Distribution of small mammals in five New Zealand forest habitats

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Abstract

This project aimed to reanalyse two large historical data sets from two different locations in New Zealand (Fiordland in the South Island and Pureora Forest Park in the North Island). The data describe populations of mice (*Mus musculus*), rats (*Rattus rattus* and *R. norvegicus*), and stoats (*Mustela erminea*) collected using standard monitoring techniques from five distinct types of forest habitat. The new analysis methods selected were an index of patchiness and Site Occupancy analysis.

The objectives of the analysis were (1) to evaluate whether the patchiness index and Site Occupancy analysis methods might contribute to improved protocols for monitoring small mammal populations in the future, and (2) to use formal tests of five hypotheses to evaluate two of the assumptions made by the conventional density index often used in small mammal studies.

I describe the results of the analyses for each species, including any problems encountered (such as the inability of the Site Occupancy method to analyse very sparse data sets). I also describe the results pooled from each of the two study locations and potential consequences for small mammal monitoring and control.

This analysis has suggested that in most cases the density index is not a rigorous measure of small mammal populations. However, both the index of patchiness and Site Occupancy analysis provided useful, new information about these populations of rodents and stoats, despite the fact that these historical data sets were not designed for use with modern methods of analysis.

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General

Many of the terms used in this thesis may have ambiguous meanings, or special meanings easily confused with common usage. For example, MacKenzie *et al.* (2002) defined a ‘season’ as a survey period, but I have used the word ‘session’ for this, retaining ‘season’ in its normal sense as a calendar season (spring, summer etc). The purpose of this glossary is to disambiguate and provide a reference for the meanings of the disparate terms and symbols used in this thesis.

Term	Meaning
Beechmast cycle	The sequence of events following a heavy seed fall (mast) of southern beech (*Nothofagus* spp.). See decline phase and seedfall phase.
Catchability	The willingness of an animal to enter a trap. May vary with age, gender and experience of traps. Also called trappability. This is *not* detectability (q.v.).
Colonisation	The likelihood that a previously unoccupied station will become occupied.
Covariates	Habitat features of a given station (for example, canopy height or distance to a road) which may or may not affect population parameters such as detectability. Sampling covariates (such as observer) were not used in this study.
Decline (phase)	The period following the peak population of mice or stoats after a beech seedfall. Usually beginning in late summer or early autumn 6-9 months after the seed falls in March-June. Mouse populations may return to normal seasonal fluctuations the following year, but stoat populations may take two years to recover. Also called the crash year.

Term	Meaning
Density index	A measure of captures per unit effort such as captures per hundred trap nights (C/100 TN). More accurately called an abundance index.
Detectability	The ability to detect an animal given that one is there. Comprised of the sum of two components: abundance of animals in the local area, and their catchability.
Detection probability	The probability of detecting a species if at least one member of it is present.
Equal detectability	The assumption that all animals are equally detectable at all times, regardless of individual, environmental or seasonal factors. One of the assumptions of the density index.
Even distribution	The assumption that all animals are evenly dispersed throughout an area at all times, regardless of environmental or seasonal factors. One of the assumptions of the density index.
Fiordland National Park	A rugged area in south west New Zealand. Data were available from two sampling areas in this region: the Eglinton Valley and the Hollyford Valley.
Index	A measurement used as a surrogate for a (difficult to measure) population parameter. Usually a count statistic.
Index of patchiness	A measure of aggregation in one dimension (Brown *et al.* 2004).
Kiore	*Rattus exulans* or Polynesian rat. Brought to New Zealand by the Maori, now found only in isolated parts of Fiordland and on offshore islands.
Local extinction	Where a previously occupied station becomes unoccupied.
Location	Wider sampling area: either Pureora or Fiordland.

Term	Meaning
Mice	*Mus musculus*. The smallest of the four rodent species found in New Zealand. Found throughout the country in all types of habitat.
Multi-season	A type of Site Occupancy model where occupancy of stations changes between sessions via colonisation and local extinction.
Non significantly patchy	A patchiness (I) value either less than one, or greater than one with a p value >0.05.
Normal (year)	A year that has no beech flowering, mast seedfall, or population disturbance as a result of mast seedfall.
Norway rat	*Rattus norvegicus*. The largest of the three rats found in New Zealand, usually found near water or in commensal habitats.
Occupancy	The proportion of trap stations occupied by the species of interest.
Original studies	Fiordland: King (1980, 1982, 1983) and King and Moller (1997) Pureora: King *et al.* (1996a, 1996b, 1996c) and Innes *et al.* (2001).
Patchiness	Non-random under-dispersion of animals along a transect trap line.
Probability of colonisation	The probability that at least one member of a species will move into the area of a previously unoccupied station.
Probability of local extinction	The probability that the species will become locally extinct from a previously occupied station.
Probability of occupancy	The probability that the station (and hence some unmeasureable local area) is occupied.
Pureora Forest Park	A state-owned forest west of Lake Taupo where native timber was logged and native forest converted to exotic plantations until the late 1970s. Now an important recreational area.

Term	Meaning
Road	All but one of the roads mentioned were simple gravel tracks. The exception was State Highway 94 from Te Anau to Milford, through the Eglinton Valley.
Sample	Data collected from one trap line during one trapping session.
Sample	Data collected from one trapping session.
Sampling period	The entire period over which sampling was carried out at a location (for example, at Pureora, this was five years).
Season	A calendar season such as summer or winter. For season with respect to Site Occupancy, see session, single-season or multi-season.
Seedfall (phase)	The period of time from the onset of heavy beech flowering in spring until the population peak following a mast seedfall 15 months later.
Seedfall status	The stage of the beech mast cycle during which a given beech forest sample was collected. Categorised as either normal, seedfall or decline.
Session	One field session, during which traps were inspected daily. Usually 3 nights for rodents, 10-14 nights for stoats. This is the same period that MacKenzie *et al.* (2002) describe as a season.
Ship rat	*Rattus rattus*. The most common of the three rat species found in New Zealand forests.
Significantly patchy	A patchiness (I) value greater than one that also has a p value of less than 0.05.
Single-season	A type of Site Occupancy model where there is no colonisation or local extinction.
Site	See station.

Term	Meaning
Site Occupancy	A statistical technique developed by MacKenzie *et al.* (2002) which estimates the proportion of stations occupied by a species explicitly accounting for the fact that the target species may not be detected even when it is present.
Station	A trap site, either one or two traps under a single tunnel.
Trap line	A continuous line of trap stations set in one type of forest: homogenous beech, heterogeneous beech, logged native podocarp-hardwood, unlogged native podocarp-hardwood or pine forest.
Trap night	One night of sampling across all habitats
Trap-out	Where all or most of the animals living in the local area are removed during the first part of the sampling session (defined as being the first six nights)

Patchiness symbols

Symbol	Meaning
I	Computed patchiness index value
P	Percentage of randomised distances greater than the observed distance

Site Occupancy symbols

Symbol	Meaning
Variable	
ψ	Probability of occupancy
γ	Probability of colonisation
ε	Probability of local extinction
p	Probability of detection
Covariates (Pureora only)	
.	Constant
t	Time
alt	Altitude
asp	Aspect
drain	Drainage
phys	Physiography
sl	Slope
CC	Canopy cover
D	Canopy density
DE	Distance to small mammal escape cover
DR	Distance to a road
GL	Forest litter cover
GV	Vascular ground cover
H	Canopy height
Tds	Trend down over a trapping session
TO	Trap out effect

Examples of symbol use:

Symbol	Meaning
p(DR)	Variation in detection probability with distance to a road
p(TO*Tds)	A decrease in detection probability during a trap out effect

Symbol	Meaning
Other	
*	Adjacent covariates have a multiplying effect
+	Adjacent covariates have an additive effect
-2logL	-2 multiplied by the log of the likelihood (*L*) value
DI	Density index
eq	Equilibrium
i	Initial sampling session (occupancy only)
L	Likelihood value
psi	ψ - probability of occupancy
w	ΔAIC weight

Trap line labels

	Pureora	Fiordland (**S**outh Island)
Rodent traps	PRE (exotic forest) PRL2 (logged native forest) PRU (unlogged native forest)	SRE (Eglinton Valley) SRH (Hollyford Valley)
Fenn traps	PFE (exotic forest) PFL (logged native forest) PFU (unlogged native forest)	SFE (Eglinton Valley) SFH (Hollyford Valley)

Chapter One:

Introduction

1.1. Overview

In this chapter I give a brief background to the study of rodents (*Rattus rattus, R. norvegicus* and *Mus musculus*) and stoats (*Mustela erminea*) in New Zealand including the history of their arrival and establishment. In addition, I describe methods used for control and monitoring of these species and some of the associated problems, such as rapid population recovery, and the shortcomings of available methods for analysing the monitoring data.

New statistical techniques offer the potential to resolve or mitigate some these problems. I describe two recently developed techniques which may be suitable and their advantages over conventional indexing methods used for the last 35 years.

In order to determine the full potential of these new methods and evaluate the problems with the old methods it is necessary to apply them to a large data set collected under consistent field routines over many years. I have applied these methods to two large existing data sets (King 1982, 1983, King *et al.* 1996a, 1996b, Innes *et al.* 2001). I describe these datasets and the conventional density index that was used to analyse the data when they were originally published. I discuss the limitations of the old and new analysis methods, and potential problems with them. I also summarise my hypotheses, aims and expected outcomes.

1.2. Literature review

1.2.1. Rodents and stoats in New Zealand

1.2.1.1. History of colonisation

New Zealand has been colonised by four species of rodents and three mustelids. The kiore (*Rattus exulans*) came with Polynesian settlers in the 13th century AD (Anderson 2000, Wilmhurst and Higham 2004); the other rodent species were unintentionally introduced by Europeans in the 18th and 19th centuries (Atkinson 1973, Guthrie-Smith 1999, Ruscoe and Murphy 2005). The mustelid species, however were introduced deliberately in the late 19th century in an effort to control rabbits (*Oryctolagus cuniculus cuniculus*) (Thomson 1922).

Although Holdaway (1996, 1999) suggested that kiore first arrived and established more than 1000 years before permanent Polynesian settlement (around 50-150 AD (Holdaway 1999)), this scenario now seems unlikely. Other sources suggest that the dating of rat bones is unreliable (Anderson 2000, Higham and Petchey 2000) and that Polynesian and kiore settlement were close to simultaneous, at around 1250-1300 AD (Anderson 2000, Wilmhurst and Higham 2004).

Kiore were once prevalent (Watson 1956) on the three main islands as well as many offshore islands, but have declined due to competition from European species (Atkinson and Towns 2005) and Department of Conservation eradication programmes (Towns and Broome 2003). Remnant populations survived in the North Island until the 1850s (Atkinson 1973), and some still remain in Fiordland as well as on a dwindling number of islands (Atkinson and Towns 2005).

Norway rats (*R. norvegicus*) were the first of the European species to become established. They were known to be present before the end of the 18th century and were common throughout the northern North Island by the 1830s and on both islands by the mid 1850s (Innes 2005b).

Mice (*Mus musculus*, Figure 1.1) were common in the Bay of Islands by 1830 (Guthrie-Smith 1999) and in South Island by the mid 1850s (Gillies 1877).

Ship rats (*R. rattus*, Figure 1.2) did not establish in natural habitats in New Zealand until after 1870s in the North Island and 1890s in the South Island (Atkinson 1973). The ship rat and house mouse are the dominant species in natural habitats at the present time (Innes 2005a, Ruscoe and Murphy 2005).

