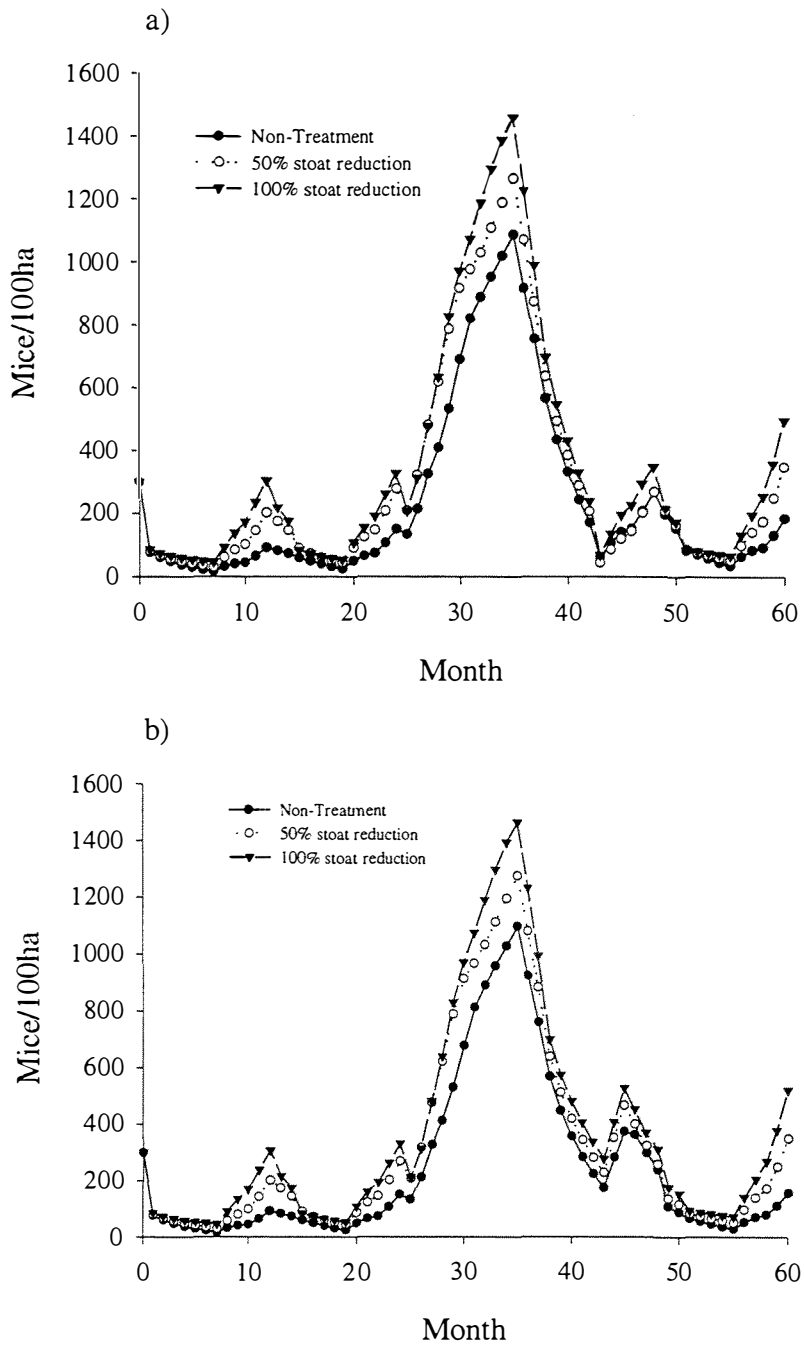

Figure 5.5 Population dynamics of mouse populations generated by the ERRPTS population model. Population dynamics were simulated with no predator reduction, 50%, and 100% stoat reduction with a) severe natural mortality, and b) less severe mortality. See text for details.

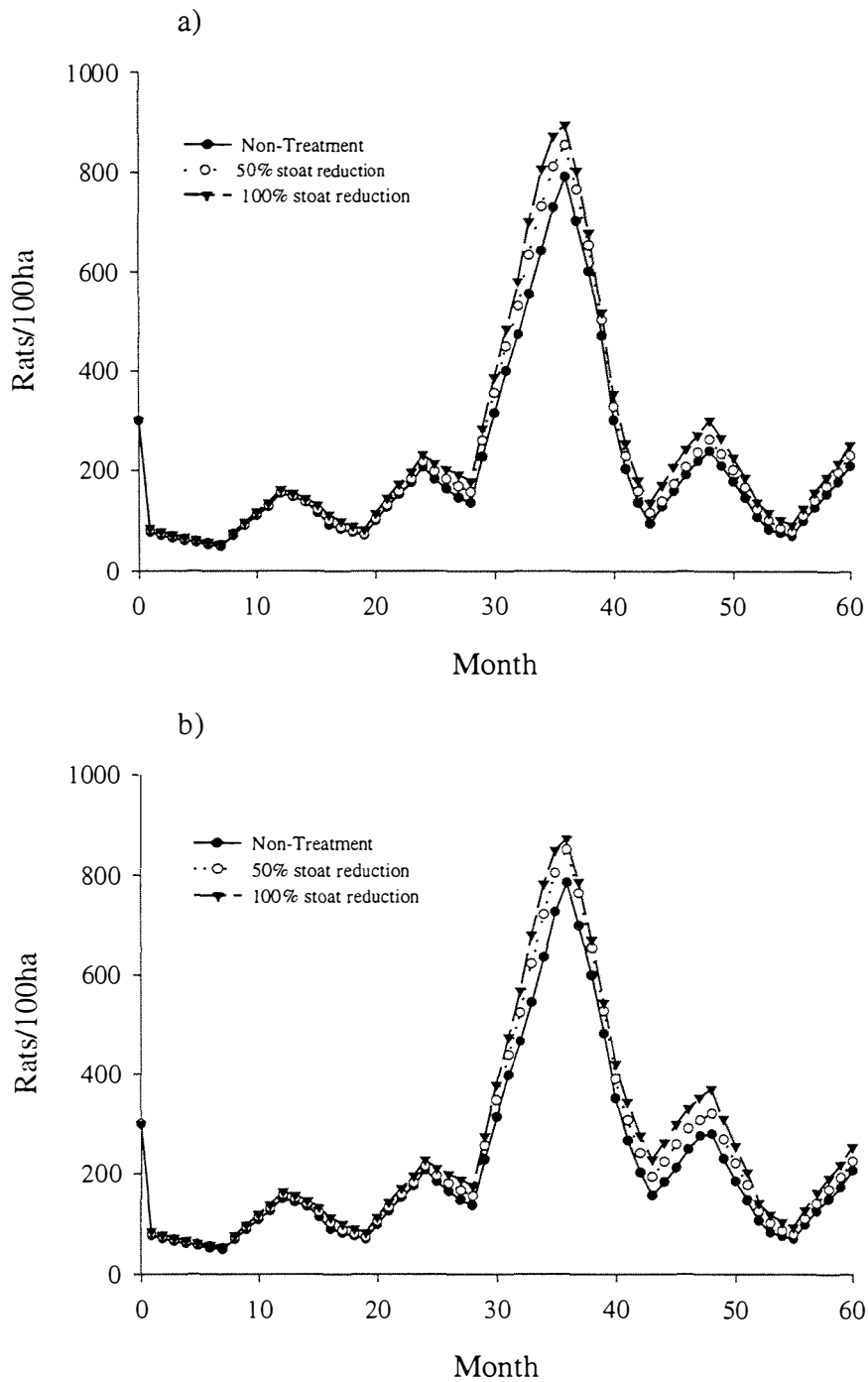

Figure 5.6 Population dynamics of ship rat populations generated by the ERRPTS population model. Population dynamics were simulated with no predator reduction, 50%, and 100% stoat reduction with a) severe natural mortality, and b) less severe mortality. See text for details.

5.4 Discussion

The ERRPTS dynamic model of mouse, ship rat and stoat population dynamics generated similar population behaviour during a simulated eruption as seen in field studies (King 1983b; Innes 1990; Fitzgerald *et al.* 1996; King and Moller 1997). The amplitude of the rat eruption in the model was smaller than that seen in the calibration field data (King and Moller 1997), although it was similar to the range in rat densities seen in the current study. While the timing and amplitude of food-driven eruption events in field situations may vary between locations, and temporally within a location, the model serves as a useful generalization of the processes occurring. It provides a framework for investigating the relative importance of food and predation in driving the observed population dynamics.

The model highlights the primary importance of food in driving the eruptive system. Mouse numbers have been shown to be significantly correlated with the size of the beech seedfall in mixed beech/podocarp forest in the Orongorongo valley in the North Island, New Zealand (Fitzgerald *et al* 1996), and in pure beech forest in the South Island (King 1983b). Similarly, rat numbers significantly increased following the beech masting in the same South Island study (King and Moller 1997), and are known to increase following heavy winter fruiting in North Island forests (Daniel 1978).

The time lags in the predator response to the rodent eruption appear to be a relatively minor component in the predator's inability to prevent a population eruption. Instead, the extended, multiple breeding in rodents (Daniel 1972; Innes 1979; King 1982a; Innes 1990; Murphy and Pickard 1990; Berry and Bronson 1992), compared to a single breeding effort by stoats (King and Moody 1982; King 1990a), appears to be the main reason why predators cannot prevent a prey outbreak.

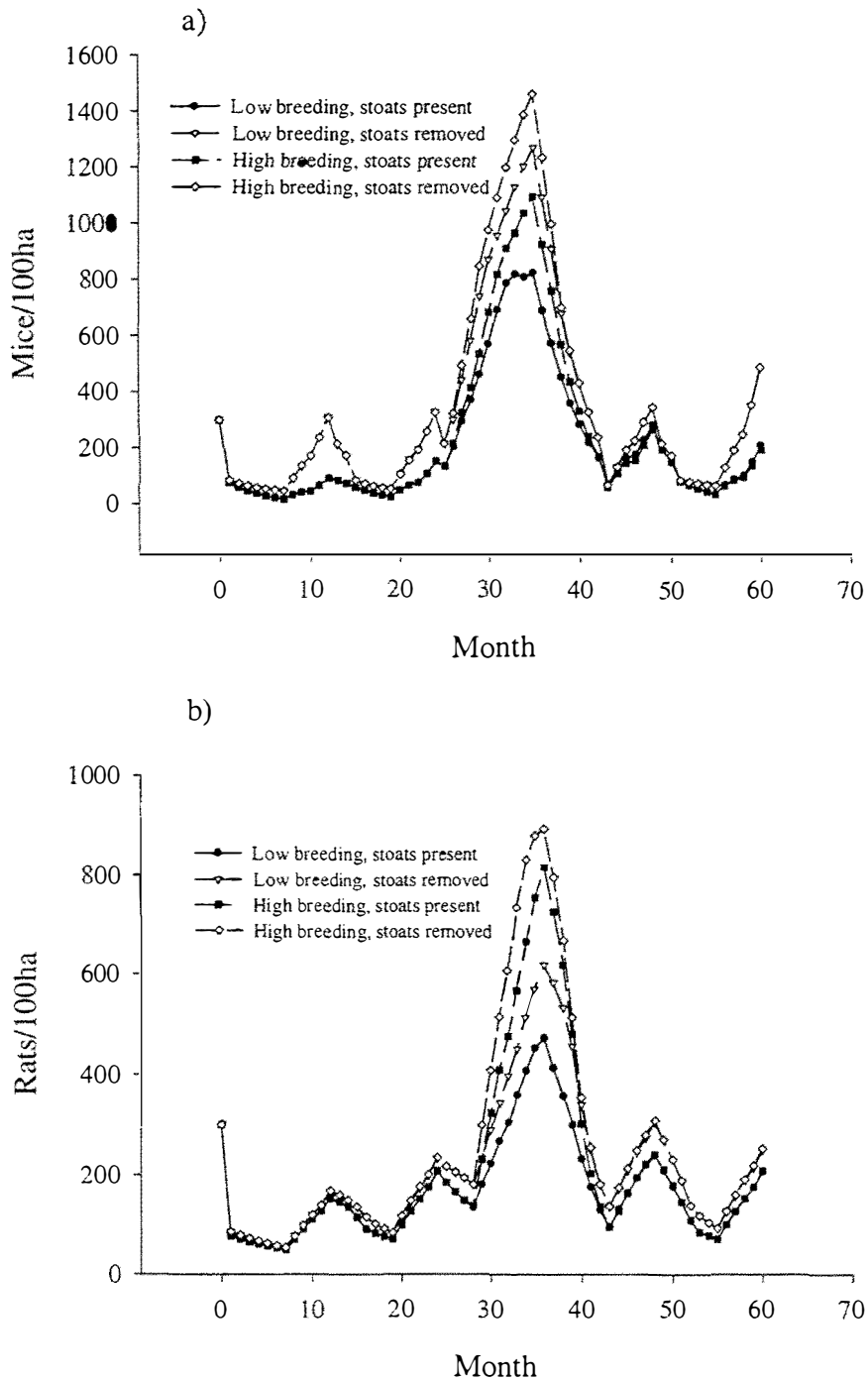

Figure 5.7 The effect of varying the mast-year breeding rate on population dynamics of a) mouse, and b) ship rat populations with predators present or removed. For mice, the low breeding rate was 2.44 young/mouse/month and the high level at 2.86 young/mouse/month. For rats the low and high breeding rates were 0.79 young/rat/month and 1.41 young/rat/month respectively.

It has been suggested that functional shifts in predation rates by year round generalist predators may keep low-density prey populations in a predator-pit from which they cannot escape (Sinclair *et al.* 1990; Pech *et al.* 1992). Such a mechanism has also been proposed to explain the lack of cyclicity in some microtine rodent populations in Fennoscandia (Hanski *et al.* 1991). In New Zealand forest systems, stoats are present in low numbers in non-mast years as the only common predator (King 1990a). This low density, coupled with a relatively slow numerical response due to a single annual litter (King and Moody 1982), may mean that stoats can only keep rodents in a "semi predator-pit". In a partial mast year where not all trees set seed (King 1982a; Fitzgerald *et al* 1996), the stoat total response may have a greater limiting effect on the rodent populations, but still cannot prevent a significant increase in prey numbers.

In the predator-pit model proposed by Sinclair *et al.* (1990) and Pech *et al.* (1992) for eruptive systems in Australia, generalist predators (red foxes, *Vulpes vulpes*, and feral cats, *Felis catus*) were present in moderate numbers year round, and their numbers were buffered by the presence of alternative prey. In their model, there was a threshold density below which predators could regulate prey populations through shifts in the predator functional response, but above which predation was non-regulating, or inversely density dependent (Sinclair *et al.* 1990). In comparison, predators (stoats) in the New Zealand system may have little capacity to prevent an eruption; so that, while they can exhibit some population limitation, there may be no threshold density below which they can regulate prey density.

The timing of the stoat population increase in the model suggests that predation will be most important during the crash and low phases following the eruption. A number of field studies of cyclic populations of small mammals have shown that predation is important during the crash and low phases of the cycle (Erlinge *et al.* 1988; Korpimaki *et al.* 1991; Reid *et al.* 1995), and that the removal of predators may stop the cyclical decline (Korpimaki and Norrdahl 1998).

In the model, predator:prey ratios were highest late in the crash phase, and stoats were eating the maximum number of rodents per stoat, so that the total predation pressure was greatest at this time. However, the model highlighted the primary importance of natural mortality over the crash phase. Stoat induced mortality will become relatively

more important with a more gradual drop in the carrying capacity, and with less food or cold induced mortality. Both mice and rats have high-energy requirements characteristic of small mammals, and are susceptible to cold stress (Innes 1990; Berry and Bronson 1992). As a result, post-mast mortality is high irrespective of predator induced mortality. Therefore, whether the response of rodents to predator removal during the crash phase is detectable under field conditions remains to be seen.

The model also predicts that predators should be able to limit prey populations in the post-crash low phase, through high predator:prey ratios, and such a response has been shown in field experiments with microtine communities in Fennoscandia (Korpimaki and Norrdahl 1998), and for eruptive rabbit/red fox associations in Australia (Newsome *et al.* 1989). Once again, the strength of predator limitation in the low phase in the New Zealand forest system will be modified by the relative strength of other limiting factors acting upon rodents at the same time. As predator numbers drop in the period following the eruption, predator limitation should also decline, so that the system becomes reset for the next eruption.

5.4.1 Future work and model development

While the model generated population dynamics and behaviours similar to those seen in field situations, a number of parameters were "best-guess" estimates, or generalized functions. Clearly a better understanding of the processes occurring in these systems, and the construction of a more robust model, requires the investigation of a number of parameters.

Information is required on the breeding biology of rodents in New Zealand, including the effects of density on reproductive behaviour and fecundity, and the breeding rates of young-of-the-year animals. More information is required on the energy requirements of stoats, and the functional responses of stoats to changes in rodent density and relative species abundance. It is not known to what extent prey switching between rodents occurs in stoats, and consequentially how accurate calculated prey consumption rates are.

The model made no estimates of spatial effects within the system, but rather used average densities in an arbitrary area. Stoats are known to be highly mobile during dispersal (King 1982b), but the effect this movement has on predation rates is unclear. Similarly, mice and rats are known to be largely solitary in low-density populations (Daniel 1972; Fitzgerald *et al.* 1981; Hooker and Innes 1995), but the social structure of high-density populations is unknown.

Therefore, while the model is a useful starting point as it stands, and generates testable predictions, the investigation of the points discussed will greatly enhance both the model, and our understanding of New Zealand forest systems, and predator/prey interactions in general.