Stoats (*Mustela erminea*, Figure 1.3) were first introduced in 1885 (Thomson 1922) to control rabbit populations and many subsequent introductions were made, initially protected by law (Thomson 1922), despite vehement objections from ornithologists (Martin 1884, Reischek 1885, Buller 1894). Eventually, in 1903 the government removed legal protection for mustelids, though they were still protected in rabbit infested areas (Thomson 1922). Stoats are now common in all types of native forest (King and Murphy 2005).

Two other species of mustelid were introduced simultaneously with the stoat: the weasel (*M. nivalis*) and the ferret (*M. furo*) (Thomson 1922). While both of these species have established wild populations, they are distributed unevenly throughout the country and often at lower density than comparable populations of stoats (King *et al.* 1996a, Clapperton and Byrom 2005, King 2005). The data sets used in this analysis contain few records of either weasels or ferrets, so they have not been considered in this project.

1.2.1.2. Why are small mammals a problem?

Rodents and mustelids represent serious ecological threats to native flora and fauna, either directly or indirectly, especially to native birds. Stoats and all three rat species are implicated, individually or in groups, in the extinction, decline, or breeding failure of a variety of species. These include invertebrates such as landsnails (Brook 2000) and weta (Ramsay 1978), and herpetofauna such as Whitaker's skink (Towns 1994), bats (Pryde *et al.* 2005b), and native birds such as the kaka (Wilson *et al.* 1998, Dilks *et al.* 2003), kakapo (Clout 2006), kiwi (McLennan *et al.* 1996), kokako (Clout and Hay 1981, Innes and Hay 1995), mohua (Elliot and Rasch 1995, O'Donnell *et al.* 1996, Dilks *et al.* 2003), saddleback (Lovegrove 1996) and North Island tomtit (Knegtmans and Powlesland 1999). There is also evidence that seedling establishment and ecosystem structure may be affected by rats (Campbell and Atkinson 2002, Towns *et al.* 2006).

Mice are known to eat arthropods (Fitzgerald *et al.* 1996) and support populations of larger predators. Among the best known examples of this are the population irruptions of mice that follow a heavy beech mast and support a much larger than usual cohort of stoats the following summer (King 1983, O'Donnell *et al.* 1996, Wilson *et al.* 1998, Dilks *et al.* 2003).

1.2.1.3. Small mammals in beech forests

Southern beech trees (*Nothofagus* spp.), like northern beech (*Fagus* spp.), are mast seeders. That is, in most years they produce very little seed. However, in some years, all beech trees in an area simultaneously produce very large volumes of seed. This is called a mast event (Wardle 1984).

As described in section 1.1.1.2, rats and stoats are known to be serious predators of native birds. During a mast seedfall event, mouse populations are able to breed over winter on the additional food supplied by beech seeds and by the following summer the population can become very large (King 1982). The mice, in turn provide an increased food supply for stoats resulting in a much larger than normal cohort of young stoats the following summer (King and McMillan 1982). Given that stoats eat proportionally the same number of birds each, regardless of the number of mice available, a larger stoat population results in increased predation of birds (King 1983).

Meeson (1884) described a plague of rats (probably kiore) in beech forest, but King and Moller (1997) found very few rats in Fiordland beech forest in the 1970s. However, in 1999/2000, 2000/01 and this summer (2006/07) ship rats have reached very high densities following the most recent beech mast event (Dilks *et al.* 2003, Department of Conservation 2006, NZPA 2006). Rats are known to have negative impacts on the breeding of native birds (see section 1.2.1.2) and bats (Pryde *et al.* 2005b) in the Eglinton Valley (Dilks *et al.* 2003, Pryde *et al.* 2005a), but very little information on their response to beech seedfall has been available until recently.

1.2.2. Control of small mammals in New Zealand

The small mammals most often targeted for control on the two main islands of New Zealand are ship rats and stoats, as both species are sufficiently widespread and predatory to pose serious risks to native birds (O'Donnell *et al.* 1996, Wilson *et al.* 1998, Towns and Broome 2003).

Ship rats are the most widespread of the three rat species and have been targeted by widespread poisoning on the two main islands either directly or indirectly as by-kill from possum (*Trichosurus vulpecula*) operations with anticoagulant poisons or 1080 (Innes 2005a). Success has been achieved in forest areas greater than 3000 ha using a combination of aerial and ground based poisoning (Innes *et al.* 1995). Because the ship rat can reach large numbers rapidly, annual control is an expensive necessity where immigration cannot be excluded (Innes 2005a). Ship rats have also been successfully eradicated from several offshore islands (Towns and Broome 2003)

Primary poisoning of stoats is not currently used as a method of control (King and Murphy 2005), though poisons targeted specifically at stoats are under development (O'Connor 2002). Secondary poisoning from 1080 or brodifacoum does assist in the control of stoat populations (Alterio 1996, Murphy *et al.* 1999). Trapping has been used for many years to control stoats, and until recently the main trap used was the Fenn trap (King and Murphy 2005). Recently new traps have been developed to meet new ethical guidelines (Murphy and Fechney 2003). Care must be taken in controlling stoats because if rats are present and not controlled concurrently, it is possible that meso-predator release (Murphy and Bradfield 1992, Courchamp *et al.* 1999) may lead to increased numbers of rats, and increased damage to the conservation resource that the operation was designed to protect.

Kiore are unable to compete with the larger ship rat and so are found in only a few locations on mainland New Zealand (Atkinson and Towns 2005). They were once common on offshore islands, but have been eradicated from many of them, including Kapiti Island (Empson and Miskelly 1999), using anticoagulant poison baits. This process has occasionally been complicated by the fact that some Maori tribes regard kiore as *taonga* (cultural treasures) (Atkinson and Towns 2005).

Norway rats are more commonly found in commensal habitats than natural ones and their distribution is very patchy (Innes 2005b). However, they have been eradicated from a number of offshore islands, the largest of which was 11300 ha Campbell Island (Towns and Broome 2003). Norway rats are seldom specifically targeted for control on the mainland because they are not often a conservation threat (Innes 2005b).

Mice do not often represent a direct threat to wildlife and are usually only by-kill in 1080 operations against possums or ship rats (Miller and Miller 1995). However, mice were specifically targeted in a successful eradication operation to protect the Cook Strait giant weta (*Deinacrida rugosa*), McGregor's skink (*Cyclodina macgregori*) and the goldstripe gecko (*Hoplodactylus chrysosireticus*) on Mana Island (Hook and Todd 1992).

Rodents are highly fecund, and under the right conditions can reach plague proportions in short periods of time (Miller and Miller 1995). After a control operation, rodent populations may recover within a few months (Miller and Miller 1995). Thus control operations must be carefully timed to provide greatest benefit to native wildlife.

1.3. Monitoring of small mammals in New Zealand

1.3.1. Analysis techniques

The conventional approach to the analysis of monitoring data so far has usually been to calculate an estimate of relative density or density index: captures per hundred trap nights (C/100 TN) for a whole line over a given sample period (usually 3-14 days) assuming that the distribution of animals and the probability of detection were equal over the whole line (Fitzgerald and Karl 1979, King 1980, 1982, 1983, Taylor and Tilley 1984, King *et al.* 1996a, King *et al.* 1996b, Choquenot and Ruscoe 2000, Innes *et al.* 2001). This was done despite the fact that the capture records showed both spatial and temporal variation in numbers of animals caught (Innes *et al.* 2001, Purdey *et al.* 2004). The assumptions of even distribution of captures and equal detectability of individuals have been repeatedly questioned (Tanaka 1960, Anderson 2001, King and White 2004), but have rarely been investigated or quantified, largely because, until recently, no techniques existed to test them.

1.3.2. Rodent sampling

The earliest established standardised rodent sampling technique used in New Zealand was set up by B.M. Fitzgerald and B.J. Karl in the Orongorongo Valley (Fitzgerald 1978, Fitzgerald and Karl 1979, Fitzgerald *et al.* 2004). Their study used a long transect line (116 trap sites) with stations at 50 m intervals. Traps were set for three nights every three months, in the last weeks of February, May, August and November. Each station had a pair of rodent kill traps (one rat trap, one mouse trap) set back to back in a tunnel and baited with peanut butter and rolled oats. This trap line was maintained for 27 years (Efford *et al.* 2006).

Other studies have used a similar arrangement but with only 36 traps per line. Traps were set for three consecutive nights every three months over a period of

approximately five years (King 1982, King *et al.* 1996b). The assumption was made that if the sampling technique was standardised, then any change in observed catch would relate directly to a change in the population.
Different measures of abundance such as the minimum number known to be alive (Krebs 1966, Ruscoe *et al.* 2004) have also been used (Ruscoe *et al.* 2001, Ruscoe *et al.* 2004) but the raw data were not available to me.

1.3.3. Stoat sampling

Long-term, consistent trapping for stoats is very laborious, and for practical reasons cannot always be maintained over the years without change. As a result, there is no standardised procedure for monitoring populations of stoats in New Zealand as there is for rodents. Estimates of absolute density have been made by live trapping capture-mark-recapture methods, predominantly using Edgar live traps (Alterio *et al.* 1999, Cuthbert and Sommer 2002, Smith and Jamieson 2005), but also Elliot live traps (Smith and Jamieson 2005) in various spatial arrangements: distributed through an area of interest (Cuthbert and Sommer 2002), at 150 m intervals on circular trap lines (Alterio *et al.* 1999), and on transect lines (Smith and Jamieson 2005). The resulting analyses have produced estimates of average home range size from 9.4 ha to 108 ha (Cuthbert and Sommer 2002, Smith and Jamieson 2005), and average densities of 2.5 to 4.2 stoats per km ^{2} (Alterio *et al.* 1999) and up to 10 stoats per km^2 in a particularly good year (King and Powell 2007).

Estimates of relative density or density indices have also been made for stoats either using transect line sampling (King 1983, King *et al.* 1996a) or simply traps dispersed through the area of interest (Taylor and Tilley 1984). This method has given values from <1 to 16 C/100 TN varying with season, habitat and prey availability (King 1980, 1983, Taylor and Tilley 1984, King *et al.* 1996a). While these indices are normally considered approximately reliable for stoats (Erlinge 1983), and are consistent with the changes in age structure that should follow real changes in density, some evidence suggests that the capture rate of stoats declines when mice are very abundant (King and White 2004).

The Department of Conservation (DOC) uses its own DOC 200/250 trap for stoats. However, the Fenn trap is still legal and is still the most commonly used trap for stoat control or removal sampling in New Zealand, outside of DOC (Purdey *et al.* 2004, Kelly *et al.* 2005, Smith *et al.* 2005, Christie *et al.* 2006) despite the fact that it is now considered inhumane (Warburton *et al.* 2002). Fenn traps can be set singly (King 1980, 1983, King *et al.* 1996a) or in pairs (Taylor and Tilley 1984).

1.3.4. Problems associated with small mammal monitoring at varying densities

Populations of small mammals are monitored for a variety of reasons, from the purely zoological investigation of a species and its ecology (Daniel 1972) to pest control (Dilks *et al.* 2003), for example, to determine if large scale eradication or control is needed and if the operation was successful. The use of traps for monitoring is dependant on the assumption that traps can effectively and representatively catch the target species whether it is at high or low density regardless of environmental conditions or habitat factors. The analysis of monitoring data is dependant on the assumption that the method is sensitive to changes which may be affecting the population structure or dynamics (see section 1.2.4).

For monitoring, capture rates up to 20 captures per hundred trap nights (C/100TN) are usually considered to be accurate (Tanaka 1960). King and White (2004) found in New Zealand *Nothofagus* forests that stoat capture rate increased with mouse capture rate until the mouse capture rate approximated 20-25 C/100TN, but after this point, stoat capture rate declined. Mouse capture rates greater than 60 C/100TN were associated with very low stoat capture rates. The explanation that King and White (2004) proposed to explain this discrepancy is that at very high mouse densities, natural prey are so easily caught that artificial baits are unattractive to stoats.

Even when the effects of carrying capacity (food availability, nesting sites etc) on maximum possible density are disregarded, trap saturation (with target or non target species) is still a potential problem. There is an upper limit to how many animals can be caught on each night of trapping: if every trap that can be reached by an animal is filled by one, it is not possible to detect any more animals even if they are present (Boulanger and Krebs 1996). All other considerations aside, once parts of the trap line become saturated, any index will stop being linearly related to actual population density.

At low population densities, a great deal of effort may be needed to catch a very small number of animals (King *et al.* 1996a), if any animals are caught at all. Traps may be placed in an area where the target species is present, but not detect any because the home ranges of individuals of the target species are so large that the probability of encountering and being caught in a trap within the few days allowed is very low.

The greatest problem however, is how to tell whether the data accurately represent the population. Has the capture rate been skewed by a plentiful food source or trap saturation, or is the species absent from the area? Is the dispersion of traps relative to the average home range size appropriate? Standard monitoring methods cannot overcome these problems, which relate to environmental and population variables which must be measured separately.

1.3.5. The problem with indices

Anderson (2001) suggests that there are two major problems with the methodology common in wildlife field studies, one of which is the use of index values. An index assumes that a given amount of effort will detect a given and approximately constant proportion of the population (Anderson 2001, Witmer 2005). This can be expressed mathematically:

$$i = pN$$

where i is the index, p the probability of detection and N is the actual population size.

Moreover, an index assumes that this detection probability is equal at any time, regardless of habitat, food availability, weather conditions or observer (Anderson 2001). In other words, an index assumes that an increase in trap-catch is always associated with an increased population, not with increased catchability. Engeman (2003) maintains that these factors may bias any wildlife study regardless of the use of indices.

Detection probability is much more likely to be variable than constant, and many new techniques explicitly account for this variation. Examples include Site Occupancy (MacKenzie *et al.* 2002), spatially explicit density estimation (Efford 2004) and the zero inflated binomial model (Tyre *et al.* 2003). Using one of these new techniques could mitigate the effect of bias introduced by variable detection probability.

Another problem with indices is that they assume that animals are evenly distributed throughout the habitat, or at the very least, that all traps are equally likely to catch an animal. However animals frequently are not evenly distributed (Brown *et al.* 2004) and each trap may have a different detection probability relative to a food source, escape cover, the centre of the nearest individual's home range or a number of other environmental factors. It is doubtful that any index would be accurate where these factors are significant.

These criticisms relate to indices of density or abundance. Density indices are a count statistic expressing numbers per unit of area or effort; abundance indices are often used where the estimation of the area sampled cannot be calculated. Both are usually considered (accurately or not) to be directly correlated with true density or abundance modified by the probability of detection.

Other types of indices are in use for specific purposes other than abundance or density, such as the index of patchiness (Brown *et al.* 2004). The patchiness index attempts to quantify mathematically the degree of aggregation along a line of observed captures (see section 1.4). While indices of this type also assume that the observed data are related in some way to the characteristics of the population of interest, they are more robust than abundance indices for three reasons. Firstly they do not use a count statistic. Secondly, they measure a relative attribute rather than an absolute one. Thirdly, they are comparing data points within the data set, rather than comparing the data set with the population parameter of interest, which is unknown.

1.3.6. Detectability

Detectability is influenced by two factors: the willingness of an animal to enter a trap (catchability) and the total number of animals available to be caught (population size). Catchability relates to other elements such as food availability and the surrounding terrain, and may vary from site to site and season to season. The effect of population size is more predictable – the larger a population the greater the probability of catching *one* individual, regardless of individual or local variation. Thus, detectability can be expected to vary with population size, but cannot be reliably separated from catchability.

1.4. Background to my approach

1.4.1. Aims

This project aims to reanalyse data collected by King (1982, 1983), King *et al.* (1996a, 1996b, 1996c) and Innes *et al.* (2001) in the 1970s and 80s in much more depth than was possible at the time. These data include information on the house mouse (*Mus musculus*) rats (*Rattus* sp.) and stoat (*Mustela erminea*). The project aims to apply to these data two new techniques, Site Occupancy analysis (MacKenzie *et al.* 2002) and an index of patchiness (Brown *et al.* 2004), which have been developed recently.

1.4.2. Objectives

1) To evaluate the assumptions made by the density index with respect to detectability and patchiness of small mammals.
2) To evaluate whether the patchiness index and Site Occupancy analysis methods might contribute to improved protocols for monitoring small mammal populations in the future.

1.4.3. Why use old data?

Meta-analysis is a useful tool where the results of two or more studies can be combined to answer a question using greater statistical power than is possible with each study individually (Everitt 2002, p. 242). The longer a particular field method has been used consistently, the greater the opportunity for a meta-analysis, especially if new techniques appear that might offer the chance to look at old data in new ways. Additionally, legacy data can provide a useful preliminary test of a new technique without incurring the time and expense of conducting a new field trial. Because this standard sampling technique has been in use in New Zealand for 35 years, these data offer a significant opportunity to test the use of Site Occupancy analysis (MacKenzie *et al.* 2002) and the index of patchiness (Brown *et al.* 2004) on these types of data.

The datasets I used for this purpose have one main advantage: they comprise a long series of systematic small mammal monitoring data, collected over a total of ten years in two different sample areas in five habitat types. Moreover, these collections have been the basis of a detailed body of published knowledge about the species against which the new conclusions may be tested. Only in one study area, the Orongorongo Valley (Choquenot and Ruscoe 2000, Efford *et al.* 2006), have rats and mice (but not stoats) been monitored by the same methods and for longer. These advantages balance (to some extent) the one obvious limitation to my approach: the data were not collected with the requirements of any new technique in mind.

The data used in this study are especially useful because they contain one particularly good example of how indices may fail. In the spring and summer of 1983-84 in the young exotic plantation in Pureora Forest Park (Figure 3.5), the mouse density index was around 15 C/100 TN in November, 5 C/100 TN in February, and over 40 C/100 TN in May (King *et al.* 1996b). Examination of the dissection data suggests that the population could not have added so many extra members by reproduction in the three months between February and May. There are two possible explanations for this discrepancy; either that the February 1984 count was too low due to an undetected decrease in the probability of detection, or there was a large immigration event.

King *et al.* (1996b), suggested that the very high population peak could have been due to an unusually large flush of insects that enhanced reproductive success in the late summer and autumn of 1984 (mice eat many invertebrates (Miller and Webb 2001) but their food supplies were not measured during this study). If true, this could also explain the low catch rate in February, as the trap baits could have been a relatively unattractive source of food in comparison to live insects.

There are no direct observations to test the insect hypothesis, and no information on either catchability or detectability, thus, it is impossible to gauge the accuracy of this suggestion in retrospect. It is problems of this nature which are driving the shift towards more complex models which are able to include estimates of variation in detectability.

The two major assumptions of the density index are even distribution and equal detectability. I wanted to test both of these assumptions as well as I could with the existing data. The patchiness index (Brown *et al.* 2004) is the only method of which I am aware that tests *one dimensional* distribution. Site occupancy is the most widely used of the recently developed methods which estimate detectability. It is also the only method which permits the use of kill trap data (D.I. MacKenzie pers. comm.). Another option would have been maximum likelihood analysis using catch effort models. I chose the Site Occupancy method over the maximum likelihood method because it provided more information about the system.

1.5. Development of hypotheses

I developed a number of hypotheses to test the two main assumptions of the density index: even distribution and equal detectability.

The first two hypotheses are that these assumptions are absolutely correct; that there is no change in detectability and no change in distribution through a session. The first hypothesis would test for decrease in detectability with the removal of samples, as well as for changes in detectability over the long term – does a trap station always sample the same proportion of the local population? The second hypothesis would test for patchiness in each habitat type to see if any were significantly patchy and if so whether all were patchy to the same extent. For example, the Hollyford Valley might be more patchy than the Eglinton Valley because it is a heterogeneous mix of silver beech (*Nothofagus menziesii*) and kamahi (*Weinmannia racemosa*) with some red beech (*N. fusca*) whereas the Eglinton Valley has an even canopy of red beech, at least along the rodent trap line (Johnson in King 1982).

The third and fourth hypotheses relate detectability back to the density index. I did not expect to find support for my first two hypotheses and so decided to test the independence of the density index from the patchiness index and detectability. The third hypothesis stated that density index and detectability were independent. If density index and detectability were not independent, then unanswerable questions arise relating to the density index: is it closely related to population size, with variation in catchability having only a small effect, or is it strongly affected by catchability but bearing little resemblance to the population?

The last hypothesis was that density index and patchiness were independent. I thought that patchiness might increase as population size decreases. For example, after a beech mast seedfall event, particularly a partial mast, individuals may cluster around beech trees as food sources while the seeds are available. Conversely, in non-seed years, patchiness could decrease as individuals spread out and enlarge their home ranges in search of food.

Hypothesis one to could be evaluated only for changes in detectability within each trapping session. The Site Occupancy method will test for p(t) (variation in detectability between sampling sessions), however just because PRESENCE (Hines 2006) will fit and select a p(.) (constant detectability) model doesn't make it a good explanation of the biological system. Given the length of time (five years) over which the data were collected, a p(.) model is unlikely to adequately describe the system.

I have, however, been able to test for two hypotheses relating to detectability within a trapping session. The first of these examines the data for a change in detectability at a given trap station within a session, tested using the p(Tds) and p(TO) models; a simple p(t) model, modified by covariates or not, has constant detectability during a session. The second of these examines the data for a change in detectability between trap stations within a session, tested using models where detectability varies with covariates; a simple p(t) model has constant detectability between trap stations within a session. This second hypothesis can be tested only on the Pureora data where records of potential covariates are available.

These hypotheses are listed formally in section 1.5.1 below. They provide the formal tests necessary to meet my first objective: to evaluate the use and assumptions of the density index. However, I also had some more open-ended questions relating to the application of the patchiness index and Site Occupancy to standard small mammal monitoring data. These I have organised as research questions and they are listed in section 1.5.2 below. The first research question evaluates the tests of the hypotheses to complete my first objective, the other question relates to my second objective: evaluating the use of the patchiness index and Site Occupancy analysis with small mammal monitoring data.

1.5.1. Hypotheses

1) That there are no changes in the detectability of small mammals at a given trap station within a trapping session.
2) That there are no changes in the detectability of small mammals between trap stations within a trapping session.
3) That small mammals are evenly distributed along each trap line during a given trapping session.
4) That the density index is independent of variations in the detectability of small mammals.
5) That the degree of patchiness in small mammal populations is independent of the density index.

1.5.2. Research questions

1) Do these data provide any new information regarding the usefulness of the density index as applied to rodents and stoats?
2) Do these techniques provide new information about the processes of change in these populations of rodents and stoats?