5.5 Summary of model outputs

A generalized model of the population dynamics of house mice, ship rats, and stoats in an eruptive system was constructed. The model tested the relative importance of food and predator limitation of rodent populations in New Zealand forests, and generated a number of outputs and predictions that could be tested under field conditions.

1. Predators can exhibit minor limitation over prey populations prior to an eruption.

2. Predators cannot prevent a rodent eruption, but may delay the increase in prey populations in response to food.

3. The inability of predators to stop a rodent eruption is due to the vastly different rates of increase between predators and prey, and the lack of alternative prey to buffer stoat numbers, rather than the time-lags in predator breeding.

4. Predators will have relatively more influence on peak prey population density in partial mast conditions. With a full mast eruption, predators should not be able to significantly limit prey population size.

5. Predators have the potential to significantly hasten the rate of decline in crashing rodent populations. The strength of predator limitation will depend on the severity of the crash in the carrying capacity.

6. Predators can limit prey populations in the post-crash low phase. The strength of the low-phase predator limitation will depend on the extent of the natural mortality during the crash phase, and on the predator:prey ratios over the crash and low-phases. Predator limitation should decline over the low phase as predator:prey ratios drop.

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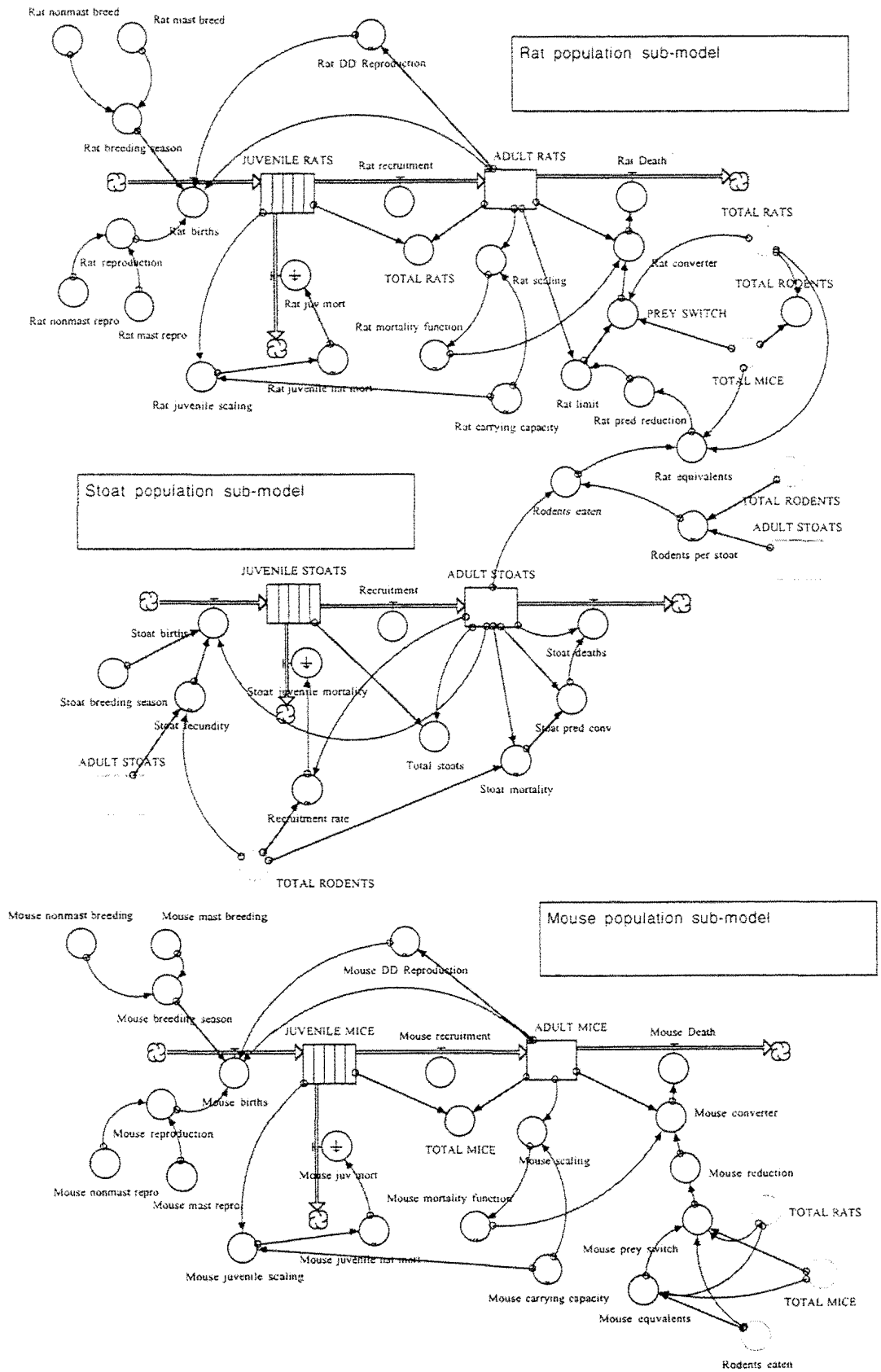
Appendix 5.1 ERRPTS population model developed in STELLA II.



Appendix 5.2 Model logic and parameters used in construction of ERRPTS population model. Sources of parameters are listed in the text.

ADULT_MICE(t) = ADULT_MICE(t - dt) + (Mouse_recruitment - Mouse_Death) * dt

INITIAL ADULT_MICE = 300

INFLOWS:

Mouse_recruitment = CONVEYOR OUTFLOW

OUTFLOWS:

Mouse_Death = Mouse_converter

ADULT_RATS(t) = ADULT_RATS(t - dt) + (Rat_recruitment - Rat_Death) * dt

INITIAL ADULT_RATS = 300

INFLOWS:

Rat_recruitment = CONVEYOR OUTFLOW

OUTFLOWS:

Rat_Death = Rat_converter

ADULT_STOATS(t) = ADULT_STOATS(t - dt) + (Recruitment - Stoat_deaths) * dt

INITIAL ADULT_STOATS = 2

INFLOWS:

Recruitment = CONVEYOR OUTFLOW

OUTFLOWS:

Stoat_deaths = ADULT_STOATS*Stoat_pred_conv

Appendix 5.2 cont'd

JUVENILE_MICE(t) = JUVENILE_MICE(t - dt) + (Mouse_births - Mouse_recruitment - Mouse_juv_mort) * dt

INITIAL JUVENILE_MICE = 0

TRANSIT TIME = 2

INFLOW LIMIT = ∞

CAPACITY = ∞

INFLOWS:

Mouse_births = Mouse_breeding_season*(ADULT_MICE*Mouse_reproduction)*Mouse_DD_Reproduction

OUTFLOWS:

Mouse_recruitment = CONVEYOR OUTFLOW

Mouse_juv_mort = LEAKAGE OUTFLOW

LEAKAGE FRACTION = Mouse_juvenile_nat_mort

NO-LEAK ZONE = 1.33

JUVENILE_RATS(t) = JUVENILE_RATS(t - dt) + (Rat_births - Rat_recruitment - Rat_juv_mort) * dt

INITIAL JUVENILE_RATS = 0

TRANSIT TIME = 3

INFLOW LIMIT = ∞

CAPACITY = ∞

INFLOWS:

Rat_births = Rat_breeding_season*(ADULT_RATS*Rat_reproduction)*Rat_DD_Reproduction

Appendix 5.2 cont'd

OUTFLOWS:

Rat_recruitment = CONVEYOR OUTFLOW

Rat_juv_mort = LEAKAGE OUTFLOW

LEAKAGE FRACTION = Rat_juvenile_nat_mort

NO-LEAK ZONE = 2.0

JUVENILE_STOATS(t) = JUVENILE_STOATS(t - dt) + (Stoat_births - Recruitment - Stoat_juvenile_mortality) * dt

INITIAL JUVENILE_STOATS = 0

TRANSIT TIME = 3

INFLOW LIMIT = ∞

CAPACITY = ∞

INFLOWS:

Stoat_births = Stoat_breeding_season*(Stoat_fecundity*ADULT_STOATS)

OUTFLOWS:

Recruitment = CONVEYOR OUTFLOW

Stoat_juvenile_mortality = LEAKAGE OUTFLOW

LEAKAGE FRACTION = Recruitment_rate

NO-LEAK ZONE = 0

Mouse_breeding_season = IF 24 < TIME AND TIME < 37 THEN Mouse_mast_breeding ELSE Mouse_nonmast_breeding

Mouse_converter = (ADULT_MICE*Mouse_mortality_function)+Mouse_reduction

Appendix 5.2 cont'd

Mouse_equivalents =

(2*TOTAL_MICE*Rodents_eaten)/(2*TOTAL_RATS+TOTAL_MICE)

Mouse_juvenile_scaling = JUVENILE_MICE/Mouse_carrying_capacity

Mouse_mast_breeding = IF 0 < ((TIME/12) - INT (TIME/12)) and ((TIME/12) - INT(TIME/12)) < 0.84 THEN 1 ELSE 0

Mouse_mast_repro = NORMAL(2.86,0.21)

Mouse_nonmast_breeding = IF 0.5 < ((TIME/12) - INT(TIME/12)) and ((TIME/12) - INT(TIME/12)) < 1 THEN 1 ELSE 0

Mouse_nonmast_repro = NORMAL(2.44,0.18)

Mouse_prey_switch = IF TOTAL_MICE >2*TOTAL_RATS THEN 2*Rodents_eaten ELSE Mouse_equivalents

Mouse_reduction = Mouse_prey_switch*1

Mouse_reproduction = IF 24 < TIME AND TIME < 37 THEN Mouse_mast_repro ELSE Mouse_nonmast_repro

Mouse_scaling = ADULT_MICE/Mouse_carrying_capacity

PREY_SWITCH = IF TOTAL_MICE > 2*TOTAL_RATS THEN 0 ELSE Rat_limit

Rat_breeding_season = IF 24 < TIME AND TIME < 37 THEN Rat_mast_breed ELSE Rat_nonmast_breed

Rat_converter = (ADULT_RATS*Rat_mortality_function)+PREY_SWITCH

Rat_equivalents =
(2*TOTAL_RATS*Rodents_eaten)/(TOTAL_MICE+2*TOTAL_RATS)

Rat_juvenile_scaling = JUVENILE_RATS/Rat_carrying_capacity

Rat_limit = IF ADULT_RATS < 100 THEN 0 ELSE Rat_pred_reduction

Rat_mast_breed = IF 0.25 < ((TIME/12) - INT (TIME/12)) and ((TIME/12) - INT(TIME/12)) < 1 THEN 1 ELSE 0

Appendix 5.2 cont'd

Rat_nonmast_breed = IF 0.5 < ((TIME/12) - INT(TIME/12)) and ((TIME/12) - INT(TIME/12)) < 1 THEN 1 ELSE 0

Rat_nonmast_repro = NORMAL(0.794,0.07)

Rat_pred_reduction = Rat_equivalents*1

Rat_reproduction = IF 24 < TIME AND TIME < 37 THEN Rat_mast_repro ELSE Rat_nonmast_repro

Rat_scaling = ADULT_RATS/Rat_carrying_capacity

Rodents_eaten = ADULT_STOATS*Rodents_per_stoat

Stoat_breeding_season = PULSE(1,7,12)

Stoat_pred_conv = IF ADULT_STOATS < 3 THEN 0 ELSE Stoat_mortality

TOTAL_MICE = ADULT_MICE+JUVENILE_MICE

TOTAL_RATS = ADULT_RATS+JUVENILE_RATS

Total_rodents = TOTAL_MICE+TOTAL_RATS

Total_stoats = ADULT_STOATS+JUVENILE_STOATS

DD_stoat_mort = GRAPH(ADULT_STOATS)

(0.00, 0.105), (5.00, 0.105), (10.0, 0.105), (15.0, 0.115), (20.0, 0.125), (25.0, 0.145), (30.0, 0.18), (35.0, 0.24), (40.0, 0.33), (45.0, 0.495), (50.0, 0.8)

Appendix 5.2 cont'd

Mouse_carrying_capacity = GRAPH(TIME)

(0.00, 1.00), (1.00, 1.00), (2.00, 1.00), (3.00, 1.00), (4.00, 1.00), (5.00, 1.00), (6.00, 1.00), (7.00, 1.00), (8.00, 1.00), (9.00, 1.00), (10.0, 1.00), (11.0, 1.00), (12.0, 1.00), (13.0, 1.00), (14.0, 1.00), (15.0, 1.00), (16.0, 1.00), (17.0, 1.00), (18.0, 1.00), (19.0, 1.00), (20.0, 1.00), (21.0, 1.00), (22.0, 1.00), (23.0, 1.00), (24.0, 1.00), (25.0, 3.34), (26.0, 5.42), (27.0, 6.92), (28.0, 8.00), (29.0, 8.00), (30.0, 8.00), (31.0, 8.00), (32.0, 8.00), (33.0, 8.00), (34.0, 8.00), (35.0, 8.00), (36.0, 8.00), (37.0, 7.43), (38.0, 6.23), (39.0, 4.97), (40.0, 3.65), (41.0, 2.57), (42.0, 1.00), (43.0, 1.00), (44.0, 1.00), (45.0, 1.00), (46.0, 1.00), (47.0, 1.00), (48.0, 1.00), (49.0, 1.00), (50.0, 1.00), (51.0, 8.00), (52.0, 8.00), (53.0, 8.00), (54.0, 8.00), (55.0, 8.00), (56.0, 8.00), (57.0, 8.00), (58.0, 8.00), (59.0, 8.00)

Mouse_DD_Reproduction = GRAPH(ADULT_MICE)

(0.00, 0.508), (50.0, 0.444), (100, 0.4), (150, 0.356), (200, 0.316), (250, 0.28), (300, 0.248), (350, 0.212), (400, 0.176), (450, 0.14), (500, 0.108)

Mouse_juvenile_nat_mort = GRAPH(Mouse_juvenile_scaling)

(0.00, 0.00), (20.0, 0.00), (40.0, 0.015), (60.0, 0.035), (80.0, 0.075), (100, 0.145), (120, 0.215), (140, 0.31), (160, 0.44), (180, 0.635), (200, 0.975)

Mouse_mortality_function = GRAPH(Mouse_scaling)

(0.00, 0.06), (20.0, 0.065), (40.0, 0.07), (60.0, 0.085), (80.0, 0.125), (100, 0.175), (120, 0.245), (140, 0.32), (160, 0.425), (180, 0.545), (200, 0.715)

Appendix 5.2 cont'd

Rat_carrying_capacity = GRAPH(TIME)

(0.00, 1.00), (1.00, 1.00), (2.00, 1.00), (3.00, 1.00), (4.00, 1.00), (5.00, 1.00), (6.00, 1.00), (7.00, 1.00), (8.00, 1.00), (9.00, 1.00), (10.0, 1.00), (11.0, 1.00), (12.0, 1.00), (13.0, 1.00), (14.0, 1.00), (15.0, 1.00), (16.0, 1.00), (17.0, 1.00), (18.0, 1.00), (19.0, 1.00), (20.0, 1.00), (21.0, 1.00), (22.0, 1.00), (23.0, 1.00), (24.0, 1.00), (25.0, 1.68),(26.0, 2.71), (27.0, 3.46), (28.0, 4.00), (29.0, 4.00), (30.0, 4.00), (31.0, 4.00), (32.0, 4.00), (33.0, 4.00), (34.0, 4.00), (35.0, 4.00), (36.0, 4.00), (37.0, 3.71), (38.0, 3.12), (39.0, 2.48), (40.0, 1.82), (41.0, 1.28), (42.0, 1.00), (43.0, 1.00), (44.0, 1.00), (45.0, 1.00), (46.0, 1.00), (47.0, 1.00), (48.0, 1.00), (49.0, 1.00), (50.0, 1.00), (51.0, 1.00), (52.0, 1.00), (53.0, 1.00), (54.0, 1.00), (55.0, 1.00), (56.0, 1.00), (57.0, 1.00), (58.0, 1.00), (59.0, 1.00)

Rat_DD_Reproduction = GRAPH(ADULT_RATS)

(0.00, 0.716), (50.0, 0.636), (100, 0.572), (150, 0.508), (200, 0.444), (250, 0.388), (300, 0.332), (350, 0.272), (400, 0.208), (450, 0.152), (500, 0.108)

Rat_juvenile_nat_mort = GRAPH(Rat_juvenile_scaling)

(0.00, 0.00), (35.0, 0.00), (70.0, 0.015), (105, 0.035), (140, 0.075), (175, 0.145), (210, 0.215), (245, 0.31), (280, 0.44), (315, 0.635), (350, 0.975)

Rat_mortality_function = GRAPH(Rat_scaling)

(0.00, 0.06), (30.0, 0.065), (60.0, 0.07), (90.0, 0.085), (120, 0.125), (150, 0.175), (180, 0.245), (210, 0.32), (240, 0.425), (270, 0.545), (300, 0.715)

Recruitment_rate = GRAPH(Total_rodents/ADULT_STOATS)

(50.0, 0.925), (65.0, 0.915), (80.0, 0.89), (95.0, 0.87), (110, 0.84), (125, 0.805), (140, 0.575), (155, 0.185), (170, 0.075), (185, 0.025), (200, 0.005)

Rodents_per_stoat = GRAPH(Total_rodents/ADULT_STOATS)

(40.0, 5.72), (86.0, 5.72), (132, 5.72), (178, 5.72), (224, 5.72), (270, 6.00), (316, 8.28), (362, 13.6), (408, 19.3), (454, 22.1), (500, 23.6)

Appendix 5.2 cont'd

Stoat_fecundity = GRAPH(Total_rodents/ADULT_STOATS)

(0.00, 1.12), (20.0, 1.12), (40.0, 1.15), (60.0, 1.20), (80.0, 1.28), (100, 1.65), (120, 2.68), (140, 3.83), (160, 4.42), (180, 4.45), (200, 4.45)

Stoat_mortality = GRAPH(Total_rodents/ADULT_STOATS)

(20.0, 0.51), (33.0, 0.375), (46.0, 0.3), (59.0, 0.24), (72.0, 0.19), (85.0, 0.15), (98.0, 0.1), (111, 0.06), (124, 0.03), (137, 0.015), (150, 0.005)

Appendix 5.3 Abbreviations used in ERRPTS population dynamics model.