1.6. Expected outcomes

I expect that this analysis will answer the question of whether or not there is a tendency towards patchiness for each species in different habitats, and if so, if it varies in any predictable way with density index or with some environmental variable.

I expect that this analysis will determine if detectability is constant within a session and if it varies with density index.

I expect to be able provide an answer, with respect to detectability and patchiness, to the question: does the density index represent reliable information about a species?

I expect to be able to provide estimates of distribution (occupancy) and detection probability for rodents and stoats in different habitats, and to identify important covariates.

I expect to be able to provide a broader and more integrated understanding of each species and their interactions where practical.

Chapter Two:

Materials and methods

2.1. Materials

2.1.1. The original studies

The data I used were originally collected in two separate studies applying the same survey methods to five quite different habitats. The results were published in six separate papers. The first of the two studies was conducted in beech forest in Fiordland National Park in the mid-70s, and the data were published by King (1982, 1983). The second study was conducted in mixed podocarp-hardwood and exotic forest at Pureora Forest Park in the mid-80s, and was published by King *et al*. (1996a, 1996b, 1996c) and Innes *et al*. (2001). King *et al.* (1996c) included an analysis of habitat covariates, but it was still very simple compared to what can be done with the modelling techniques now available.

The survey technique used for rodents in all study areas was based on that used at the Orongorongo Valley (Fitzgerald and Karl 1979, Choquenot and Ruscoe 2000, Efford *et al.* 2006). Transect lines for rodents (coded R) consisted of 36 stations set at 50 m intervals over a total of 1.8 km. Each station had a pair of wooden 'Ezeset' break-back rodent traps (one rat trap, one mouse trap, Figure 2.1) set back to back in a tunnel and baited with a mixture of peanut butter and rolled oats. Traps were set for three nights every three months – in the last week of February, May, August and November. Because mice can be easily caught in both rat and mouse traps, each sample represents 216 trap nights. Each sample represents 108 trap nights for ship rats caught in rat traps.

Figure 2.1: A rat and mouse trap pair set at Pureora (tunnel removed)

For Fenn (F) trap (Figure 1.3) sampling in each area the basic procedure (trap type, baiting etc) was always the same, but the number of traps and the number of nights over which traps were set varied between trap lines, depending on the area of habitat available and the length of the access track. Each sample from Pureora represents between 320 and 612 trap nights, and each sample from Fiordland represents between 400 and 480 trap nights. The density indices in both the original and this analysis are expressed in terms of captures per hundred trapnights (C/100 TN), corrected for unavailable traps, and all values for this study have been recalculated to allow for small variations in the data set.

Fenn traps were set in separate transect lines but at different spacings in each study: 300 m spacings were used at Pureora (King *et al.* 1996c), 400 m spacings in Fiordland (after March 1976, but variable prior to this (King 1980, 1983)). Fenn traps were set over at least 10 nights per month (varying up to 14 nights per month in Fiordland and 12 at Pureora) and baited with fish-based cat food.

Because such long distances had to be covered by a few staff during each daily check, only one of the five Fenn trap lines was set through untracked forest (PFU), and the other four were set along roads. All of these were simple gravel tracks carrying little traffic; the exception was SH 94, the road from Te Anau to Milford via the Eglinton Valley.

All of these data, for both rodents and stoats, refer to dead animals, and the populations were therefore sampled without replacement.

2.1.1.1. Pureora

Three types of habitat were sampled at Pureora. Two of these habitats were in native podocarp-hardwood forest, of which one had been subject to selective logging (L) and the other was untouched (U) (Figure 2.4). The third habitat was in a large *Pinus radiata* plantation (E) divided into compartments planted at different times (Figure 2.4). The naming conventions from the original Pureora papers (King *et al.* 1996a, 1996b, 1996c, Innes *et al.* 2001) have been continued here to prevent confusion, with two exceptions; the addition of a prefix for study area (P), and the aggregation of FE1 and FE2 into one dataset (PFE) for the Site Occupancy analysis (Figure 2.4).

In the logged native forest, the Fenn trap line (PFL) consisted of 39 traps (11.4 km) and was set along a gravel road. However, the rodent line (PRL2) was set in a circle in the forest interior; the closest trap was 20 m from a road (Figure 2.4).

One rodent and one Fenn trap line were set in the unlogged native forest (Figures 2.2 and 2.3). Both lines were set in loops and only the ends of these lines approached any kind of road (Figure 2.4); the first trap on the Fenn trap line (PFU) was 10 m from the nearest road, but the first trap on the rodent line (PRU) and the second trap on the PFU line were both 100 m from the nearest road. The Fenn trap line in this area had 32 traps (9.9 km).

One rodent and one Fenn trap line were set in the exotic forest which comprised many different compartments with trees of different ages. The rodent line (PRE, Figure 2.4) was entirely in a young area of plantation (six year old trees at start of sampling) where the canopy had not closed. The grassy undergrowth in this area was very thick (Figure 2.5), even at the end of the sampling period when the trees were older (Figure 2.6)

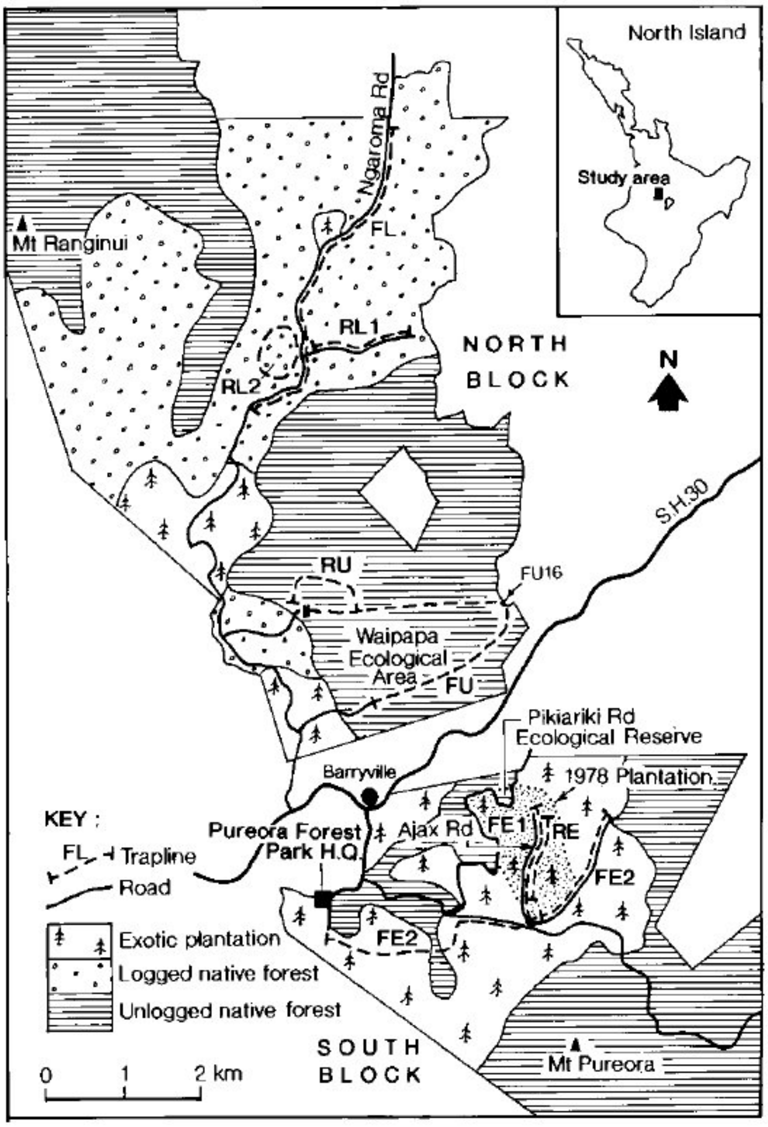

Figure 2.4: Pureora trap line layout (map from King *et al.* (1996c))

The Fenn trap line was set in a T shape and so was split in two at the boundary between the older and younger forest (Figure 2.4). The down stroke of the T (PFE1) was in the younger part of the exotic forest and consisted of only 10 traps (3 km). The crossbar of the T (PFE2) was the longer of the two split lines with the remaining 41 traps (12.6 km) and was in the older (12 year old trees at start of sampling), closed canopy portion of the exotic forest. PFE1 and PFE2 were analysed together for the Site Occupancy analysis as PFE because the spatial arrangement of traps is irrelevant for this technique.

All trapping at Pureora was conducted at three month intervals. However, rodent and Fenn traps were sampled in different months for different periods of time. Rodent lines were sampled in the last week of February, May, August and November. Fenn trap lines were sampled in late January, April, July and October; initially for 12 nights, but after July 1984, for 10 nights.

2.1.1.2. Fiordland

The two habitats sampled in Fiordland were very different; the Hollyford Valley (Figure 2.7) is a heterogeneous mix of silver beech (*Nothofagus menziesii*) and kamahi (*Weinmannia racemosa*) with some red beech (*N. fusca*) whereas the Eglinton (Figure 2.8) is fairly homogenous red beech (Johnson in King 1982). Note that this description applies only to the areas in which rodent traps were placed; there are areas in both valleys for which no information on vegetation is available. The Eglinton Fenn trap line started with 50 traps, reduced to 48 from November 1974; the Hollyford had a line of 40 Fenn traps (Figure 2.9).

Rodent lines in Fiordland overlapped with Fenn trap lines and were sampled for three nights at three month intervals in the last weeks of February, May, August and November. Fenn trap lines were sampled, initially for 14 nights and from April 1976 for 10 nights at the start of every month. Data with variable trap spacings were unsuitable for use with either technique: the patchiness index assumes equal spacing between all traps and Site Occupancy assumes that all trap stations are in the same place throughout sampling, whereas in this data set trap number represented a different station after the spacings were changed. Thus, data with variable trap spacings were discarded and all of the Fenn trap data used for Fiordland was collected over 10 nights.

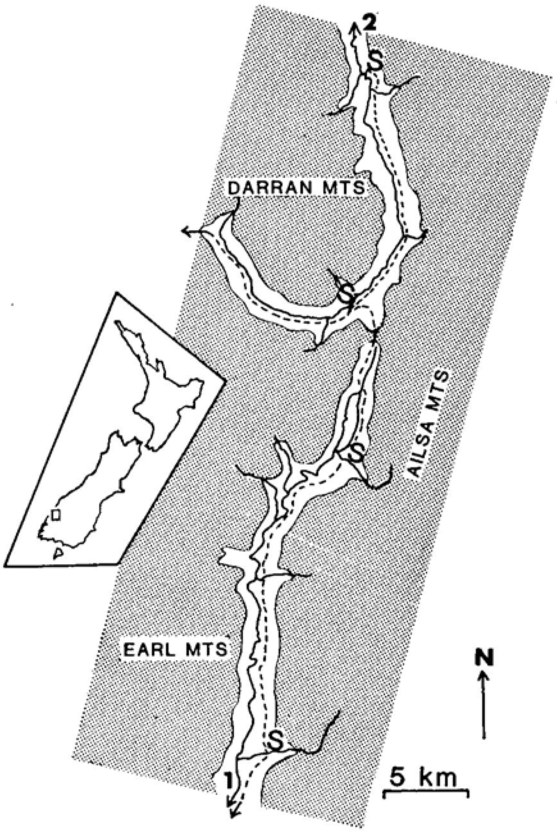

Figure 2.9: Map of the Eglinton (1) and Hollyford (2) Valleys. The two Fenn trap lines are marked S to S, one in each valley. Rodent trap lines sampled 1.8 km of each 20 km (approx) Fenn trap line. Rivers are marked by solid lines, and the roads are marked by dotted lines; State Highway 94 enters at the bottom of the figure and leaves via the Homer tunnel at the left (map from King and McMillan (1982))

According to the seed tray data (Figure 2.10), the silver beech in the Hollyford Valley had a partial mast year in 1975, though there was no apparent response by mice and stoats to it. In 1976, mice and stoat numbers in both valleys increased in response to a mast event, but the seedfall trays could not detect a mast event (though a higher proportion of sound red beech seed was detected than in the two preceding years, see Figure 2.10). This suggests two possible scenarios: either the seed trays in the Eglinton Valley failed to accurately sample the red beech seedfall in that valley; or the mouse and stoat populations responded to something other than a red beech seedfall.