Parameter	Description
Rats	
Rat nonmast breed	Length of the breeding season in a non-mast year
Rat mast breed	Length of rat breeding season in a mast year
Rat nonmast repro	Number of young/rat/month in a non-mast year
Rat mast repro	Number of young/rat/month in a mast year
Rat DD reproduction	Function giving the proportion of rats breeding in relation to density
Rat juvenile scaling	Adjusts the carrying capacity dependent on whether a non-mast or mast year
Rat juv. mort	Juvenile rat mortality
Rat scaling	Adjusts the carrying capacity dependent on whether a non-mast or mast year
Rat limit	Sets density below which rat mortality is zero
Rat pred reduction	Allows modification of predation intensity to simulate predator reduction
Rat equivalents	Calculates number of rats eaten given 2:1 mouse:rat consumption by stoats
Rat carrying capacity	Function that sets population size at which natural mortality is maximal
Mice	
Functions for mice are the same as for rats above	
Stoats	
Stoat pred converter	Sets density below stoat mortality is zero

Chapter 6: The role of predators in ship rat and house mouse population eruptions: Drivers or passengers?

6.0 Abstract

Four hypotheses regarding the role of predation in the population dynamics of eruptive small mammal communities are presented, and tested using the small mammal assemblage found in mixed forests in New Zealand. Large-scale (750 ha) predator removal was conducted, targetting stoats (*Mustela erminea*). House mouse (*Mus musculus*) and ship rat (*Rattus rattus*) population dynamics during an eruption were compared in areas with and without predator reduction. The success of predator reduction was measured by comparing live-capture rates of predators on treatment and non-treatment areas, and by recruitment rates of the threatened northern brown kiwi (*Apteryx australis mantelli*). Overall, predator reduction was successful, although there was a continual low rate of invasion onto the treatment area. The predictions and results were that 1) *Predators cannot prevent a population eruption due to time lags in breeding.* Supported: Populations of mice and rats erupted to high densities in areas with and without predator reduction, following synchronous southern beech (*Nothofagus* spp.) seeding. 2) *Predators cannot truncate peak prey population size.* Supported: Peak densities of mice and rats were not significantly different between treatment and non-treatment areas. 3) *Predators can hasten the rate of decline in prey populations during the crash phase.* Not supported: There was evidence of populations of mice and rats declining slower in areas with predators removed, but none of the trends were significant. 4) *Predators can limit low-phase prey populations.* Equivocal: Populations of rats in beech forest, and populations of mice and rats in coastline habitats were significantly higher in areas with predators removed, but were not significantly different in tawa-podocarp forest. Therefore, the role of food in driving the early stages of the mouse and rat eruption was demonstrated, but the role of predation in the decline and low phases remains unclear.

6.1 Introduction

The relationship between food and predation in regulating small mammal population dynamics has been the focus of much recent ecological research (Lidicker 1988; Sinclair 1989; Newsome 1990; Batzli 1992; Krebs 1996). Numerous studies have shown that variation in predation intensity may drive the decline and low phases of cyclic populations of microtine rodents in Fennoscandia (Hanski *et al.* 1991; Hanski *et al.* 1993; Korpimaki and Norrdahl 1998), and snowshoe hares (*Lepus americanus* L.) in North America (Sinclair 1986; Murray *et al.* 1994; Krebs *et al.* 1995; Rohner 1995). Australian studies have highlighted the importance of predators in limiting low-density prey populations, but the inability of predators to prevent a food-driven prey eruption (Newsome *et al.* 1989; Newsome 1990; Sinclair *et al.* 1990; Pech *et al.* 1992).

New Zealand forests contain a relatively simple, human derived, small-mammal predator prey system, that exhibits eruptive population dynamics (Innes 1990; King 1990; Murphy and Pickard 1990). Populations of feral house mice (*Mus musculus* L.) and ship rats (*Rattus rattus* L.) are generally present at low densities, but exhibit short-term eruptions (12-16 months duration, King 1983) following heavy synchronous seeding of *Nothofagus* species (Daniel 1978; Fitzgerald 1978; King 1983; Fitzgerald *et al.* 1996; King and Moller 1997). Following the rodent eruption, populations of predators, especially stoats (*Mustela erminea* L.), increase greatly in number, increasing predation on both rodents and endemic species (King 1982, 1983).

Small-mammal population regulation theories predict that in an eruptive system driven by bottom-up food limitation, predators should be able to limit low-phase prey population density through functional shifts in feeding rates and keep prey in a predator pit (Sinclair *et al.* 1990, Pech *et al* 1992). However, the predator numerical response should lag behind that of the prey during a population eruption, due to different intrinsic rates of increase and relative food availability. Peak prey population density during the eruptive phase should be set largely by the food availability during the rodent breeding season, with predator limitation playing only a minor role during the increase phase (Chapter 5).

Time lags in predator numerical responses mean that predation pressure will be greatest at, or just after, the rodent population peak. Consequently predation should cause prey populations to crash more rapidly, and to a lower density than that set by food limitation alone following the eruption (Newsome *et al.* 1989; Newsome 1990; Reid *et al.* 1995).

Little work has focused on the regulation of eruptive small mammal communities in New Zealand. While the observed population dynamics of house mice, ship rats and stoats appear to conform to current theories, there has been no concerted effort to test these theories in the New Zealand setting. As a first step to understanding the role of predators in the eruptive system, a computer model of the house mouse/ship rat/stoat community was constructed, and used to generate a range of predictions (Chapter 5).

Four predictions regarding the role of predators in the population dynamics of eruptive rodent species in New Zealand are presented and tested in this study. These predictions are based on published studies of other small mammal/predator associations, the predictions of the model (Chapter 5), and on current knowledge of ship rats, house mice and stoats. It is assumed that, in New Zealand forests, the rodent/predator system is driven from the bottom up by large, periodic energy inputs (King 1983; Fitzgerald *et al.* 1996) and that the basic physiology and biology of these species have not changed following their introduction into New Zealand (Innes 1990).

The predictions are as follows:

1. *Predators are unable to prevent outbreaks in prey populations.* Differences in both reproductive biology and potential intrinsic rates of increase between rodents and their mustelid predators mean that house mice and ship rats can increase earlier than mustelids in response to a beech masting (Output 2, 3; Chapter 5). Such time lags in mustelid responses to rodent prey have previously been reported from European studies (Pearson 1966; Pearson 1971; Korpimaki *et al.* 1991; Korpimaki 1993). Consequently prey populations with and without predators present should erupt at a similar time and rate following a beech masting.

2. *Predators do not determine peak prey population sizes during eruptions.* Due to the time lags hypothesised in Prediction 1, peak rodent densities in a full-mast year will be largely set by food availability and the length of the breeding season (Output 4, Chapter 5), with predator numbers peaking at, or after, the rodent population peak. Peak population density will fluctuate from year to year, depending on the size of the winter and spring food supplies (Jensen 1982; Fitzgerald *et al.* 1996). Therefore, peak prey-population densities should be similar in areas with and without predator removal.

3. *Predators can significantly hasten the rate of decline following an outbreak.* In New Zealand, stoat numbers are highest just following the peak in rodent populations (King 1982), and stoats show large functional shifts in diet, feeding almost exclusively on rodents when abundant (Korpimäki *et al.* 1991). Similarly, voles have been shown to constitute almost the entire weasel diet in cyclic populations of voles in northern Fennoscandia (Henttonen *et al.* 1987; Korpimaki *et al.* 1991). Therefore I predict that predation can significantly hasten and extend the decline phase of eruptive rodent populations, with prey populations declining more slowly in areas with predators removed. The strength of predator limitation during the crash phase will be influenced by the severity of food limitation over the same period (Output 5, Chapter 5).

4. *Predators are able to limit prey population size during the low phase.* Predator:prey ratios should be highest in the post-crash phase, so that predators are able to limit prey populations during the low phase (Newsome *et al.* 1989; Reid *et al.* 1995). Predator:prey ratios should decline in the seasons following the crash, as the low phase progresses, as a result of heavy characteristic winter mortality in stoats (King 1990), so that predator limitation of prey populations becomes less severe as predator:prey ratios decline (Output 6, Chapter 5).

The system under study provides an excellent test of the factors influencing eruptive small mammal populations, due to the artificial and relatively simple nature of the

predator-prey-habitat association, and allows the examination of predator-prey dynamics on a large scale in the field (May 1999).

6.2 Methods

6.2.1 Study site and location

The study was conducted at Lake Waikaremoana (38° 47′ S 177° 05′ E), situated at the south-eastern corner of Te Urewera National Park (212,000 ha), in the North Island of New Zealand (Figure 1.1, Chapter 1). This study was part of a larger project investigating the dynamics of the small mammal/predator system, and the implications this has for the threatened northern brown kiwi (*Apteryx australis mantelli* Bartlett).

The lake covers 5,170 ha and is 582 m a.s.l. The catchment is steep and almost entirely forested, and has no history of timber logging. The forest consists of mixed stands of southern beech (*Nothofagus fusca*, *N. truncata*, *N. menziesii*, *N. solandri*), podocarp (Podocarpacae) and tawa (*Beilschmiedia tawa*) forest at lower elevations, rising to pure beech forest at higher altitudes (800-1000 m a.s.l). The lake margin is covered with a mix of introduced grasses, sedges, and regenerating manuka (*Leptospermum scoparium*) scrub, growing on the old lake bed that was exposed in the 1940s when the lake level was lowered to allow hydroelectric power generation (McLennan 1997).

Introduced small mammals present in the area include three rodent species: house mice, ship rats and Norway rats (*R. norvegicus* Berkenhout.); four predator species: weasels (*M. nivalis* Erxleben), stoats, ferrets (*M. furo* L.) and feral domestic cats (*Felis catus* L.), and three species of herbivore: Australian brush-tailed possums (*Trichosurus vulpecula* Kerr), European rabbits (*Oryctolagus cuniculus* L.), and European hares (*Lepus europaeus* de Winton). Large mammals, present in low numbers, include red deer (*Cervus elaphus* Lonnberg) and feral pigs (*Sus scrofa* L.).

Of the small mammals, ship rats and possums are seasonally present in moderate numbers, although house mice and ship rats increase to high population densities after southern beech seeding. Of the four predators present, stoats are the most common, with weasels, ferrets and cats present at low densities.

6.2.2 Previous predator indexing and trapping

Predator-monitoring transect lines were established in 1994 through the bush and around the coastline on two peninsulas, Puketukutuku (750 ha) and Whareama (400 ha). Footprint tracking tunnels (King and Edgar 1977) were placed at 200 m intervals, and live-capture cage traps (for stoats, ferrets and feral cats) at 300 m intervals, along the bush lines on each peninsula, and at each of the coastline stations (100-200 m spacing). Tracking tunnels were set in the evening, baited with peanut butter, and checked the following day. Any rodent or predator tracks found were recorded, and the species identified when possible, using knowledge on the shape, structure and size of feet of the species present in the study area (King *et al.* 1994). The monitoring effort was irregular until October 1995, after which tunnels were usually run for three consecutive nights each month. Results are expressed as the proportion of tunnels tracked for a given time period. Live capture cages were run concurrently with the tracking tunnels. In each trapping session, the traps were baited with rabbit meat and run for three consecutive nights. The location, date of capture, species and sex (where possible) of any animals caught were recorded, and individuals were either released (in non-treatment areas) or euthanased (in treatment areas).

In September 1994, Mk 4 and Mk 6 Fenn kill traps (FHT Works, Redditch, England) were placed at 150 m intervals along each of the transect lines on Puketukutuku peninsula, and on several additional ridges between transects. Traps were placed at 25 m intervals across the neck of the peninsula, in an attempt to intercept any predators moving into the trapped areas. Fenn traps were also placed at each of the coastline stations on Puketukutuku peninsula. All traps were placed under wooden covers to prevent capture of non-target animals, and were baited with either hen's eggs or rabbit meat. Traps were run continuously from May 1995, and were checked every 7-10

days on the main trap-lines. A small number of the lines were checked less frequently, with intervals between inspections of 2-4 weeks. The species, sex, capture date and location of all animals caught was recorded.

6.2.3 Small mammal population monitoring

In order to study the potential impacts of predator removal on prey population dynamics, rodents were intensively monitored in five "Rodent-monitoring" areas on the two peninsulas from January 1996 to March 1998. On Puketukutuku peninsula, lines of tracking tunnels were established in both the podocarp-tawa forest (Treatment area 1; T1), and the beech forest (Treatment area 2; T2). A third line was established in podocarp-tawa forest on the treatment peninsula in October 1996 (Treatment area 3; T3). On the non-treatment Whareama peninsula, lines were established in corresponding forest types (Non-treatment area 1; NT1, podocarp-tawa forest; Non-treatment area 2; NT2, beech forest). A sixth line (Non-treatment area 3; NT3) was established in April 1996 (Figure 1.1, Chapter 1), to examine any peninsula effects.

In each of the six areas, tracking tunnels were placed at 100 m intervals along lines running from the lake edge up into the bush, before looping around to enclose areas of 15-20 ha. Each tunnel was baited with peanut butter, and run for a single night each month. Results are expressed as the proportion of tunnels tracked for a given period.

It has been shown elsewhere that tracking tunnels are influenced by sampling effort and target species activity (Chapter 2). Therefore, tracking rates were calibrated with levels of rat by-catch in Fenn traps placed in the tawa-podocarp and beech forest. Data from tracking tunnels were directly compared between treatment and non-treatment areas located in the same habitat type, and were used to compare only population trends between habitat types.

6.2.4 Statistical analysis

Differences in tracking rates between seasons and between areas were analysed using the Genmod procedure in SAS (SAS Inc. 1996). An individual tunnel could be either tracked or untracked, so a binomial analysis was used. Differences between periods were analysed using a repeated measures design, to investigate temporal trends in the data. The Genmod analysis produces a X^2 statistic that can be compared with the critical value from the X^2 distribution with the appropriate degrees of freedom.

Tracking rates of mice on the large predator-monitoring lines were expressed as monthly averages (Non-treatment area, 4 transect lines; Treatment area, 5 transect lines) and were compared between treatments and seasons using the Genmod procedure in SAS.

Capture rates in live capture cage traps were low throughout the study. The numbers of traps and trap-nights were similar between treatment and non-treatment areas, so differences in numbers of predators caught were compared using the Mann-Whitney test, which is a non-parametric analogue of a two-tailed *t*-test (Zar 1974).

Fenn trap capture rates were low relative to the number of trap-nights run. Differences in capture rates between areas and years were analysed using the Genmod procedure in SAS, with a binomial approximation, and an auto-regressive correlation matrix, which correlates the trapping data with the previous value only.

Numbers of rats and stoats caught on the Fenn lines were used to calculate predator:prey ratios for tawa-podocarp and beech forest areas separately, and differences in predator:prey ratios between treatments and years were analysed using an analysis of variance in SYSTAT (SPSS Inc. 1996).

6.3 Results

The general trends in rat population tracking rates in the rodent-monitoring areas are shown in Figure 6.1. Synchronous southern beech seed-fall occurred in autumn 1995 (Dr C. Ward, pers. comm.). Following this large energy input, rat tracking rates increased to high levels in rodent-monitoring areas. Tracking rates peaked in autumn/winter (May-August) 1996 in all areas before declining to low levels by autumn 1997 (Figure 6.1a,b, refer to Appendix 6.2, 6.3).

In tawa-podocarp forest, tracking rates were consistently lowest in Treatment area 1, and differences were significant in all seasons except summer 1996/1997 (Figure 6.1a). In the beech forest sites, all areas showed similar trends over the 1996 peak, although Non-treatment area 3 tracking rates were slightly lower than in the other two areas. Through the low period (August 1997 to March 1998), tracking rates were similar in non-treatment areas, and significantly lower than in the treatment area (X^2 = 183.3, df = 2, $P < 0.001$; Figure 6.1b).

Rat tracking rates on the large predator-monitoring lines were more variable than those observed on the smaller scale rodent-monitoring lines (Figure 6.2a, b). Rats on predator-monitoring beech forest lines also showed high densities in 1996 following the autumn 1995 mast seeding (Figure 6.2b). Rat numbers declined in late 1996 on predator-monitoring lines, and were fairly low for the rest of the study.

Mouse numbers were high on all lines in treatment and non-treatment areas throughout 1995 and early 1996 (Figure 6.3a, b), and were declining rapidly at the time monitoring commenced in the rodent-monitoring areas in January 1996. In both treatment and non-treatment areas on the rodent-monitoring lines, mouse tracking rates were higher in beech forest than in tawa-podocarp forest, but declined to zero in all areas by spring 1996, with only the occasional mouse print recorded after this time (Figure 6.3b). On the predator-monitoring bush lines, there were no significant differences in peak mouse population densities. In the peak phase, mouse tracking rates on the coastline were not significantly different between treatment and non-treatment areas, although the treatment and non-treatment areas did differ during the post-crash low phase.

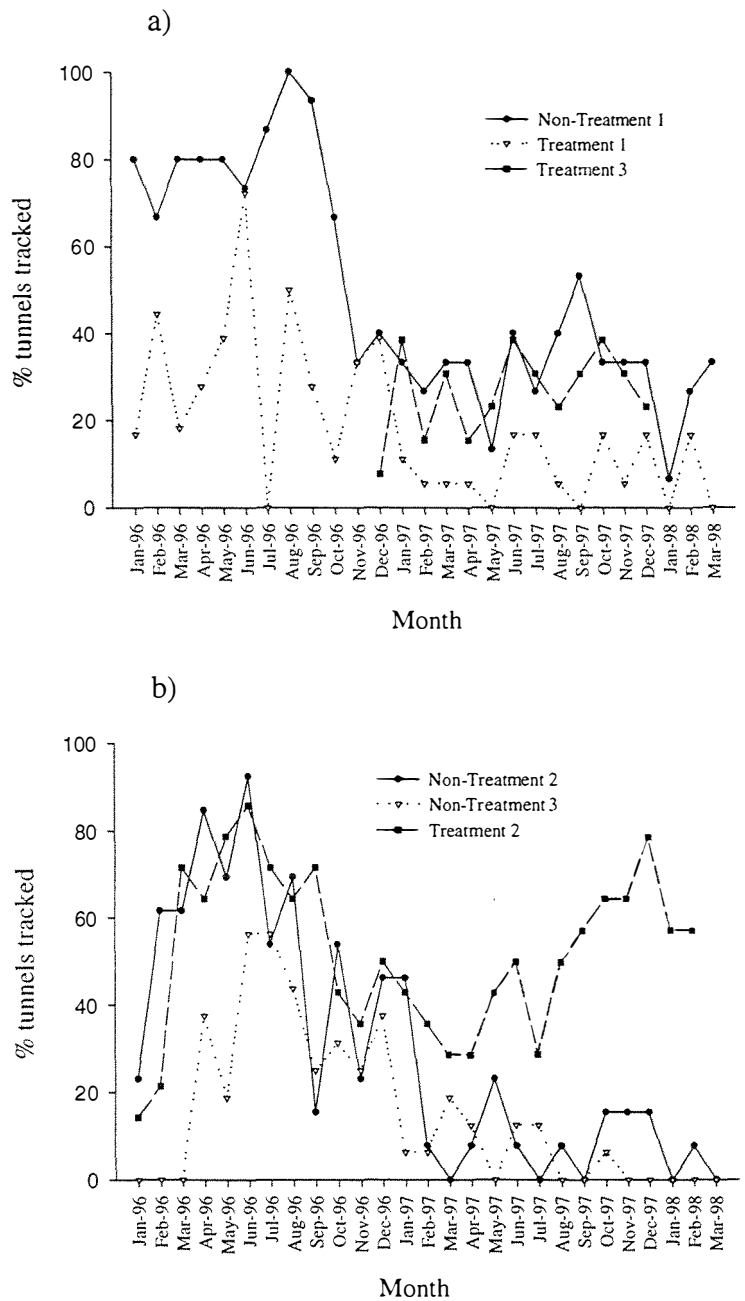


Figure 6.1 Monthly tracking rates (% tunnels tracked) for ship rats on a) tawa-podocarp forest, and b) beech forest index lines. Predator trapping commenced in May 1995 and continued throughout the study. Tracking tunnels were run for a single night each month, and were run in the same habitat on the same night to control for activity.

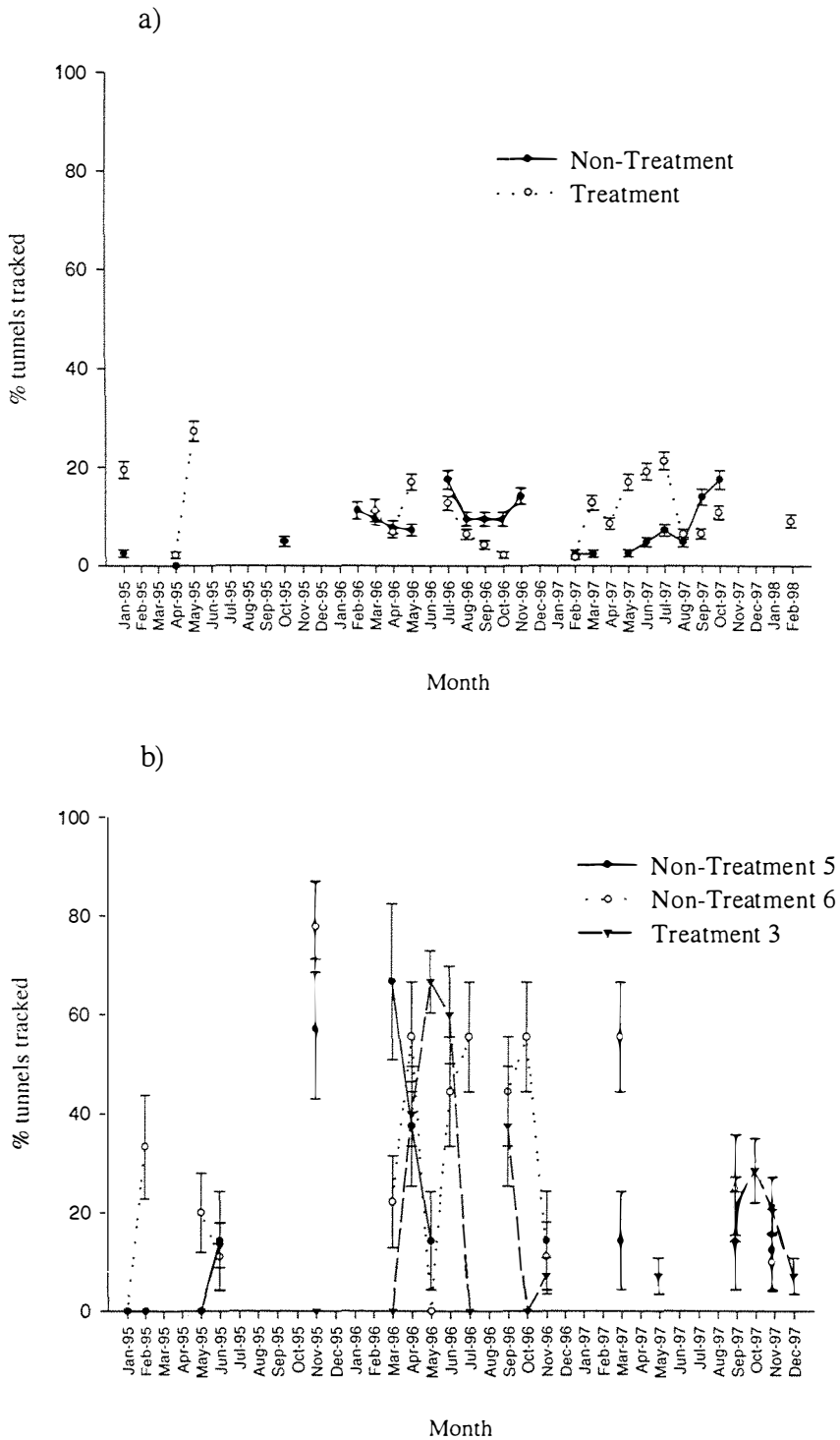


Figure 6.2 Monthly tracking rates of ship rats in treatment and non-treatment areas, on a) coastline and b) beech forest predator-monitoring transect lines. Predator trapping was conducted from May 1995 until the end of the study in treatment areas.

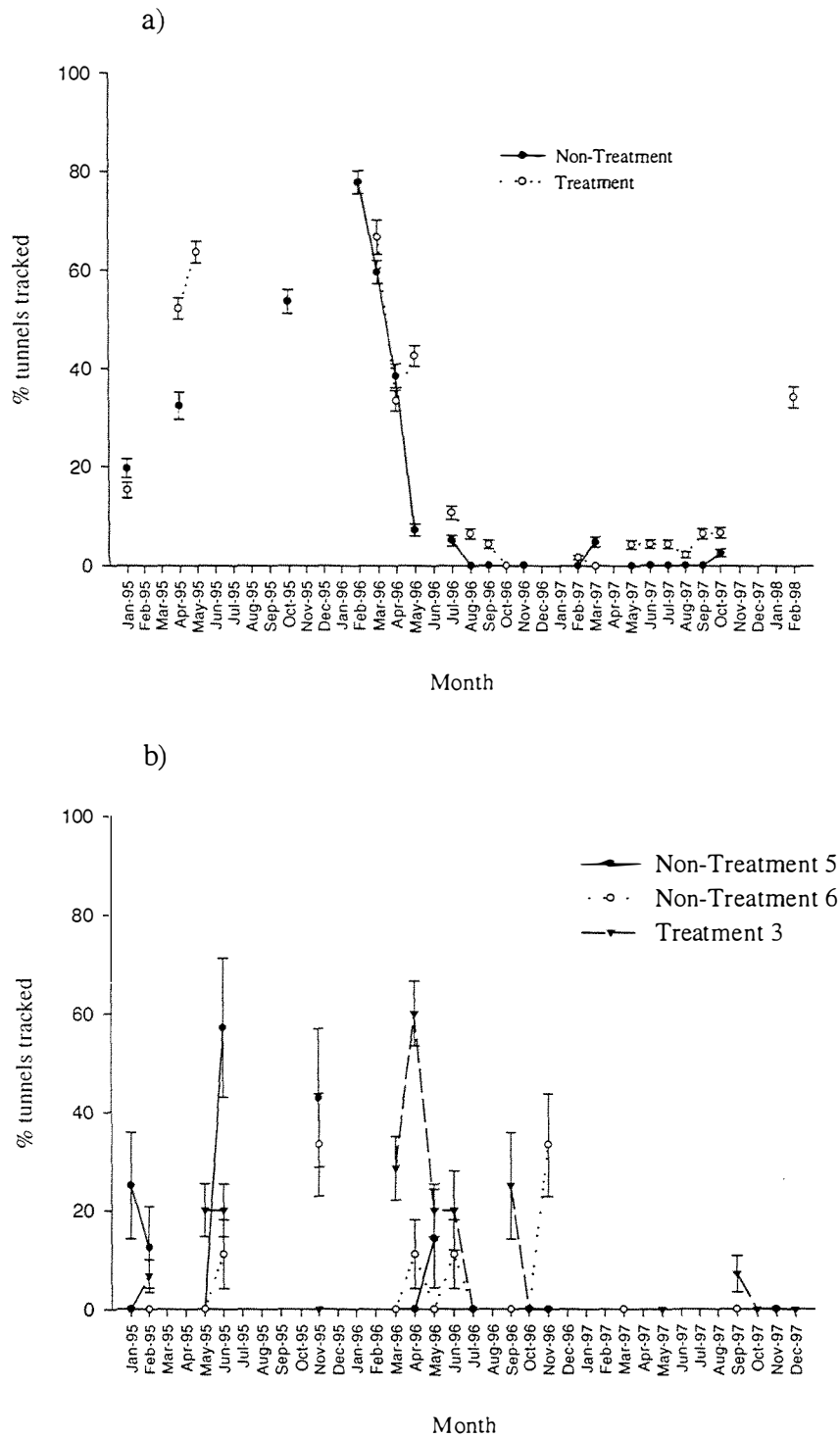


Figure 6.3 Monthly tracking rates of mice in treatment and non-treatment areas, on a) coastline and b) beech forest predator-monitoring transect lines. Predator trapping was conducted from May 1995 until the end of the study in treatment areas.

6.3.1 Predator population dynamics

Captures of predators in live-capture cage traps were erratic throughout the study (Table 6.1). Before trapping began in May 1995, captures of predators in cage traps in non-treatment and treatment areas were not significantly different (Mann-Whitney U = 10, $P > 0.05$). In 1996, overall live capture rates of predators were significantly higher in the non-treatment area than in the treatment area where predator kill trapping was carried out (Mann-Whitney U = 106.5, $P = 0.03$; Table 6.1). In 1997, seven predators (two cats and five ferrets) were caught in cage traps in non-treatment areas, compared to the capture of only one cat in treatment area cage traps (Mann-Whitney U = 97.0, $P = 0.06$).

Captures of stoats in treatment and non-treatment areas were vastly different. Two stoats were caught in treatment area cage traps before kill trapping commenced, and none in non-treatment areas (Mann-Whitney U = 7.5, $P > 0.05$). In comparison, after kill-trapping commenced, nine stoats were caught in the non-treatment area, and none in the treatment area (Mann-Whitney U = 108.0, $P < 0.01$). All nine were caught in 1996, the year of highest rat densities (Figure 6.1, 6.2).

Captures of predators in the kill-traps on the treatment peninsula over the course of the experiment are shown in Appendix 6.1. Captures of stoats were highly seasonal, with the majority of animals caught between May and December each year (Figure 6.3). In the tawa-podocarp forest Fenn trap lines, stoat capture rates were highest in summer 1995/96, and relatively lower in the following two summers ($X^2 = 30.39$, $df = 2$, $P < 0.001$).

Table 6.1 Numbers of predators caught in live cage traps in treatment and non-treatment areas in each year of the predator trapping experiment at Lake Waikaremoana. Kill trapping commenced in treatment areas in May 1995, and continued for the remainder of the study. TN refers to the number of trap nights set, corrected for sprung traps by subtracting half a trap-night for any cages that caught animals. A linear correction for sprung traps was used when the number of sprung traps was small compared to the total number of trap-nights.

	Non-treatment				Treatment			
Year	Cat	Stoat	Ferret	TN	Cat	Stoat	Ferret	TN
1995	4	0	1	622.0	0	2	4	999.5
1996	1	9	1	558.0	3	0	0	995.0
1997	2	0	5	645.5	1	0	0	876.5
1998	0	0	2	310.0	1	0	0	82.5
Total	7	9	9	2135.5	5	2	4	2953.5

Non-target animals that were caught in the cage traps were not included in the analyses, and included a total of 48 possums, 8 magpies (*Gymnorhyna tibicen*) and 3 harriers (*Circus approximans*) in non-treatment areas, and 52 possums and 6 harriers in treatment areas.

On the beech forest trap-lines, numbers of stoats caught were generally lower than on tawa-podocarp forest trap-lines (Appendix 6.1), although the fewer number of traps run in beech forest means that captures per 100 trap-nights (C/100TN) were not vastly different (Figure 6.4a, b). Over the years of the study, stoat captures/100TN in beech forest Fenn traps were low in summer 1995/96, higher in the summer of 1996/97 and low in summer 1997/98 ($X^2 = 6.632$, $df = 2$, $P = 0.04$). Stoats were caught more frequently in autumn and winter 1997, so that overall captures were higher in 1997, although the difference was not significant ($X^2 = 1.86$, $df = 1$, $P = 0.17$).

6.3.2 Prediction I: Predators are unable to prevent outbreaks in prey populations.

Captures of rats and stoats, and the resulting predator:prey ratios from Fenn traps in the tawa-podocarp forest across the neck of the peninsula and in the beech forest at the end of the peninsula (trap lines surrounding Treatment area 2) are shown in Figure 6.4. In tawa-podocarp forest, both stoat captures and predator:prey ratios were low throughout the large ship rat population increase in 1996 (Figure 6.1a, 6.4a), and did not increase until the period from November 1996 to June 1997, subsequent to the rat population eruption. Stoat captures were then low until January 1998, when predator:prey ratios increased again.

Capture rates of rats and stoats in Fenn traps were lower in beech forest than in tawa-podocarp forest in 1996 (Figure 6.4b). Following an increase in stoat captures in November 1996, predator:prey ratios increased on the beech trap lines, before dropping in March 1997. There was a general increase in rat and stoat captures from May 1997, that resulted in a corresponding increase in the predator:prey ratio. The ratio was especially high in August 1997, before dropping again, and remaining low for the rest of the study.

There were no significant differences in predator:prey ratios recorded in 1996 and 1997 on either the tawa-podocarp forest trap-lines ($F_{1,6} = 0.322$, $P = 0.59$) or on the beech forest trap-lines ($F_{1,6} = 0.052$, $P = 0.83$). Over the course of the study, predator:prey ratios were not significantly different on trap-lines in tawa-podocarp or beech forest ($F_{1,12} = 0.86$, $P = 0.37$). In both the tawa-podocarp and beech forest, predator prey ratios never increased before the rise in rat captures, and were driven by stoat captures lagging 3-4 months behind rat population increases.