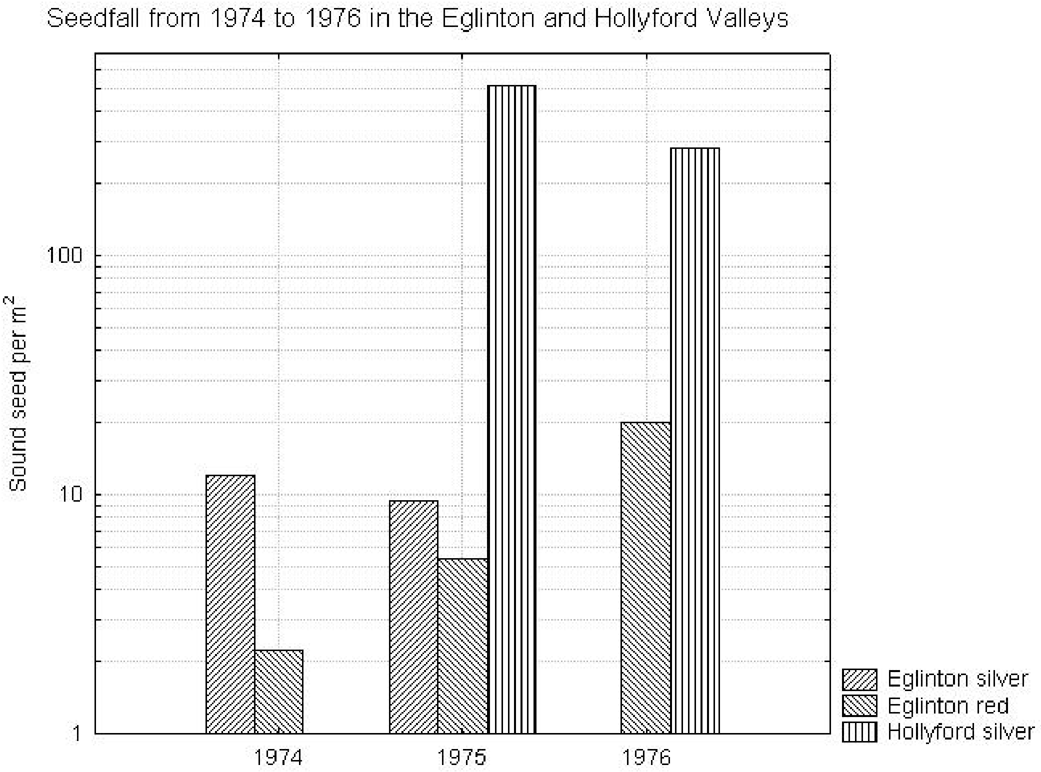

Figure 2.10: Seedfall of silver and red beech in the Eglinton and Hollyford Valleys as detected by eight round trays (C.M. King unpubl. data). A seedfall is considered to be a partial mast above 500 sound seeds per m^2 and a full mast above 4000 sound seeds per m^2 (Wardle 1984).

Both scenarios are possible; Wardle (1984) shows that full masts were observed in both red beech (Rahu Saddle) and silver beech (Rowallan State forest) in 1976, and although there were few silver beech trees close to the trap lines, there was a great deal of silver beech further up the valley sides (C.M. King pers. comm.). It is also possible that mice and stoats responded to a combination of partial seedfalls in both silver and red beech. Red beech seeds are larger than silver beech seeds (7 and 5-6 mm respectively (Wardle 1984)) and have a higher concentration of nutrients (Beggs 1999); a small number of red beech seeds may have been sufficient to promote a mouse population irruption.

2.1.1.3. Trap line labelling

In this analysis the data are labelled according to the line they represent. The first letter indicates the study area (P for Pureora, S (South Island) for Fiordland). The second letter gives trap type (R for rodent traps, F for Fenn traps). The third letter gives the trap line from which the sample was taken, named for forest type at

Pureora (E for exotic, L for logged native and U for unlogged native) and for the valley name in Fiordland (E for Eglinton and H for Hollyford).

2.1.2. Limitations of the data set

As much as possible, I have attempted to use exactly the same data as the original studies (King 1982, 1983, King *et al.* 1996a, 1996b, 1996c, Innes *et al.* 2001), using the same definition of a capture (counting a severed body part as a capture but not a simple tuft of fur on its own) as in the original analysis. Occasional discrepancies (such as the omission of records that did not include the trap number) were few in comparison to the total number of records (n = 3043). These discrepancies arose because Site Occupancy analysis and the patchiness index require the exact location of each capture, whereas the original analysis pooled all the data collected on each trap line for each night of sampling.

Portions of the data set have not been used or have been removed from certain parts of the analysis. The line designated RL1 in the original study (King *et al.* 1996b, King *et al.* 1996c, Innes *et al.* 2001) was not used at all because it was not sampled for the full five year period. The data for stoats from the PFE1 line were not used in the patchiness analysis because only one animal was caught during the whole five year period. These data were incorporated into the Site Occupancy analysis because the unusual shape of the line did not affect the analysis as it did the patchiness index.

The data from the Hollyford Valley (SFH) were not used for the Site Occupancy analysis because the forest in that area is very heterogeneous and no site specific habitat covariates were recorded. No habitat covariates are available for the Eglinton Valley either, but the forest there is much more homogenous, at least along the trap line. Data collected from the Fenn trap lines in Fiordland before April 1976 were not used for either analysis because the trap spacings were variable.

Some of the remaining data could not be used for Site Occupancy because PRESENCE could not accurately estimate the beta parameters for the model (section 2.2.5.2). These lines were stoats on the PFL and PFU lines, Norway rats on the PFL line and ship rats on the PRE and SRE lines.

Kiore were found only in Fiordland and their sample sizes were insufficient for analysis with either technique.

2.1.3. Brown's index of patchiness

2.1.3.1. Usefulness of patchiness

Data provided by the conventional methods for rodents and stoats have never been formally analysed for evidence of patchy distributions. However clumping is sometimes visible even to casual inspection of raw data. For example, Innes *et al.* (2001) found that of forty three Norway rat (*Rattus norvegicus*) captures in nine traps, thirty five (81%) came from a single trap. Also, Purdey *et al.* (2004) found most of the stoats they captured, and most of the radio-tracking records, were concentrated along a section of nine traps in the middle of their transect line (of 30 traps) in the Grebe Valley. These observations imply different catch rates in different parts of the trap line, but until recently there has been no way to measure clumping in transect line data. The index of patchiness (Brown *et al.* 2004), developed from the two-dimensional SADIE method (Perry 1995), attempts to quantify mathematically one-dimensional (transect line) patchiness.

2.1.3.2. Description of patchiness analysis

The method developed by Brown *et al.* (2004) generates an index of patchiness, calculated in two sections. Firstly, captures are averaged over all the available traps, by moving a portion of each capture along the trap line until each station contains the same proportion of the available captures. For example, if there were two captures on a 10 trap line:

0 1 0 1 0 0 0 0 0 0

Fractions of the two capture records in the second and fourth trap would need to be spread around all traps until there was 0.2 of a capture in each. The distance that each portion of each capture has had to be moved in order to do this is calculated and summed; this is D_{ob} (the observed distance). In this example D_{ob} is 5.4.

Secondly the data are randomised (999 times in Brown *et al.* (2004)). For each randomisation, D is calculated again, and the average randomised distance is D_{av}. This gives an estimate of how the data would be distributed if the real distribution of the animals had been totally random. The percentage of random D values greater than D_{ob} generated during the randomisation process gives the percentile (P).

The index of patchiness given by Brown *et al.* (2004) is:

$$I = D_{ob}/D_{av}$$

Values of I greater than one are considered to be patchy, that is if $D_{ob} > D_{av}$ because, if the observed captures need to move a greater distance than average to be evenly distributed, they must have been aggregated. The calculated I value is considered significant only if P exceeds the usual 1% 5% or 10% levels of significance. Thus lines where the computed patchiness index is less than one can be considered to have a relatively even distribution of animals along the whole line. Values of I greater than one, with a P value greater than 0.1 are considered to be aggregated, but not significantly so.

2.1.4. Introduction to Site Occupancy analysis

2.1.4.1. Description of Site Occupancy analysis

Site Occupancy analysis is a statistical technique that utilises simple binary presence-absence (as opposed to ranked abundance) data collected over many repeated surveys, defined as a ‘season’ (MacKenzie *et al.* 2002) (referred to in this thesis as a session). It provides an estimate of the proportion of trap stations occupied while taking into account false absences, the probability of detection, and seasonal variation in the behaviour of animals (MacKenzie *et al.* 2002). The analysis is usually run using a program called PRESENCE (Hines 2006). The technique assumes that each station is independent and that all stations are closed to changes in occupancy within a session (MacKenzie *et al.* 2002).

PRESENCE (Hines 2006) uses the likelihood approach (MacKenzie *et al.* 2006), which simply estimates the probability of observing the sampled data, to produce a mathematical description of the observed data and generate a model (Hines 2006). For example, suppose a station had the detection history (over three sampling periods within a session) of:

$$h = 101$$

MacKenzie (2002) describes this mathematically as:

$$P(h = 101) = \psi p_1(1 - p_2)p_3$$

where ψ is the probability of occupancy and p is the probability of detection (given that the species is present). This means that the probability of observing a given detection history, h, is equal to the probability of occupancy multiplied by the probability of detection for survey 1, the probability of not detecting the species in survey 2 $(1 - p_2)$, and the probability of detection for survey 3 (Hines 2006).

Extensions of the method include (1) the use of site or sampling covariates in the model which allow for the investigation of which habitat variables play a pivotal role in the likelihood a station is occupied, or that the species is detected at that station (MacKenzie *et al.* 2006); and (2) multi-season models, which add the parameters γ and ε representing the probabilities of colonisation (that a previously unoccupied station becomes occupied) and local extinction (the reverse) (MacKenzie *et al.* 2003).

2.1.4.2. Types of model

This analysis had the potential to generate five kinds of model. Unfortunately, one could not be used due to a bug in PRESENCE. All of the other four types fit at least one of the data sets tested.

When a model is named, the parameters used to estimate each variable are inserted into brackets following the variable. A full stop indicates a constant, t indicates time and T indicates a trend (in this analysis Tds –downwards trend through a session). For example, $\psi(.)p(t)$ would be a model with constant occupancy and variation in detectability over time.

The first type of model estimates ψ (probability of occupancy) and p (probability of detection), using a simple single-season occupancy model. Single-season models assume that all data entered represent a system where there is no change in occupancy between sessions. This type of model can be used on data from several sessions, the model simply assumes that each station is closed to changes in occupancy for the whole of the sampling period, effectively setting the probabilities of colonisation and local extinction to zero.

For dynamic populations such as rodents and stoats, a single-season model would usually be inappropriate over a long sampling period. However, Norway rats from the PFU line provide a good example of the use of this model. All the captures for Norway rats on this line were from a single trap. No animals were ever detected anywhere else on this line during the five years of sampling, so the most likely scenario is that there is no colonisation or local extinction for this line. In this case, the best model is a single-season model (see Chapter four for more information).

A second type uses Markovian dynamics to construct a multi-season model, which can be either stationary or non-stationary. A Markovian model is one where initial occupancy (denoted $\psi(i)$) is estimated by the program, but occupancy in subsequent sessions is implicit (defined by the parameters) by MacKenzie's (2006) equation:

$$\psi_{t+1} = \psi_t(1 - \varepsilon_t) + (1 - \psi_t)\gamma_t$$

where ψ_t is the occupancy in the first session, ψ_{t+1} is the occupancy in the second and ε_t and γ_t are the local extinction and colonisation probabilities in the first session. This calculation can be solved iteratively until ψ is calculated for each session. When ε and γ are constant, it is a stationary Markov process – it will eventually reach equilibrium occupancy. MacKenzie *et al.* (2006) defined equilibrium occupancy as:

$$\psi_{Eq} = \gamma/(\gamma + \varepsilon) \qquad \textbf{(2.1)}$$

When either of these two variables is not constant for example, $\gamma(t)$, it is a non-stationary Markov process – it will never reach equilibrium occupancy. For example $\psi(i)\gamma(t)\varepsilon(.)p(t)$ is a non-stationary Markovian model with constant probability of local extinction and variation in colonisation and detection probabilities over time. Markovian models are suitable for use in this analysis because they describe a system where occupancy changes between sessions in a relatively predictable way which may or may not reach an equilibrium level.

A third type of model, random-occupancy, assumes that the probabilities of local extinction and colonisation sum to one:

$$\gamma + \varepsilon = 1$$

and the occupancy state of a station at time t is not dependant on its state at time $t - 1$. This type of model usually has no equilibrium occupancy. For example, $\psi(i)\gamma(t)\{\varepsilon = 1 - \gamma\}p(t)$ is a model with no equilibrium where occupancy is estimated initially, colonisation probability is estimated and random, probability of local extinction is not calculated but implicit ($\varepsilon = 1 - \gamma$), and detectability varies over time. Random occupancy models are suitable for use in this analysis because they describe a system where there is no pattern or consistency to occupancy, as would be expected in a species with low site fidelity or wide juvenile dispersal.

The final type of model assumes seasonal occupancy and colonisation. In this model, ε is implicit, described by MacKenzie *et al.* (2006) using the equation:

$$\varepsilon = \gamma(1 - \psi)/\psi \qquad \textbf{(2.2)}$$

The probability of occupancy may vary over time, with covariates, or be constant in this model. For example $\psi(.)\gamma(.)p(t)$ is a dynamic constant occupancy model with constant probability of colonisation (and consequently constant probability of extinction as calculated by Equation 2.2) and variations in detectability over time. The proportion of stations occupied remains constant but the particular stations which are occupied changes. This model is suitable for use in this analysis because it describes a situation where the proportion of sites may either remain constant or change over time while the particular stations that change are able to vary between sessions depending on the probabilities of colonisation and local extinction.

Most rodent species, such as mice, have inherently unstable populations, and would not normally be considered to have a population equilibrium. However, equilibrium occupancy refers to the proportion of stations occupied by the species, and this may vary independently of population size. For example it is possible to have either a large or small number of stations occupied by either a small number or a large number of individuals. It is possible for the Site Occupancy of a species to be at equilibrium even when the population size is not.

2.1.4.3. Usefulness of Site Occupancy analysis

Little more than four years after its initial publication (MacKenzie *et al.* 2002), the Site Occupancy technique is already a commonly used tool in conservation management. Most of the published examples of its application concern rare or cryptic species, where it can provide estimates of such things as, the proportion of potential breeding sites in an area that is occupied (MacKenzie *et al.* 2003) or the monitoring of population trends (Joseph *et al.* 2006). This study is one of the first attempts to use this technique on abundant pest species. However, even common species cannot be detected with certainty, and so Site Occupancy offers the same potential advantages to pest management and zoology as it does to conservation of rare species.

The potential advantages of this technique include:

- It does not require accurate count data of undisturbed populations, which is expensive to obtain and not available in the existing data sets;
- It overcomes the issue of trap saturation;
- The ability to analyse habitat or sampling covariates is inbuilt into the model;
- Either single or multi-session data can be used;
- It automatically calculates detectability;
- It may be used instead of abundance to monitor population trends, given certain assumptions (not applicable to this data set);
- It can calculate changes in occupancy such as site colonisation or local extinction, which may or may not be linked to changes in abundance;
- It can give insight into site fidelity within the population.

2.1.4.4. Potential problems with Site Occupancy

One criticism of the application of Site Occupancy to kill-trap data is that removal sampling precludes independence – that removing an animal decreases the probability of the same species being detected at the same station later. This decrease in detectability is expected with the use of kill-trapping. This problem can be addressed by using a model incorporating a downwards trend in detectability during a session (as p(Tds)).

This decreasing detectability model may not be adequate if all detectable individuals are removed from the local area during the trapping period. Thus, on the Fenn trap lines which were set for at least ten nights, I also tested a trap-out model (p(TO)) which showed that the probability of detection was higher for the first six days of trapping than for the rest of the sampling period. It is not necessary to recapture individual animals, as occupancy asks only if there is a member of a given species present.

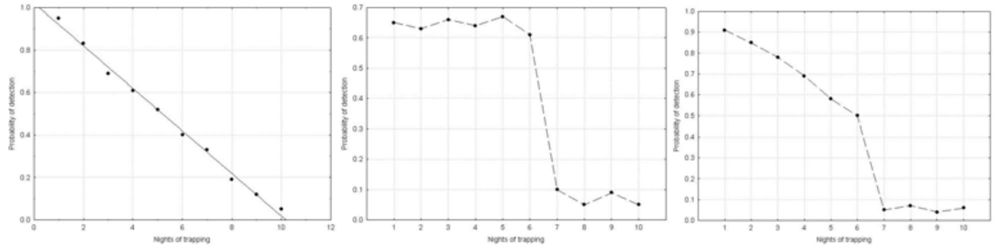

Figure 2.11: Theoretical examples of: a decrease in detectability over a trapping session (left); a trap-out effect (centre); and a combination of both (right).

It has also been suggested (MacKenzie and Bailey 2004) that there must be only one trap in an individual's home range in order to meet the assumption of independence. The Cambridge Dictionary of Statistics has the following definition of independence: "two events are said to be independent if knowing the outcome of one tells us nothing about the other" (Everitt 2002, p. 187). In terms of trap catch this suggests that, in order for two captures to be independent, that the second animal (or no animal) was not caught simply because the first one was. Or, more generally that capturing an animal in a trap does not prevent another animal from being captured again later (make the probability of a second capture 0), or make the probability of another capture certain (equal to 1) and that a capture does not effect the probability of capture in neighbouring traps (either positively or negatively).

This could be a problem when sampling using live trapping (i.e. sampling with replacement) because individuals may become trap-happy or trap-shy after capture affecting subsequent detection probabilities. However, with kill trapping, no individual can be detected in more than one trap and there is no opportunity to develop a learned behaviour. Colonial populations complicate this issue, but the fact remains that aside from a general decrease in detectability during each session, because each individual encountered is removed, capturing one individual does not make a subsequent capture certain or impossible.

2.2. Methods

2.2.1. Procedure

1) All data were digitised (section 2.2.3.)
2) Two copies of the digitised data were created:
    - one was summed by season and converted to a Comma Separated Values (CSV) file for the patchiness index analysis (appendix D)
    - the other was modified to presence/absence data (all records of two or more captures were converted to a 1 in the data sheet) for Site Occupancy analysis
3) Both analyses were run on their respective data sets (section 2.2.4)
4) The results of both analyses were carefully examined and suspect results removed:
    - All samples with fewer than two captures were removed from the patchiness results (section 2.2.5.1)
    - All Site Occupancy models with large or unlimited standard errors within the beta parameters of the model were removed from the set of candidate models (section 2.2.5.2)
5) The results were then displayed (section 2.2.5)

2.2.2. Additional methods

Not all techniques applied to the data were universally valid across all data sets. Occasionally, where the analysis produced an unexpected result, additional methods were used to explore the result further. These are described within the relevant chapters.

2.2.3. Data digitisation

The field data sheets were used to generate a Microsoft Excel file of captures. An untouched trap was designated 0, capture of a target animal was designated 1 (or occasionally 2) and when the trap was sprung or caught a non-target animal it was designated –. Mice could be caught in either rat or mouse traps so both traps had to be unavailable to mice for the station to be designated as an unavailable station (thus rats were counted as non-target animals within the mouse analysis, and stoats were non-target animals for the rat analyses etc).

Brown's (2004) original description of the index of patchiness involved determining the D_{ob} for each night of a sampling session, summing these, repeating this procedure for D_{av} and using the two summed values to produce an I value for the whole sampling session. However, P is the proportion of the randomised distributions which were used to calculate D_{av} that are greater than D_{ob}. Thus if D_{ob} is calculated nightly, then P must be calculated nightly and I could find no means of generating a sessional P value from several nightly P values.

Thus, the patchiness analysis was conducted with the data summed for each session as there should be no change in underlying patchiness during a trapping session. Only rarely was a trap station unavailable for the whole sampling period, however in Fiordland, some trap stations were occasionally washed out, snowed in or stolen.

The Site Occupancy analysis used the data as they were entered, the only exception being that every case where two animals were caught together was converted to a 1, as the analysis deals only with presence or absence, not numbers of animals.

2.2.4. Patchiness program

The original method developed by Brown *et al*. (2004) requires the status of every trap to be recorded as occupied or not on every possible trapping occasion. Brown's method does not allow for unavailable traps (for example where a trap was sprung but no animal caught, or only a non-target animal was caught). These situations were common in all the available data sets. In addition, one line had a change in the number of traps during the study (Eglinton in Fiordland changed from 50 to 48) and a few traps were unavailable for a whole session. After some discussion, thought and communicating with Dr Brown about this problem, I decided that it would be best solved by writing a new program capable of dealing with the unavailable traps. This was also an opportunity to add the ability to analyse whole spreadsheets of data, as compared to just one line at a time, as well as to increase the number of times the data are randomised.

Thus, I requested assistance from friends knowledgeable in the field of programming. The result of this is IOPUT (Uznanski and Watkins 2006), or Index of Patchiness with Unavailable Traps, which we have tested to ensure that it gives the same results as Brown's original program. A detailed description of the program and a hard-copy of its source code are available in appendix D. A working version of the program, some example data and the software required to run it are included with this thesis. When this program encounters an unavailable trap, it treats the data as if the trap was not there in the field; the distance between the neighbouring stations is doubled but the unavailable station cannot be randomised nor does it receive part of the redistributed catch when calculating the average distance as an empty trap would. Even though these data were eventually analysed as aggregates for the whole trapping session, the ability to deal with unavailable traps was still useful (for example to deal with the change in the number of traps set in the Eglinton Valley).