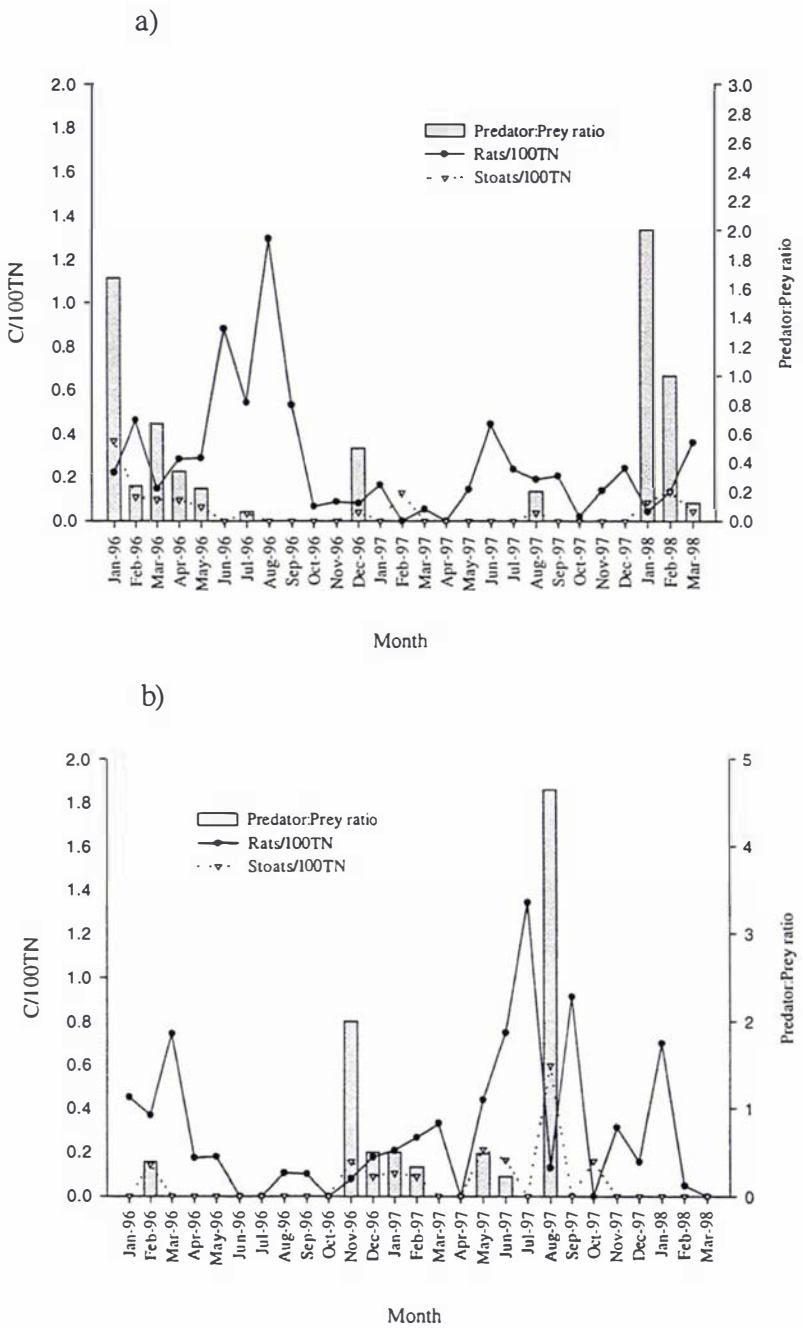


Figure 6.4 Monthly rat and stoat captures per 100 trap-nights (C/100TN) in Fenn traps in a) tawa-podocarp and b) beech forest at Lake Waikaremoana. Rat and stoat captures were used to calculate predator:prey ratios for months where both species were caught.

6.3.3 Prediction 2: Predators do not truncate peak prey population sizes during eruptions.

On the smaller-scale rodent-monitoring lines, tracking rates in the tawa-podocarp areas in autumn/winter 1996 were significantly higher in Non-treatment area 1 (NT1) than in Treatment area 1 (T1) (Average % tunnels tracked ± 95%CI: NT1, 83.3 ± 7.7%; T1, 33.6 ± 8.8%; $X^2 = 44.02$, $df = 1$, $P < 0.001$; Figure 6.1a). In the beech forest areas, tracking rates were not significantly different between Non-treatment area 2 (NT2) and Treatment area 2 (T2) over autumn/winter 1996 (Average % tunnels tracked ± 95% CI: NT2; 71.8 ± 10.2%; T2; 72.6 ± 9.7%; $X^2 = 0.17$, $df = 1$, $P = 0.68$). However, the average tracking rate in Non-treatment area 3 (NT3; 42.5 ± 10.8% tunnels tracked) was significantly lower than in either Non-treatment area 2 or Treatment area 2 ($X^2 = 17.05$, $df = 2$, $P =<0.01$; Figure 6.1b).

On the larger-scale predator-monitoring lines, mouse tracking rates were not significantly different between treatment and non-treatment areas on either the beech forest lines ($X^2 = 3.16$, $df = 2$, $P = 0.21$), or on the coastlines ($X^2 = 0.31$, $df = 1$, $P = 0.58$; Figure 6.3a, b). Similarly, tracking rates of ship rats were not significantly different between treatment and non-treatment areas in the beech forest ($X^2 = 1.49$, $df = 2$, $P = 0.47$), or on the coastlines ($X^2 = 3.17$, $df = 1$, $P = 0.08$; Figure 6.2a, b).

6.3.4 Prediction 3: Predators can significantly hasten the rate of decline following an outbreak.

Irrespective of predator manipulation, numbers of ship rats declined sharply in all areas following their peaks in winter 1996 (Figure 6.5a,b). The rates of decline in treatment and non-treatment rodent-monitoring areas from winter 1996 to autumn 1997 were not significantly different between treatments, either in tawa-podocarp or beech forest (Table 6.2). In both forest types there was a slight, consistent trend for greater rates of decline in non-treatment areas, where predators were still present (Figure 6.5a, b). This trend was not significant in either forest type.

The data are more erratic on the predator-monitoring lines, so the decline phase population dynamics were compared for the mouse and rat populations on the coast lines only. Over the decline period (April 1996 to November 1996 for mice; Figure 6.3a), there was a trend for monthly tracking rates to be higher in treatment areas than in non-treatment areas (treatment effect: $X^2 = 2.93$, $df = 1$, $P = 0.09$). Over the decline period in the ship rat populations on the coastline (July 1996 to January 1997; Figure 6.2a), tracking rates were significantly higher on the treatment peninsula than in the non-treatment area ($X^2 = 5.88$, $df = 1$, $P = 0.02$).

Table 6.2 Binomial repeated measures analysis of differences in tracking rate recorded between September 1996 and April 1997 in treatment and non-treatment rodent-monitoring areas. Lines in tawa-podocarp and beech forest were analysed separately. Refer to text for details.

Source	Deviance	*df*	X^2	*P*
Podocarp				
Treatment	23.57	1	9.65	0.002
Month	7.80	6	15.63	0.012
Treatment by Month	0.00	6	7.90	0.246
Beech				
Treatment	35.74	2	13.37	0.001
Month	10.08	7	25.66	0.006
Treatment by Month	-0.00	14	10.08	0.757

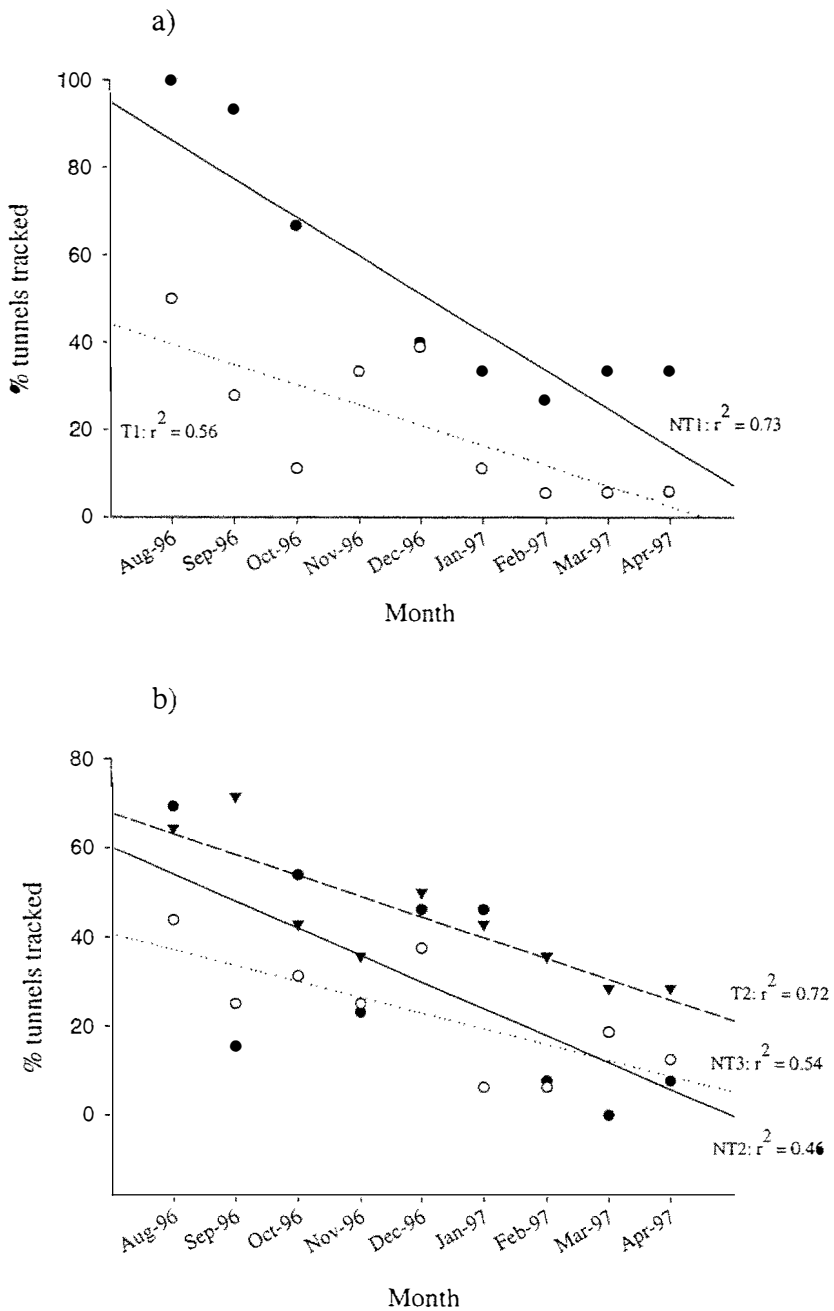


Figure 6.5 Decline in ship rat seasonal tracking rate following the winter 1996 population peak on a) tawa-podocarp forest and b) beech forest indexing lines. Filled circles and triangles denote non-treatment areas; open circles denote treatment areas. Lines are linear regression equations, and r^2 values are shown for each area. All regressions are significant at the $P = 0.05$ level.

6.3.5 Prediction 4: Predators are able to limit prey population size during the low phase.

Following the population decline in 1996, tracking rates in the rodent-monitoring beech forest area climbed throughout autumn/winter 1997, so that from August 1997 to the end of the study, tracking rates were significantly higher in beech forest with predators removed (T2), than in non-treatment areas (NT2, NT3) in the same forest type (average % tunnels tracked ± 95 % CI: T2; 64.3 ± 9.1%; Pooled non-treatment; 4.7 ± 2.8; X^2 = 183.30, df = 2, P < 0.001; Table 6.3, Figure 6.1b). In the tawa-podocarp forest, tracking rates and population trends in NT1 and T3 were similar throughout the low phase. Numbers of rats tracked in T1 were consistently significantly lower than in either T3, or in the non-treatment area throughout the low phase (May 1997 to March 1998; X^2 = 28.30, df = 2, P< 0.001; Table 6.3).

On the predator-monitoring coastline transects, tracking rates were significantly higher over the low period in treatment areas, both for mice (low period December 1996 to February 1998; X^2 = 4.34, df = 1, P = 0.04; Figure 6.3a) and rats (low period February 1997 to February 1998; X^2 = 13.31, df = 1, P < 0.01; Figure 6.2a).

On the predator-monitoring beech forest lines, rat tracking rates were significantly higher in treatment areas than in non-treatment areas (X^2 = 21.22, df = 2, P < 0.01). Mouse tracking rates on the predator-monitoring beech forest lines were too low for analysis over the low phase.

Table 6.3 Binomial repeated measures analysis of differences in tracking rate recorded between May 1997 and March 1998 in treatment and non-treatment rodent-monitoring areas. Lines in tawa-podocarp and beech forest were analysed separately. Data were analysed using a general linear model with binomial data.

Source	Deviance	*df*	X^2	*P*
Podocarp				
Treatment	32.73	2	28.30	0.0001
Month	18.94	10	13.79	0.183
Treatment by Month	0.00	17	18.94	0.332
Beech				
Treatment	36.544	2	183.30	0.0001
Month	23.76	10	12.79	0.236
Treatment by Month	0.00	18	23.76	0.163

6.4 Discussion

6.4.1 Assumptions of the study

Interpretation of results from this study relies on the indices of rodent and predator density giving an accurate picture of true density levels, and of changes in the study populations. Therefore, there are four assumptions that must be tested before valid conclusions can be drawn. These are discussed below:

1) Footprint indexing gives an accurate picture of population trends. It has been shown previously that tracking tunnel indices correlate closely with rodent numbers estimated by removal trapping (Brown *et al.* 1996), although the accuracy of the index can be influenced by activity levels, sample size and tracking tunnel arrangement (Chapter 2). These limitations can be reduced by the use of a consistent experimental protocol. However, tracking rates can only confidently be compared between areas in

similar forest types, although overall trends in population density can be compared between habitat types.

2) Due to a high by-catch of ship rats in Fenn traps in tawa-podocarp forest during the rodent peak in trapped areas, it is possible that no response in rodents to predator removal at this time was a result of stoat predation being replaced by "trap predation". Mice are too light to trigger the Fenn traps, and therefore do not turn up as a by-catch. The lack of a positive response by mice to stoat removal therefore suggests that absence of a rat response to predator reduction is a true one.

3) For predation to be important in determining prey population dynamics, stoats must in fact be consuming rodents. The majority of stoat and other predator carcasses were quite decayed when the traps were inspected and not kept, so only a small proportion of the stoats caught were available for stomach contents analysis. Of these, rat remains were found in 24% of 17 stoat stomachs (Dr Kay Clapperton, pers comm.). A previous survey from this area found ship rat remains in 29% of stoat stomachs examined, and mice in 24% of stomachs (King and Moody 1982). Several other New Zealand studies have noted the importance of rodents in the stoat diet (see King 1990).

4) In order for responses in rodent populations to be due to a reduction in predation pressure, predator control on the treatment peninsula must have been successfully achieved. There are two lines of evidence that suggest that this was the case. 1) Captures in cage traps were significantly higher on the non-treatment peninsula than on the treatment peninsula over 1996 and 1997. Numbers of cage trap trap-nights were similar on both peninsulas, so that the reduction in predator captures, especially stoats, on the treatment peninsula suggests a true reduction in predator number in the treatment area. 2) The survival of kiwi chicks in treatment areas with predator trapping was significantly higher than in the non-treatment areas. On the treatment peninsula in this study, 17 of 30 monitored chicks (58%) were recruited into the adult population. In comparison, in non-treatment areas 2 of 26 monitored chicks (7%) were recruited into the adult population, with the majority of deaths due to stoat predation (Dr J. McLennan, pers. comm.). In unmanaged populations of kiwi on mainland New Zealand, approximately 95 % of chicks fail to reach adulthood, with stoat predation

accounting for up to 60% of juvenile mortality (McLennan *et al.* 1996). It has been shown that an 80% reduction in stoat numbers is required to increase juvenile kiwi recruitment rates to 20%, in order to prevent a continued decline in kiwi numbers (Basse *et al.* 1999).

6.4.2 The role of predators in eruptive rodent population dynamics

In this study, role of predation in the dynamics of periodic small mammal population eruptions in New Zealand was investigated using large-scale predator reduction experiments. The results supported two predictions regarding the role of predators in this system (Prediction 1: Predators cannot prevent a prey outbreak; and Prediction 2: Predators cannot truncate peak prey population size), and provided evidence for the fourth prediction (Predators can limit low-phase prey populations). However, the study failed to find significant support for the Prediction 3; that predators can hasten the decline in prey numbers during the crash phase.

6.4.3 Prediction 1: Predators are unable to prevent outbreaks in prey populations.

The changes in predator:prey ratios throughout the rodent eruption demonstrate that predators are unable to prevent the build-up of rodents during the increase phase. This is influenced largely by key differences in the reproductive biology of the species involved, and by the relative simplicity of the system under investigation.

Murid rodents are characterised by very plastic breeding biology. The length of the breeding season is variable, and affected by food quality and quantity (Bomford and Redhead 1987; Berry and Bronson 1992). In New Zealand, the recorded breeding season for the ship rat lasts from mid September to mid April, occasionally extending into winter, following heavy seed-fall (Best 1969; Daniel 1972; Innes 1979). House mice have similarly been recorded breeding year round on Macquarie Island (Berry and Peters 1975) and Marion Island (Berry *et al.* 1978) in the sub-Antarctic. In beech

forest, mice can breed through the winter after a heavy seed fall in response to food (Murphy 1992). Year round breeding has been recorded in commensal populations of *M. musculus* (Murphy and Pickard 1990), *R. rattus* (Storer and Davis 1953; Ewer 1971) and *R. norvegicus* (Leslie *et al.* 1952).

In comparison, breeding in stoats is controlled by day length (King 1990) and female stoats exhibit delayed implantation of embryos, so that the maximum potential number of young produced in a breeding season is fixed in the preceding autumn. The survival of young is determined by the food available in the summer (King 1982). In the North Island, New Zealand, litters of between 6 -13 young are produced from late September to early October (King 1990). Newly independent young are not caught until mid to late January (King 1983) so prey numbers are already high by the time most young of the year become active. While this increases the probability of there being ample food for young stoats, it may also mean that stoats do not significantly influence the dynamics of the increase or peak phases of a rodent eruption (King 1983).

In relatively undisturbed forest areas in New Zealand, the two most prevalent small mammals are the ship rat and the stoat, with the other rodent and predator species present at only very low densities. House mouse numbers increase to very high densities following beech masting, especially in pure beech forest in the South Island (Fitzgerald 1978; King 1983; Fitzgerald *et al.* 1996), with subsequent increases in stoats and weasels. However, in the mixed forest in this study, the mouse population response was not as severe as in the South Island, and had largely dissipated when this study commenced. This lack of diverse prey base, and the absence of year-round generalist predators, as found in intact northern hemisphere systems (Hanski *et al.* 1991; Korpimaki *et al.* 1991), means that rodents can rapidly respond to increased food supplies without any significant predator limitation or regulation.

Simulation runs of the ERRPTS population dynamics model (Chapter 5) showed that predators still could not prevent a prey-population outbreak with the time-lags in predator breeding removed (Output 3: Chapter 5). This highlights the primary importance of differences in reproductive biology between predator and prey species in precluding any major predator limitation of the prey species during the increase

phase of the eruption. However, the model does predict some minor, but significant, predator limitation of prey populations during the increase phase. Prey populations with predators present should increase slightly later in response to food than populations without predators present, but still attain similar peak population densities. There was some evidence for this from mouse populations on the coast lines, with mice on the non-treatment peninsula coast line increasing significantly more slowly than on the treatment peninsula. This response to predator reduction was not seen in any of the other areas, so the strength of predator limitation in the increase phase under field conditions still requires clarification.

6.4.4 Prediction 2: Predators do not truncate peak prey population size during eruptions.

The lack of a significant difference in peak house mouse and ship rat numbers between trapped and untrapped areas in the beech forest and on the coastlines shows that predators do not truncate peak rodent population size during a full eruption. The reduced tracking rate of rats recorded in Treatment 1 may be due in part to the large localised by-catch of rats in the Fenn traps.

On both peninsulas there was a large response to the energy input during the beech masting, with populations of rodents subsequently declining as this food resource was depleted. Fitzgerald *et al.* (1996) found a strong correlation between the numbers of viable beech seed produced and the density of house mice in the following spring. Similarly, Jensen (1982) found a strong relationship between the quantity of northern beech (*Fagus sylvatica* L.) seed produced and the density of the bank vole (*Clethrionomys glareolus*) in a study in Denmark, while bank vole and wood mouse (*Apodemus sylvaticus*) breeding can be extended into winter following mast seeding of oak (*Quercus ruber*) (Smyth 1966) and ash (*Fraxinus excelsior*) (Flowerdew and Gardner 1978) in English woodlands.

Ground invertebrate numbers also increased following the 1995 beech seeding (Chapter 4). These animals make up a very important component of the summer diet of rodents in New Zealand (Daniel 1972; Innes 1979; Clout 1980; Dick 1985; Baden

1986; Miller and Miller 1995; Chapter 3). Fitzgerald *et al.* (1996) also found a positive correlation between beech seed fall and densities of litter-feeding moth larvae.

As a result of the primarily bottom up regulation of this system, it is not surprising that stoats are unable to greatly affect the peak rodent population, given the large unidirectional movement and assimilation of energy through the system following the beech seed-fall.

6.4.5 Prediction 3: Predators can significantly hasten the rate of decline following an outbreak.

Predation may be expected to play a significant role in determining the dynamics of the rodent population at, or just after, the population peak, as predator numbers are highest at this time (Prediction 3). Erlinge *et al.* (1988) found significantly lower rates of declines in *Microtus* voles in areas with mustelid predators removed, and Korpimäki *et al.* (1991) concluded that least weasels (*Mustela n. nivalis* L.) were important in shaping the decline phase of cyclical vole populations in western Finland.

In the computer model of the mouse/rat/stoat assemblage in New Zealand, predators were able to cause a small but significant increase in the rate of decline in prey populations during the crash phase. The strength of this effect is relative to the severity of the natural mortality in the prey population over the crash phase. King (1983) suggested that stoat predation may hasten the rate of decline in post-eruption mouse populations, although this has not been tested until now. In this study, no evidence was found for a consistent difference in ship rat densities between trapped and untrapped areas in beech forest during the decline, but in the rodent-monitoring areas, there was slight evidence for slower declines in rat populations in areas with predators removed. Populations of rats declined more rapidly in two of the untrapped areas (NT1, NT2) irrespective of forest type, where predators were still present, although the trends were not significant. There was also a tendency for mouse numbers to be higher over the decline phase on the coastline of the non-treatment peninsula, as predicted by King (1983). The higher tracking rates recorded by rats on

the non-treatment peninsula are, however, contrary to predictions. No detailed site descriptions were conducted for the coastline trapping and tracking sites, so the cause of differences in rat tracking rates between treatments on the coastline remains unclear.

There are several possible reasons why the predicted effect of predators on the rate of prey decline between winter 1996 and autumn 1997 was not observed in the field data. During the period of the rodent decline (i.e. late winter to spring), the environment is harsh with cold wet conditions and severely limited rodent food causing rodent mortality which can exceed 90-95% of all individuals (Innes 1990). Stoats may be able to crop only a relatively small proportion of the rat population, even if feeding almost exclusively on rodents, so that the observed prey population crash in areas with and without predators present may not be significantly different.

It is also possible that the sampling methods were not sensitive enough to detect small but real differences in predation rates. In this case, predators may hasten the decline in rodent populations, but the noise inherent in small mammal population censusing, as opposed to the noise inherent in small-mammal population dynamics, may make this difficult to observe. This problem could be partially overcome by the use of more intensive monitoring of rodent communities, such as mark-recapture techniques. Information on the diet of predators captured, and a subsequent estimation of any functional response could also assist in determining the impact of predators during the decline phase, and indeed, the entire rodent eruption.

It is therefore uncertain whether the effects of predators on prey populations during the crash phase, predicted in the literature and the by model, can be observed under field conditions in the food-driven New Zealand system.

6.4.6 Prediction 4: Predators are able to limit prey population size during the low phase.

Several studies have shown that predators can limit population size during the low phase of a population cycle or eruption (Newsome *et al.* 1989; Sinclair *et al.* 1990;

Meserve *et al.* 1993; Reid *et al.* 1995). Newsome *et al.*'s (1989) study was similar to this one in that the predator-prey-habitat association was also human-derived, yet exhibited similar, bottom up control.

The ERRPTS population dynamics model predicts that predators can limit low-density prey populations following the post-eruption crash (Chapter 5). The model predicts a small but significant effect of predator limitation during the low phase, that will reduce in intensity as the low-phase progresses, and stoat numbers and predator:prey ratios drop.

Evidence of low-phase predator limitation of house mice and ship rats on the coast lines was found in this study. However, detailed vegetation surveys and estimates of food availability in the coastline habitats were not conducted. As a result, it is difficult to completely separate the roles of reduced predator limitation and possibly increased food availability or habitat suitability in producing higher rodent numbers on the treatment peninsula coastline.

However, house mice and ship rats have been shown to differ significantly in both their habitat requirements (Innes 1990; Murphy and Pickard 1990; King *et al.* 1996; Chapter 4) and dietary preferences and selection (Daniel 1973; Innes 1979; Innes 1990; Murphy and Pickard 1990; Chapter 3). Ship rats and house mice also rarely co-occur in the same habitat (King 1983; Murphy and Pickard 1990; King *et al.* 1996; Chapter 4). The treatment peninsula coastline has more grassed areas than the non-treatment peninsula (J. McLennan, pers comm.), a habitat which can support larger mouse populations (Murphy and Pickard 1990; King *et al.* 1996). Ship rats are not commonly found in grassland habitat (Innes 1990), so this cannot explain increased rat tracking rates on the treatment peninsula. Consequentially, increases in both mice and rats on the treatment coastline must either be due to changes in a range of habitat variables and food availability that did not occur on the non-treatment peninsula, or due to the removal of a common predator. The observation that mouse and rat numbers both increased on the treatment coastline is consistent with the prediction that predators can limit low-density prey populations.

The lack of response in rodents to predator removal in podocarp forest during the low-

phase may be the result of a high localised rat by-catch in predator traps in area T1 (Area T1 was adjacent to the 25 m spaced trap lines across the neck of the peninsula), or due to continuous re-invasion of the trapping area by stoats at this point, and consistently high predator:prey ratios in these areas. The rodent-monitoring areas also had a relatively small number of tracking tunnels running, so that variability in the tracking tunnel indexing method may mask the relatively small increase in rodent numbers predicted following predator removal.

The increase in rat numbers in the rodent-monitoring beech forest area (Treatment 2) with predators removed is significantly larger than that predicted by the ERRPTS population dynamics model. In the model, the only way to produce an increase in the post-crash prey population similar to the one observed in Treatment 2 was to raise the carrying capacity, through a simulated increase in food availability. Total predator removal with a post-crash carrying capacity will only produce a small increase in prey density. Therefore, the response in rats in Treatment 2 to predator removal, while influenced by predator reduction, must also be modulated by a concurrent increase in the carrying capacity.

Food availability, as assessed by pitfall trapping of invertebrates did not significantly differ between rodent-monitoring beech forest sites. Thus, the exact cause of the large increase in ship rats in Treatment 2 remains unclear, but highlights the importance of multiple factors in shaping prey population dynamics (Liddicker 1988: Sinclair *et al.* 1990).

6.4.7 The role of predation in New Zealand eruptive systems

The role of predation in determining small mammal population dynamics has been widely studied globally, but has received scant attention in New Zealand. Using knowledge of the biology and ecology of small mammalian predator and prey species present in New Zealand and elsewhere, four predictions were made regarding the role of predators in the food-driven eruptive population dynamics exhibited by house mice and ship rats in forest in New Zealand. It was shown that predators cannot prevent a rodent population eruption following a large energy input, and cannot truncate the

peak prey population size. However the evidence for decline and low phase predator limitation was equivocal. There were no significant indications that predators can hasten the rate of decline of crashing prey populations, although trends in the data were consistent with the prediction. There was evidence of low-phase predator limitation of mouse and rat populations from the coast lines, and from the rodent-monitoring beech forest areas, but not from the larger scale beech forest lines. Therefore, while prey population dynamics during the increase and peak phases of the population eruption appear to be largely driven by food availability, the role of predators in the decline and low phases of the rodent eruption in New Zealand forests should be investigated further.

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Appendix 6.1 Numbers of predators caught in Fenn traps on trap lines in tawa-podocarp and beech forest from May 1995 to March 1998. Transects 1, 11 and 12 were in tawa-podocarp forest across the neck of the trapping peninsula. Transects 3 and 31 were in beech forest at the distal end of the trapping peninsula. TN = Trap nights.

Line	Year	Rats	Stoats	Weasels	Ferrets	TN
Podocarp						
Transect 1	1995	36	6	0	1	8033.5
	1996	93	23	0	0	23209.5
	1997	31	5	0	0	20987
	1998	11	5	0	0	6025.5
	Total	171	39	0	1	58255.5
Transect 11	1995	27	1	0	0	1985.5
	1996	18	1	0	0	3900.5
	1997†	3	0	0	0	2787
	1998	-	-	-	-	-
	Total	48	2	0	0	8673
Transect 12	1995	-	-	-	-	-
	1996	-	-	-	-	-
	1997‡	18	7	0	0	28317
	1998	3	3	0	0	10329
	Total	21	10	0	0	38646
Podocarp	Total	240	51	0	1	105574.5
Beech						
Transect 3	1995	27	2	1	0	2561.5
	1996	22	3	0	0	6557
	1997	24	2	1	0	6596
	1998	1	0	0	0	1704.5
	Total	74	7	2	0	17419
Transect 31	1995	3	0	0	0	733.5
	1996	2	1	0	0	6827
	1997	3	4	0	0	1821.5
	1998	1	0	0	0	491.5
	Total	9	5	0	0	9873.5
Beech	Total	83	12	2	0	27292.5

† Transect 11 was removed in June 1997. ‡ Transect 12 was run from January 1997.

Appendix 6.2 House mouse and ship rat tracking rates in treatment rodent-monitoring areas. For each month the number of tunnels in each area that recorded footprints is given, along with the number of tunnel-nights run.

	Treatment 1			Treatment 2			Treatment 3		
Month	mice	rats	tunnels	mice	rats	tunnels	mice	rats	tunnels
Jan 1996	2	3	18	3	2	14			
Feb 1996	2	8	18	0	3	14			
Mar 1996	2	2	18	4	10	14			
Apr 1996	2	5	18	2	9	14			
May 1996	6	7	18	3	11	14			
Jun 1996	6	13	18	2	12	14			
Jul 1996	1	0	18	1	10	14			
Aug 1996	0	9	18	0	9	14			
Sep 1996	0	5	18	0	10	14	0	0	12
Oct 1996	0	2	18	0	6	14	0	0	12
Nov 1996	0	6	18	0	5	14	0	0	12
Dec 1996	0	7	18	0	7	14	0	1	12
Jan 1997	0	2	18	0	6	14	0	5	12
Feb 1997	0	1	18	0	5	14	0	2	12
Mar 1997	0	1	18	0	4	14	0	4	12
Apr 1997	0	1	18	0	4	14	0	2	12
May 1997	0	0	18	0	6	14	0	3	12
Jun 1997	0	3	18	0	7	14	0	5	12
Jul 1997	1	3	18	0	4	14	0	4	12
Aug 1997	0	1	18	0	7	14	0	3	12
Sept 1997	0	0	18	0	8	14	0	4	12
Oct 1997	0	3	18	0	9	14	0	5	12
Nov 1997	0	1	18	0	9	14	0	4	12
Dec 1997	0	3	18	0	11	14	0	3	12
Jan 1998	0	0	18	0	8	14	-	-	-
Feb 1998	0	3	18	0	8	14	-	-	-
Mar 1998	0	6	18	0	12	14	-	-	-

- Tunnels not run.

Appendix 6.3 House mouse and ship rat tracking rates in non-treatment rodent-monitoring areas. For each month the number of tunnels in each area that recorded footprints is given, along with the number of tunnel-nights run.

	Non-treatment 1			Non-treatment 2			Non-treatment 3		
Month	mice	rats	tunnels	mice	rats	tunnels	mice	rats	tunnels
Jan 1996	2	12	15	6	3	12			
Feb 1996	0	10	15	1	8	12			
Mar 1996	0	12	15	0	8	12			
Apr 1996	0	12	15	2	11	12	0	6	16
May 1996	0	12	15	0	9	12	0	3	16
Jun 1996	1	11	15	1	12	12	2	9	16
Jul 1996	0	13	15	1	7	12	0	9	16
Aug 1996	0	15	15	0	9	12	2	7	16
Sep 1996	0	14	15	0	2	12	0	4	16
Oct 1996	0	10	15	0	7	12	0	5	16
Nov 1996	0	5	15	0	3	12	0	4	16
Dec 1996	0	6	15	0	6	12	0	6	16
Jan 1997	0	5	15	0	6	12	0	1	16
Feb 1997	0	4	15	0	1	12	0	1	16
Mar 1997	0	5	15	0	0	12	0	3	16
Apr 1997	0	5	15	0	1	12	0	2	16
May 1997	0	2	15	0	3	12	0	0	16
Jun 1997	0	6	15	0	1	12	0	2	16
Jul 1997	0	4	15	0	0	12	0	2	16
Aug 1997	0	6	15	0	1	12	0	0	16
Sept 1997	0	8	15	0	0	12	0	0	16
Oct 1997	0	5	15	0	2	12	0	1	16
Nov 1997	0	5	15	0	2	12	0	0	16
Dec 1997	0	5	15	0	2	12	0	0	16
Jan 1998	0	1	15	0	0	12	0	0	16
Feb 1998	0	4	15	0	1	12	0	0	16
Mar 1998	0	5	15	0	1	12	0	1	16

- Tunnels not run.

Chapter 7: General Discussion

Numerous mechanisms and processes have been suggested as important in shaping the population dynamics and ecology of small mammals (Batzli 1992; Krebs 1996) but recent work has focused on the roles of food and predation, and the interactions between the two (Newsome *et al.* 1989; Korpimäki *et al.* 1991). Such an approach, that considers the influence of, and interactions between, a number of potential regulating factors (Sinclair 1986; Lidicker 1988), is crucial in understanding small-mammal population dynamics under field conditions (May 1999). However, most studies reported in the literature have investigated complex predator/prey systems (Erlinge *et al.* 1983; Sinclair 1986; Boutin *et al.* 1995) where many factors and interactions cannot be controlled. Thus, the conclusions have often been equivocal.

Introduced small-mammal communities in New Zealand forests exhibit eruptive population dynamics driven by periodic energy inputs (King 1983, Murphy 1992; King and Moller 1997), and present an ideal situation in which to test the relative roles of food and predation in small-mammal population regulation. Only two prey species are present in the majority of areas, and only one predator (the stoat) is at all common. Thus, predator/prey associations can be studied without the confounding effects of a large secondary prey base, or interactions between sympatric predators. The predator/prey association is also human derived, with a unique combination of predator and prey species, and so allows us to test current theories in population ecology in a novel species-assemblage experiment.

Although the New Zealand predator/prey system is ideal for testing theories regarding population regulation, to date, very little work has been conducted within this framework.

Here, I used a large-scale predation reduction experiment to investigate the potential roles of food and predator limitation in prey population dynamics, and compared the demographics and ecology of prey populations in areas with and without predators present over a food-driven population eruption.