2.2.5. Display of analysed data

2.2.5.1. Patchiness

No distribution can be considered significantly patchy when only one animal has been caught (Brown *et al.* 2004). Thus, all samples with less than two captures were discarded from the analysis. Once the data were analysed using the patchiness index, the results were grouped and graphed against density index using STATISTICA (StatSoft Inc. 2006) according to several categories:

1) By whether or not the patchiness value was significant.
2) By line of capture
3) By season
4) By seedfall status (Fiordland data only)

Each of these groupings was also analysed using a Kruskal-Wallis ANOVA in STATISTICA (StatSoft Inc. 2006) to give an indication of whether or not there were significant differences between the groups.

For the seasonal groupings, data which were collected every three months were labelled according to month of collection. Data which were collected every month were labelled by season (so December, January and February comprise summer etc) but graphed individually, consequently there are up to three points graphed for every season from Fiordland.

For the seedfall status grouping of rodents, data collected before the onset of flowering were considered part of a normal year (data up until August 1975, from rodent lines only; see section 1.4.4.4). Data collected from the onset of flowering to the density index peak the summer after seedfall were considered to be part of a seedfall year (data collected from September 1975 to February 1977). Data collected after this point were considered part of the decline phase.

Because of delayed implantation, stoats are not able to take immediate advantage of the increase in rodent numbers following a seedfall (King and Powell 2007). Obviously, the definition of a seedfall event for stoats will be different to that of rodents because they are biologically unable to respond in the same way. A normal year for stoats was defined as being up until the emergence of young stoats (data up until November 1976), and the seedfall phase included the population peak and dispersal (December 1976 to February 1977). Data collected after this time were considered to be part of the decline phase.

2.2.5.2. Site Occupancy

Site Occupancy analysis uses the beta distribution to estimate each variable (MacKenzie *et al.* 2006). Sometimes, the model cannot accurately fit a beta parameter to the data, resulting in a very large or infinite standard error for the beta parameter. Occasionally, this was found in one of the session-specific detectability betas (under a p(t) model each session has a different beta parameter) because no animals had been caught in that session. This was expected and ignored. However, large or infinite standard error values were also found in other beta parameters or in multiple session specific detectability beta parameters. These models were regarded as highly suspicious and deleted from the set of candidate models.

Estimated detectability of the model with the lowest AIC was graphed against density index using STATISTICA (StatSoft Inc. 2006), and a line of best fit applied if appropriate, in order to answer the fourth hypothesis. If occupancy was modified by a habitat covariate, this relationship was also graphed including temporal changes if this was appropriate.

Where detectability was affected by covariates, each station had different detectability values during each sampling session and thus each station had a different line of best fit. In these situations detectability was either averaged across all stations (single-season models) or displayed only for a small number of stations (multi-season models). Detectability at different stations could not be averaged for multi-season models because not all data were output by PRESENCE (only first 200 estimates printed).

Chapter Three:

Patchiness and Site Occupancy of Mice (*Mus musculus*) in five New Zealand forest habitats

3.1. Overview

The purpose of this chapter is to test the two main assumptions of the density index as applied to mice (*Mus musculus*) in five different habitats (pine forest, logged and unlogged mixed podocarp-hardwood forest, homogenous beech forest and heterogeneous beech and podocarp forest) using formal tests of five hypotheses. In addition this chapter aims to investigate the usefulness (or not) of Brown's index of patchiness (Brown *et al.* 2004) and Site Occupancy analysis (MacKenzie *et al.* 2002) for extracting information about mouse populations from these data.

In order to assist with visualisation of these data, the raw counts have been graphed in a three-dimensional plot over time. The third dimension is represented by a colour denoting how many animals were caught at that location at that time. These graphs are available in appendix A, Figures A.1 to A.5.

3.2. Additional methods

One line (PRU) initially had no captures, so had to be removed from the data set for the Site Occupancy analysis. This was because the models (particularly Markovian models where occupancy after session one is implicit) were inaccurate where initial detection was zero.

3.3. Patchiness

If a line caught less than two mice during a trapping session it was discarded because no line with only one capture can be significantly patchy (Brown *et al.* 2004). Of the 93 samples collected, 26 have been discarded from the analysis for this reason, leaving a total of 67 samples.

3.3.1. Results

Patchiness values

Taking all 5 study areas together, the patchiness index ranged from 0.5 to a little over 2.4. Eight points from a total of 67 (12%) were significantly patchy (Figure 3.1); the patchiness values were evaluated for significance at the 5% level. The majority (91%) of the data points have density index values less than 15, and these are spread over most of the range of patchiness index values (Figure 3.1).

There was no observable correlation between the patchiness index and density index. Despite the expected significant difference between the patchiness values of the significantly patchy and non-significantly patchy groups (Table 3.1), there were no significant differences between the density index values of these groups (Table 3.1).

Table 3.1: p values from Kruskal-Wallis ANOVAs of each grouping for both patchiness and density index values

Grouping	Patchiness	Density index
Patchiness significance	**<0.001**	0.474
Trap line	**0.066**	**<0.001**
Season	0.280	0.452
Seedfall status	0.197	**0.013**

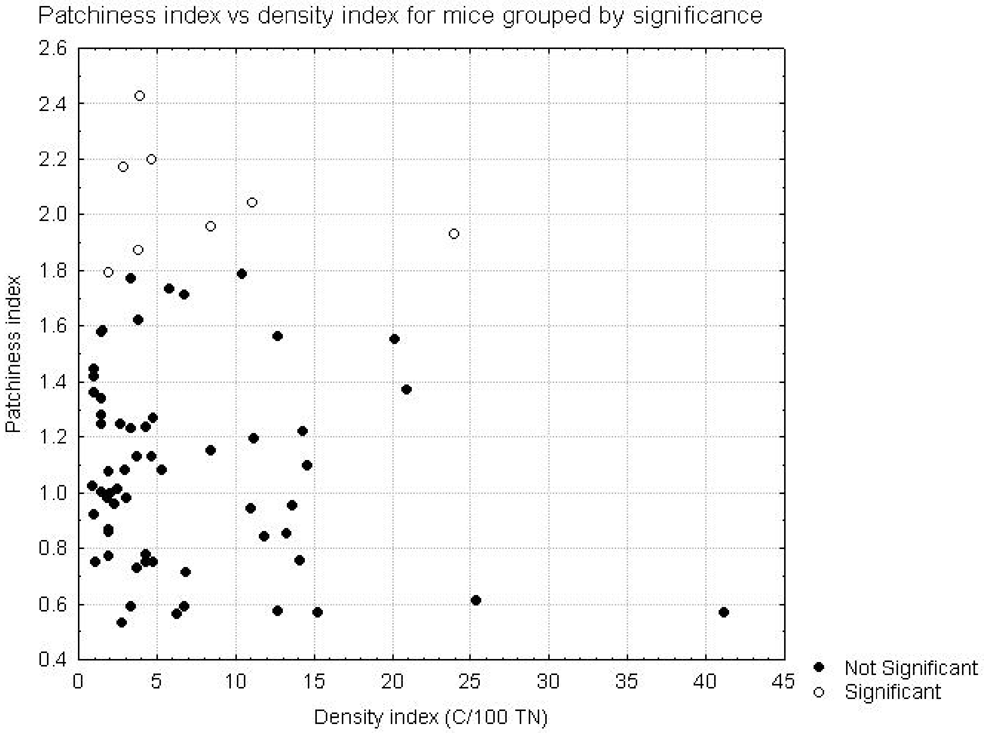

Figure 3.1: Distribution of significantly patchy and non-significantly patchy mouse samples

Trap line

Four of the eight of the significantly patchy samples were from SRH, two from SRE and one each from PRL2 and PRE (Figure 3.2). Only five samples (7%) had density index values greater than 20 and only one of these five was significantly patchy (from the SRE line (Figures 3.1 and 3.2)). There were significant differences between both the density indices and the patchiness values of the five lines, though the patchiness values had a low level of significance (Table 3.1).

Season

No seasonal trends were observable – each season had at least one point with significant patchiness or a high (>20) density index value (see Figure A.8). There were no statistically significant differences between each season for either patchiness or density index values.

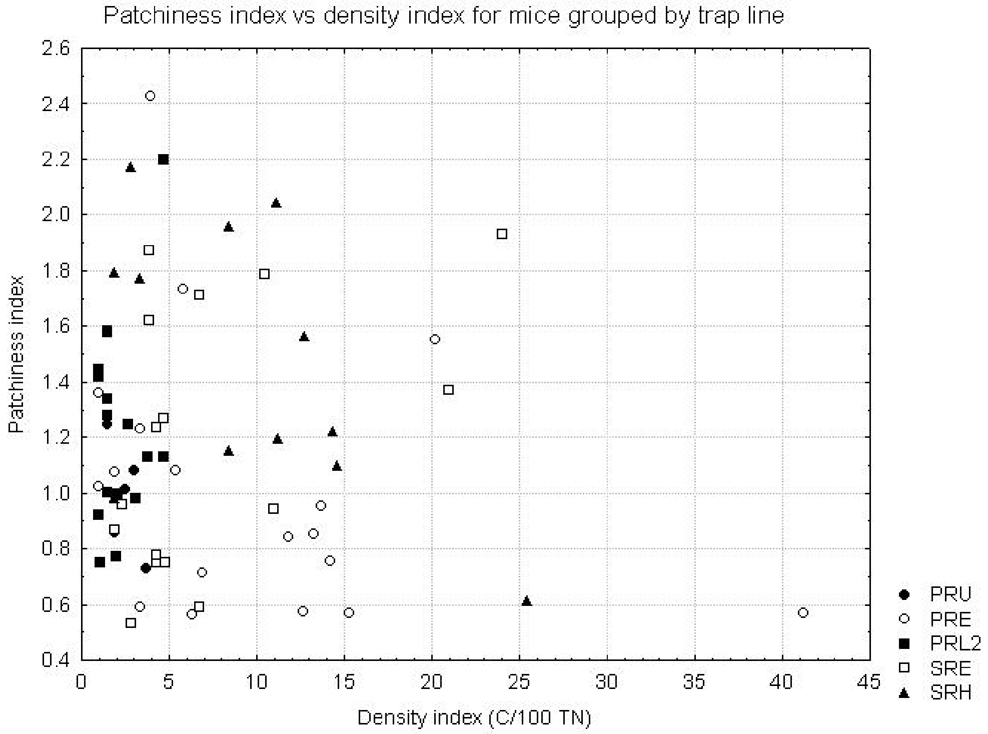

Figure 3.2: Distribution of patchiness and density index values for mouse samples from each trap line

Seedfall status

Seven of the 31 (23%) Fiordland samples were recorded during the decline phase of the beech mast cycle (Figure 3.3). Of these, five samples (71%) had high patchiness values (three (42%) were significantly patchy) and two samples (29%) with very low patchiness values. There were significant differences between the density index values of the three seedfall phases, but not between the patchiness values of these (Table 3.1).