Footprint tracking tunnels are the most commonly used density index in research and management situations in New Zealand (King and Edgar 1977; Brown *et al.* 1996). Before using this index to investigate changes in population dynamics, I tested the reliability and repeatability of tracking tunnels against two kill-trap indices (rodent snap traps, and predator Fenn traps), under two experimental protocols. Tracking tunnels were more accurate when run using a grid system than a trap-line, and their accuracy improved as the sample size increased. Tracking tunnel indices were more tightly correlated with snap trap indices when run on the intensive trapping grid than on a trapping line, and were more closely correlated with the Fenn trap indices when run in a habitat with higher rat densities, than in a lower density rat population. I showed that tracking tunnels provide a simple to use reliable index that can be used to examine changes in relative population density and behaviour in prey populations.

Increases in food availability are closely followed by increases in the species consuming the resource. Although evidence for this relationship is often correlational (King 1983; Fitzgerald *et al.* 1996), it is generally accepted that eruptive systems are driven by variation in food supply (Jensen 1982; Newsome *et al.* 1989). For food to be the primary factor driving an eruptive system, the diet of the species must either consist largely of the temporally abundant food source (Jensen 1982), or must show broad dietary preferences and an ability to alternate feeding behaviour between temporally or spatially abundant food (Clark 1980, 1982).

In this study, a low-phase population of ship rats ate a wide range of foods throughout the year (Chapter 3). Invertebrates were the most common items in the diet, and analysis of trends in invertebrate population dynamics showed that species that were frequently consumed by ship rats in the study were significantly more abundant in the summer of peak rodent densities than in the post-eruption years. It is not clear if the increase in rat numbers during the eruption was driven by increases in palatable invertebrates or by the vast quantities of *Nothofagus* seed available on the ground following the mast seeding (King and Moller 1997). However, the catholic tastes exhibited by ship rats in the study are an important factor in the species' ability to respond rapidly to large, irregular increases in food availability. No stomachs from house mice were analysed during the study, but like ship rats, increases in house mice during an eruption may also be influenced as much by increases in invertebrates, as by

the availability of beech seeds (Fitzgerald *et al.* 1996). Thus, as with other studies of eruptive systems (Newsome 1970; Newsome *et al.* 1989; Pech *et al.* 1992), small-mammal population eruptions in New Zealand are triggered by large increases in food availability.

The ability of a species to respond to temporal and spatial variation in food availability (Braithwaite and Gullan 1978; Moro 1991) should be reflected in observed habitat use (Chapter 4). Theory predicts that habitat specialist and habitat generalist species should respond to distribution determinants in different ways (Rosenzweig 1981; Seamon and Adler 1996). In areas with no predator-reduction in the current study, ship rats showed broad-scale habitat preferences for tawa-podocarp forest, which was shown to have significantly higher levels of both rat-palatable invertebrates, and fruiting-tree species, than beech forest. The increase in rat density in the mast year was associated with increases in rat-palatable foods. The removal of predators corresponded with large increases in rats in the treatment beech forest area, which may have been due to a combination of reduced predation and increased food availability.

House mice were closely associated with a greater number of microhabitat variables than ship rats. During the population eruption, mice were common in most habitats in the study area, and were associated with both micro- and macro-habitat variables. In comparison, in the low-density years during the study, mice were generally scarce in all areas, and were too few to allow quantification of habitat preferences. The habitat appears to be largely unsuitable for mice in most years, either through food shortage, or competition or predation from ship rats, but becomes temporally suitable following the large energy input (from seed fall and invertebrates) during a beech masting.

I classified house mice and ship rats as habitat generalists that will persist in any habitat that provides sufficient resources (primarily food). These habitat preferences, like their diet, are flexible, and can change as different areas become suitable, and allow the large, rapid increases in population size during an eruption. Therefore, the suitability of a particular habitat for house mice and ship rats is determined largely by the amount of food available, but can potentially be modified by the presence of competitors or predators.

Following the increased rodent densities during an eruption, populations of predators also increase (King 1982, 1983; Newsome 1990). Elsewhere, these large increases have lead several authors to suggest that predation may be important in shaping the population dynamics of prey species during an eruption. The predator pit model (Sinclair *et al.* 1990; Pech *et al.* 1992) proposes that there is a threshold prey density below which predators can regulate population size, but once prey erupt, predation cannot regulate the population. Similarly, the concept of environmentally modulated predation (Newsome *et al.* 1989) also predicts that predators cannot prevent a prey eruption, but can affect the timing and extent of the crash phase. Previously, eruptive small-mammal systems in New Zealand have not been considered within such a framework. King (1983) suggested that predators might hasten the crash in prey populations following an eruption, but did not test this hypothesis.

As a first step in examining the effects of predation in New Zealand eruptive systems, a computer simulation model of the population dynamics of house mice, ship rats and stoats was constructed (Eruptive Rodent Predator Theoretical Simulation, ERRPTS; Chapter 5). The model output predicted that predators should produce minor limitation during the pre-eruptive phase, but that predator limitation should not prevent an eruption, or limit the peak population size. This inability is primarily due to differences in reproductive biology, rather than time-lags in breeding. The output of the ERRPTS model for New Zealand situations predicts that there is no threshold prey density below which predators can regulate prey populations. This is due to low stoat density in non-eruption years, and differences in breeding rates between predators and prey. The predator pit model relies on a significant year-round predator presence and a large alternative prey base, something that does not occur in New Zealand systems.

Recent studies of cyclic small-mammal communities in the northern hemisphere have shown that predation may be sufficient to trigger the decline in peak-prey populations (Henttonen *et al.* 1987; Reid *et al.* 1995; Korpimäki and Norrdahl 1998), in these systems. In eruptive systems in New Zealand, the ERRPTS simulation model predicts that food limitation rather than predation triggers decline, but that predation should be able to drive prey populations down more quickly, and to a lower density than food limitation would allow. The strength of this effect will depend on the severity of

natural mortality over the crash and low phases, and may not be detectable under field conditions. Therefore, the ERRPTS model highlighted the overall importance of food in driving the eruptive system, but suggests key periods where predation may be important in shaping prey population dynamics.

The predictions of the ERRPTS model were tested under field conditions, using large-scale predator reduction to examine the importance of predator reduction throughout a prey population eruption (Chapter 6). As predicted by the ERRPTS model, populations of house mice and ship rats erupted in all study areas with or without predators reduction, although mice increased more slowly in coastline habitat with predators present, suggesting that predators may be able to slow the increase in prey populations. Peak population sizes did not differ in areas with and without predator reduction, so that predation may not be important during the increase phase of the eruption. Thus I conclude that the predator-pit model (Sinclair *et al.* 1990; Pech *et al.* 1992) does not apply in New Zealand systems. Food limitation rather than predation triggered the prey species decline in the study, although there was some evidence of predator limitation during the crash and low phases. In most areas this effect was small, as predicted by the ERRPTS model. The large increase in ship rat numbers in one of the treatment beech forest areas may have been due to reduced predation, and a concurrent increase in food availability. Therefore, both the ERRPTS computer simulation and the field data support the contention that food availability is the primary determinant of rodent population dynamics in this system, with predation important only at certain times, namely during the crash and low phases of the population eruption.

The predator pit model proposed for Australian systems relies on both a broad prey base and a diverse generalist predator population. Predators are able to regulate low-density prey populations through large functional responses to changes in prey density. In comparison, the eruptive system in New Zealand differs from that found elsewhere in having a small prey base and a single dominant predator, with a constrained numerical response. Thus predators in New Zealand systems cannot regulate low-density prey populations in a predator pit prior to an eruption, but can limit prey populations during the post-eruption low-phase.

7.1 Further work and directions

The current study serves two complementary functions. It illustrates the relative importance of food and predation in shaping rodent population dynamics in New Zealand forests and presents information on the mechanisms by which these factors may influence rodent demography and ecology. Additionally, the study highlights areas in our understanding of predator/prey systems in New Zealand where knowledge is lacking. Further work is required at both the intra- and inter-specific level if a fuller understanding of the factors driving and regulating small-mammal population dynamics is to be gained. This includes the investigation of:

1. Responses of rodent species to increased food availability during a population eruption. Studies have shown that house mouse and ship rat population dynamics are significantly correlated with changes in food availability (King 1983; Murphy 1992; King and Moller 1997). This response in mice may be due as much to changes in invertebrate abundance as to changes in seed availability (Fitzgerald *et al.* 1996) although the exact nature of these responses for both species is unknown. Specifically, it remains unclear if ship rats are responding to beech seed itself, or to increased invertebrate numbers during the eruption.

2. Ecology of rodents during the eruption. Information is required on the reproductive behaviour of mice and rats during a population eruption. This includes information on breeding and recruitment rates of rats in beech-mast years, and the effect of population density on the proportion of mice and rats breeding in the population.

3. Interactions between mice and rats. The nature of the relationship between mice and rats in New Zealand is unclear. The generally mutually exclusive distributions of mice and rats could be the result of competition, different habitat choice, or predation of mice by rats. The paucity of records listing mouse remains in rat stomachs suggests that predation by rats is not a major factor in shaping mouse spatial distribution. The relative importance of habitat selection and competition in shaping rodent habitat use could be examined through selective species removal

experiments in coastline areas at Lake Waikaremoana during low-density years. If mice move into the bush from the coastline following rat removal, this would suggest that competition from rats is more important than differential site selection in shaping mouse habitat use.

4. The role of predation. Information is also required to clarify the role of predators in the eruptive cycle. Specifically, shifts in the functional response of stoats following changes in rodent density require clarification. King (1983) suggested that stoats may switch their feeding from mice to birds during the crash phase, but the extent to which stoats switch between mice and rats is unknown.

7.2 Summary

In conclusion, the eruptive population dynamics of house mice and ship rats in forest ecosystems in New Zealand are driven primarily by spatial and temporal variation in food supply. Both rodent species show flexibility in feeding behaviour and habitat use that allows them to respond rapidly to changes in habitat suitability following irregular energy input into the system. Predation on these species by a single, common predator is not sufficient to regulate prey in a low-density predator pit. However, predation is potentially important during the food-limitation triggered crash and low phases of the population eruption. Predation can play a significant role in shaping the fine-scale responses of rodent populations, but the effect of predation will always be minor relative to the coarse-scale influence of variation in rodent food supply.

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Addendum to Chapter 5

2. Methods

2.1. Model overview

A three-species dynamic model consisting of house mouse, ship rat and stoat populations (termed ERRPTS, Eruptive rodent/predator theoretical simulation) was constructed using the STELLA II modelling package (High Performance Systems, Inc 1990) (Figure 5.1; Appendix 5.1, 5.2, 5.3). The STELLA II programming language uses an iconographic interface to facilitate construction of dynamic system structures (Costanza and Gottlieb 1998).

In order to keep the model as parsimonious and general as possible, a number of assumptions were made in the construction of the model. Each species was separated into juvenile and adult age classes, and the same basic model structure was used for mice and rats, with the insertion of appropriate parameters. It was assumed that immigration and emigration were negligible (or equal), and mortality functions were modified so that no species went extinct in the model over the course of the simulation. Predation by species other than stoats is known to be minimal in most forest habitats in New Zealand (King 1990a, b), and was assumed to be zero in the model. The model was run for 5 years in each simulation.

2.2. Parameters and model construction

Parameters for the model were gained from the literature on mice, rats, and stoats in New Zealand where available (Table 5.1), and generalized functions for density dependent reproduction or mortality were used from the literature if no specific information was available.

2.3. Mouse population

Both mice and rats were divided into juvenile and adult age classes. Numbers of juvenile mice present in the model were given by

JUVENILE_MICE(t) = JUVENILE_MICE(t - dt) + (Mouse_births - Mouse_recruitment - Mouse_juv_mort) * dt

(Equation 1)

where Mouse_juv_mort = juvenile mouse natural mortality.

Natural mortality of mice is high in all years, and is largely controlled by food availability (Fitzgerald 1978; Fitzgerald *et al.* 1981) and environmental conditions (Bronson 1979). The carrying capacity and the resulting level of mortality were set by an arbitrary function that allowed a six-fold variation in density between mast and non-mast years (King 1983; Murphy 1992). Mortality was set as a function of mouse numbers, with mortality ranging from 1.5% per month at low densities, to 97.5% per month at levels above the carrying capacity (Figure Add.1a).

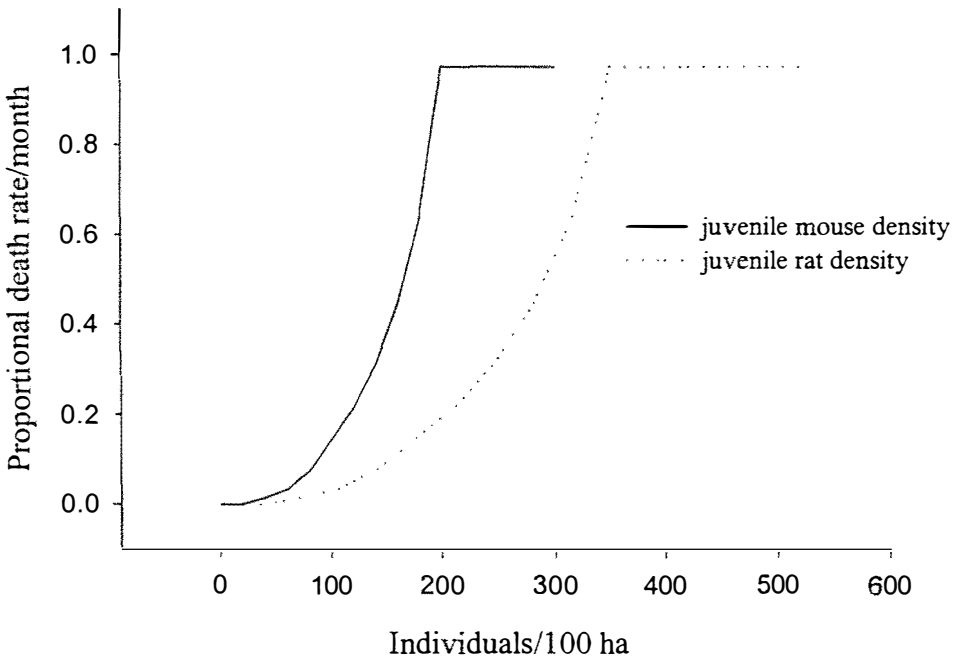
Mice were classified as juveniles for two months (Murphy and Pickard 1990), after which time they entered the adult population and could breed. The number of adult mice in the model was given by

ADULT_MICE(t) = ADULT_MICE(t - dt) + (Mouse_recruitment - Mouse_Death) * dt

(Equation 2)

Breeding rates varied depending on whether the year was a mast year or non-mast year. In a non-mast year, mice breed between September and March (Fitzgerald 1978), and produce an estimated 34.2 young/female over that period (average litter size 5.72, 6 litters/female). In a mast year, mice start breeding earlier (April-May), stop breeding in January or February (King 1982a), and produce an estimated 57.2 young/female over that period (average litter size 5.72, 10 litters/female; Murphy and Pickard, 1990). The breeding rate of mice ranges from 30% of females breeding in low-density populations, to 10% breeding in high-density populations (Fitzgerald 1978; King 1982a), so the proportion of mice breeding in the population was scaled to density.

a)



b)

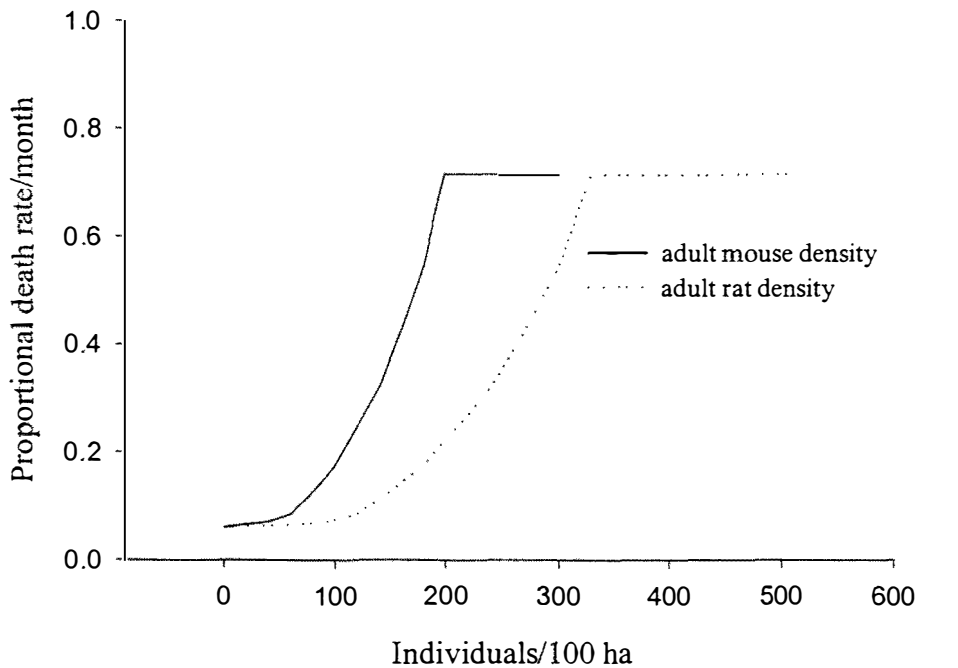


Figure Add.1 Natural mortality rates for a) juvenile mice and rats, and b) adult mice and rats, used in the STELLA ERRPTS model. The same general functions was used for mice and rats, although the densities over which the functions acted differed in the model between mice and rats.

Thus, mouse births were given by

Mouse_births = Mouse_breeding_season*(ADULT_MICE*
Mouse_reproduction)*Mouse_DD_Reproduction

(Equation 3)

where Mouse_reproduction = mouse reproductive rate, expressed as young per mouse, and Mouse_DD_Reproduction = the density dependent proportion of the mouse population breeding (Figure Add.2).

The numbers of mice recruited into the adult population were given by

Mouse_recruitment = JUVENILE_MICE - (JUVENILE_MICE*
mouse_juv_mortality)

(Equation 4)

Adult mouse mortality was a function of natural mortality and predation due to stoats, and was given by

Mouse_Death = Mouse_converter = (ADULT_MICE*
Mouse_mortality_function)+Mouse_reduction

(Equation 5)

where Mouse_mortality_function = density dependent adult mouse natural mortality scaled to the carrying capacity, with mortality ranging from 6% at low density, to 71.5% at densities above the carrying capacity (Figure Add.1b).

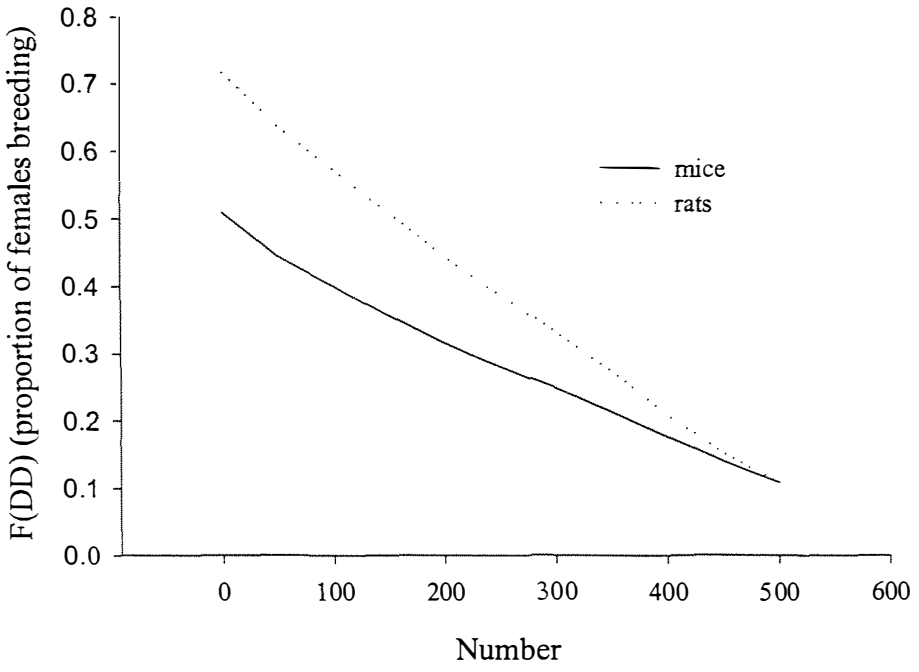


Figure Add.2 The proportion of female mice and rats breeding as a function of population size for that species. Parameters for high and low density breeding rates were estimated from published New Zealand studies (see sections *5.2.3*, *5.2.4*).

Mouse_reduction gives the numbers of mice removed by stoats. In Britain, stoats are known to eat c. 23% of their body weight per day for males, and c. 14% per day for females (Day 1968), although consumption rates in New Zealand are unknown. The average size of stoats in New Zealand is 324.4 g for males, and 207.2 g for females (King 1990). Daily food requirements equate to 75 g/food/day for male stoats, and 30 g/food/day for female stoats. Rats make up c. 30% of the diet of stoats in the study area, and mice c. 24% of the diet (King and Moody 1982a). Therefore, male stoats eat approximately 22.5 g rat/day, and female stoats eat approximately 9 g rat/day. Given an average meal size for stoats of 20 g per rat and 10 g per mouse (Day 1968), this gives an average consumption rate of 1.13 rats/stoat/day for males, and 0.45 rats/stoat/day for females, giving an overall average of 0.79 rats/stoat/day, or 23.6 rats/stoat/month. The

same calculation for mice, assuming an average meal size of 10 g, gives a consumption of 47.3 mice/stoat/month.

Mustelids are known to show functional shifts in feeding as preferred foods change in abundance (Tapper 1979; Hanski *et al.* 1991; Korpimaki *et al.* 1991; Murphy and Bradfield 1992). Therefore, stoat predation was set to switch between low and high rodent consumption rates over a threshold range of 350-450 rodents per stoat, which allowed maximal predation during a mast year. It was assumed that rats are twice as profitable as mice (Day 1968), and that mouse numbers greatly exceed rat numbers during an eruption (King 1983; Murphy and Pickard 1990; Murphy 1992). Therefore stoat predation switched entirely onto mice when the ratio of mice to rats was greater than 2:1. Thus, with mouse:rat ratios greater than 2:1, the number of mice was given by

Mouse_reduction = 2*(ADULT_STOATS*Rodents_per_stoat)

(Equation 6)

where Rodents_per_stoat is a function relating the number of rodents eaten by each stoat to the ratio of total rodents:adult stoats (Figure Add.3a). At mouse:rat ratios lower than 2:1, mice and rats were consumed in the ratio of 2 mice for every rat;

Mouse_reduction = Mouse_equivilents = {2* TOTAL_MICE*
(ADULT_STOATS* Rodents_per_stoat)}/ (2*TOTAL_RATS
+TOTAL_MICE)

(Equation 7)

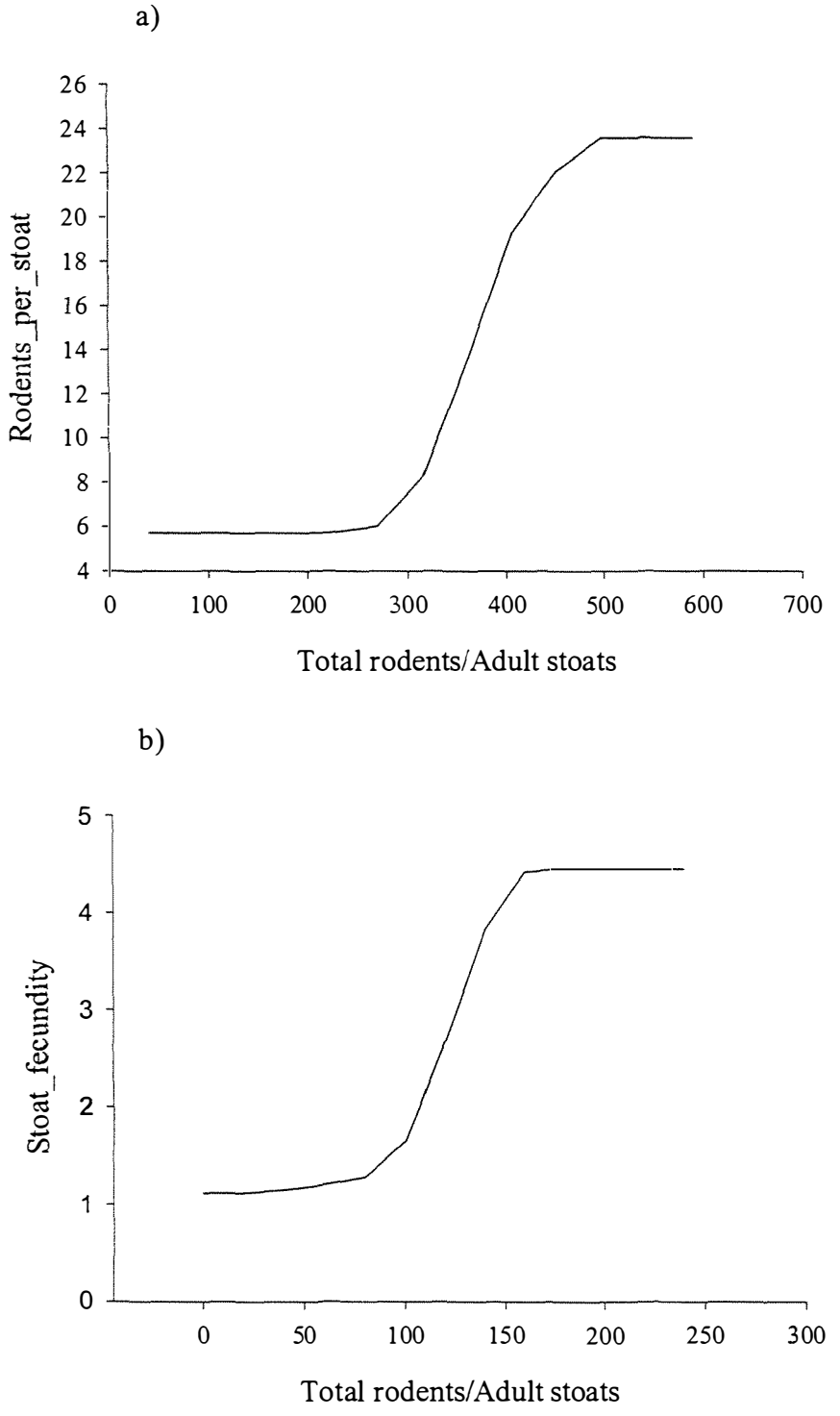


Figure Add.3 Functions used to model stoat population dynamics in STELLA ERRPTS model a) The number of rodents eaten per stoat as a function of the ratio of Total rodents to Adult stoats. b) Fecundity of stoats in the model as a function of the Total rodent:Adult stoat ratio. For sources of parameters see sections *5.2.5* and *5.2.6*.

2.4. Rat population

The rat population was structured in the same way as the mouse population (Appendix 5.2), although rats were classified as juveniles for three months (Innes 1990), at which time they entered the adult breeding population. Rat breeding was structured in the same way as for mice. The non-mast breeding season extended from September to March, with an estimated production of 11.1 young/female in that period (average litter size 5.6, 2 litters/female; Innes, 1990). The mast breeding season extended from June to March, with an estimated production of 28.1 young/female (litter size 5.6, 5 litters/female; Innes, 1990). The density dependent proportion of rats breeding ranged from 71.6% breeding at low density to 10.8% at high densities. This breeding proportion was required to generate population fluctuations similar to those seen in the field, given the rat breeding rates used in the model.

Natural mortality of juvenile and adult rats used the same functions as for mice (Appendix 5.2), but were scaled to allow a four-fold variation in the carrying capacity between mast and non-mast years.

Adult rat mortality was a function of natural mortality and stoat predation on rats, and was given by;

Rat_Death = Rat_converter = (ADULT_RATS*Rat_mortality_function) + PREY_SWITCH

(Equation 8)

where Rat_mortality_function = density dependent adult rat natural mortality (Figure Add.1b), and PREY_SWITCH = the number of rats eaten by stoats. As stated in **Equation 6**, if mouse:rat ratios were greater than 2:1, stoat predation switched entirely onto mice. Under these conditions;

PREY_SWITCH = 0

Under field conditions, rats do not become extinct over large areas, due to immigration and prey switching by predators, so a minimum number of 100 rats (1/ha) was set,

below which no stoat induced rat-mortality occurred. At rat densities higher than 1/ha, And with mouse:rat ratios lower than 2:1, The number of rats eaten was given by;

PREY_SWITCH = Rat_equivilents = {2* TOTAL_RATS*
(ADULT_STOATS* Rodents_per_stoat)}/ (TOTAL_MICE
+2*TOTAL_RATS)

(Equation 9)

2.5. Stoat population

Adult stoats present in the model were given by;

ADULT_STOATS(t) = ADULT_STOATS(t - dt) + (Recruitment - Stoat_deaths)
* dt

(Equation 10)

In comparison to the two rodent species, stoat breeding is initiated by day-length (King 1990), so that only one litter is produced in late September-early October (King 1982b; King and Moody 1982b; King 1983). On average, pregnant female stoats produce 8.8 embryos (King 1990). Both the birth and recruitment rates, however, are highly dependent on food availability, and can range from 0-2.6 young/female in a poor-food year, to 10-13 young/female in a mast year (King 1983). Therefore, numbers of juvenile stoats were given by;

JUVENILE_STOATS(t) = JUVENILE_STOATS(t - dt) + (Stoat_births -
Recruitment - Stoat_juvenile_mortality) * dt

(Equation 12)

The numbers of stoats born in each iteration was given by;

Stoat_births = Stoat_breeding_season*(Stoat_fecundity*ADULT_STOATS)

(Equation 13)

where Stoat_fecundity was a function that varied from 2.2 young per female in low food years to 8.8 young per female in high food years, and was mediated through the total rodent:adult stoat ratio (Figure Add.3b).

Juvenile mortality is closely correlated with food availability, with mortality of up to 90% recorded in non-mast years (King 1990). Thus, recruitment into the adult population was given by;

Recruitment = JUVENILE_STOATS - (JUVENILE_STOATS* Recruitment_rate)

(Equation 14)

where Recruitment_rate = density dependent juvenile mortality mediated by the ratio of total rodents:adult stoats (Figure Add.4a).

Adult stoat mortality was set at 0 at densities below 3 stoats/100 ha to prevent extinction of stoats in the model. At densities greater than 3/100 ha, adult stoat mortality was given by;

Stoat_death = ADULT_STOATS* Stoat_mortality

(Equation 15)

where Stoat_mortality = the proportional stoat death rate, mediated by the total rodent:adult stoat ratio (Figure Add.4b).

Variation in mast and non-mast year breeding rates of rodents (mean ± SD from published studies) was incorporated into the model to add a measure of stochasticity into the model, but the model still remained primarily deterministic.

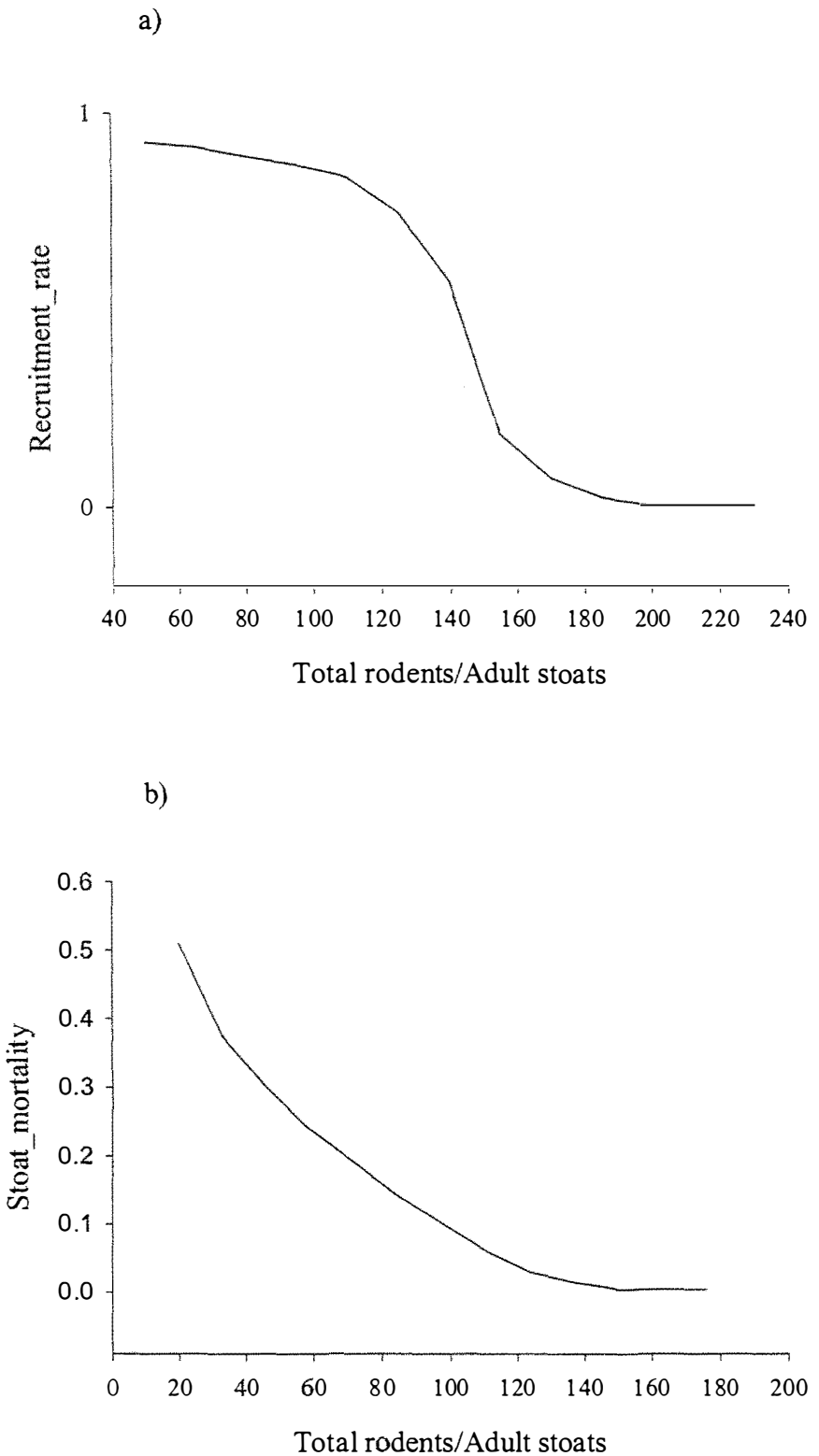


Figure Add.4 Functions used to model stoat population dynamics in STELLA ERRPTS model a) juvenile stoat mortality as a function of the Total rodent:Adult stoat ratio, and b) Adult mortality as a function of the Total rodent:Adult stoat ratio. For sources of parameters see section *5.2.5*.

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