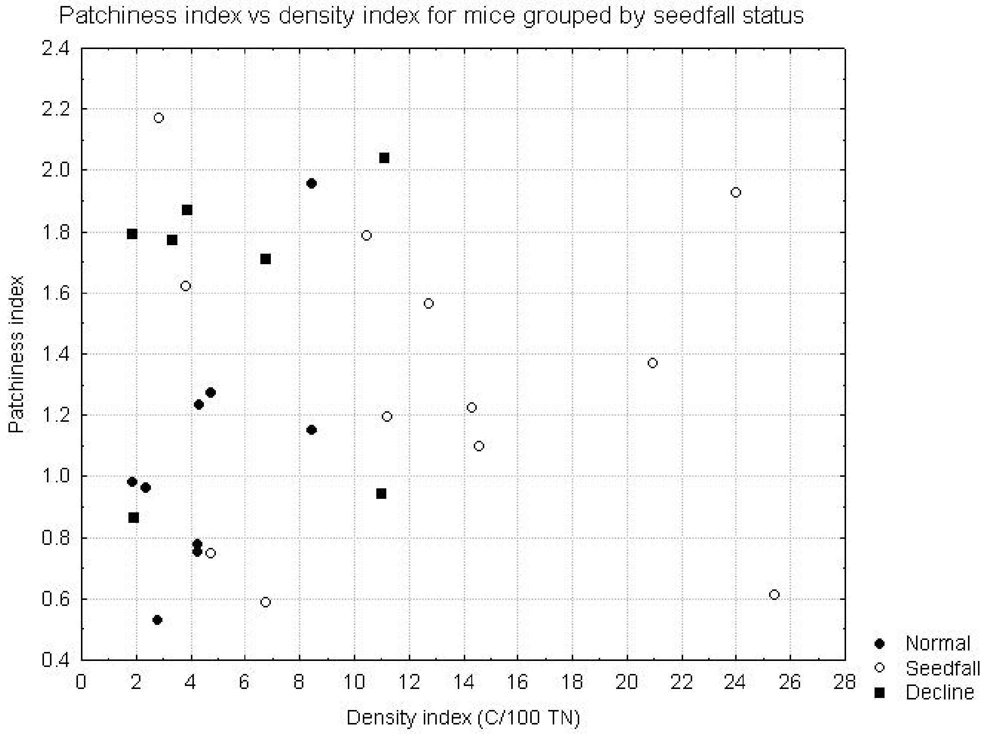

Figure 3.3: Distribution of patchiness and density index values for mouse samples from each seedfall phase (Fiordland only)

3.4. Site occupancy

Definitions for all symbols may be found in the glossary (pages xiv and xv). Table 3.2 shows, for each line, all models with ΔAIC values less than two. Additional models with ΔAIC values up to ten can be found in Table A.1.

3.4.1. Results

PRE (Pureora exotic forest)

The best fit model for PRE, $\psi(DR)\gamma(.)\varepsilon(.)p(t)$ indicates that the probability of occupancy differed between sites depending on the distance from the trap to the logging road (Figure 3.4). Of the four models for the PRE line which have good fit, three of them are Markovian.

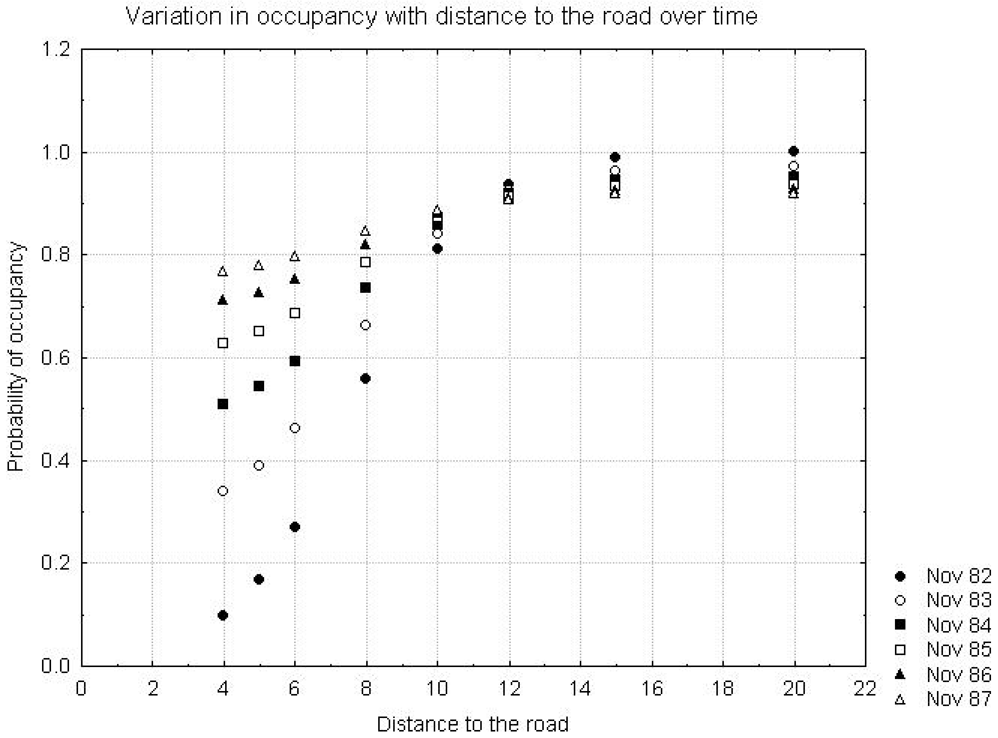

Figure 3.4: Variation in occupancy with distance to the gravel road (DR) on the PRE line for each of the six November trapping sessions using the $\psi(DR)\gamma(.)\varepsilon(.)p(t)$ model

Detectability and density index are closely correlated on the PRE line, showing a strong linear relationship (Figures 3.5 and 3.6). This is reasonable because one of the factors affecting detectability is population size: clearly, the more animals present, the greater the chance that one will be caught. The same feature can be seen on other lines, for example, PRU (Figure 3.8).

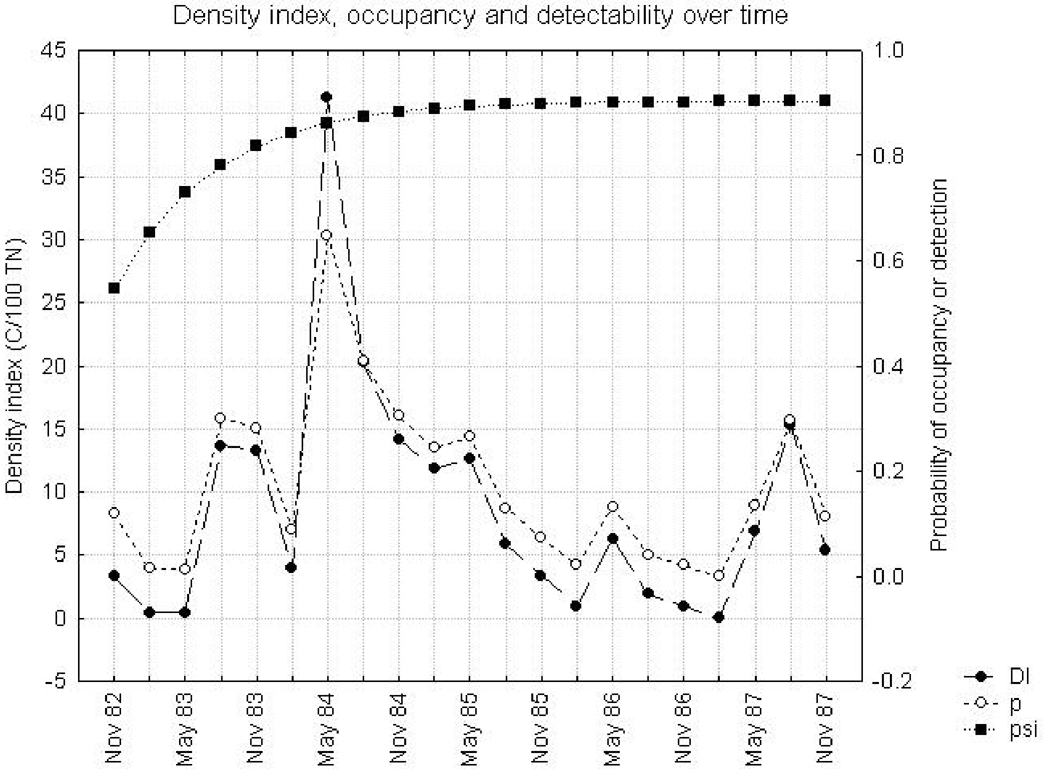

Figure 3.5: Detectability, occupancy and density index on the PRE line for the ψ(DR)γ(.)ε(.)p(t) model

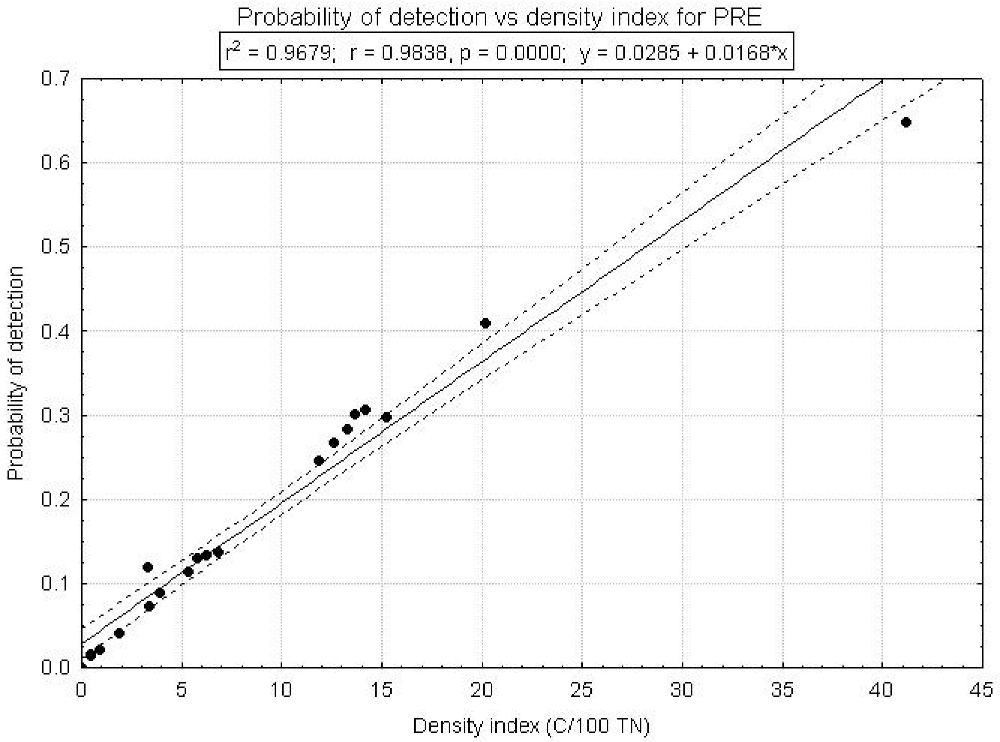

Figure 3.6: Probability of detection against density index including 95% confidence interval for mice on the PRE line using the ψ(DR)γ(.)ε(.)p(t) model

PRL2 (Pureora logged native forest)

The models for the PRL2 line showed strong support for variation in detection probability through a trapping session, and between trap sites according to distance from a road, canopy cover, vascular ground cover and distance to small mammal escape cover. The four best models all had ΔAIC values less than 0.76 indicating that their ability to describe the data is very similar.

The best model, $\psi(.)\gamma(.)p(Tds+DR+CC+GV+DE)$ is a multi-season dynamic constant occupancy model with detectability decreasing during each trapping session (Figure 3.7) and variations in detectability with distance to the logging track, canopy cover, vascular ground cover and distance to small mammal escape cover. Probability of detection from station two is graphed against density index for each of the three trap nights. PRESENCE returned complete data sets for only ten of the 36 stations in this model. This station was selected and graphed because it was representative of the other results obtained and averaging across traps was inappropriate.

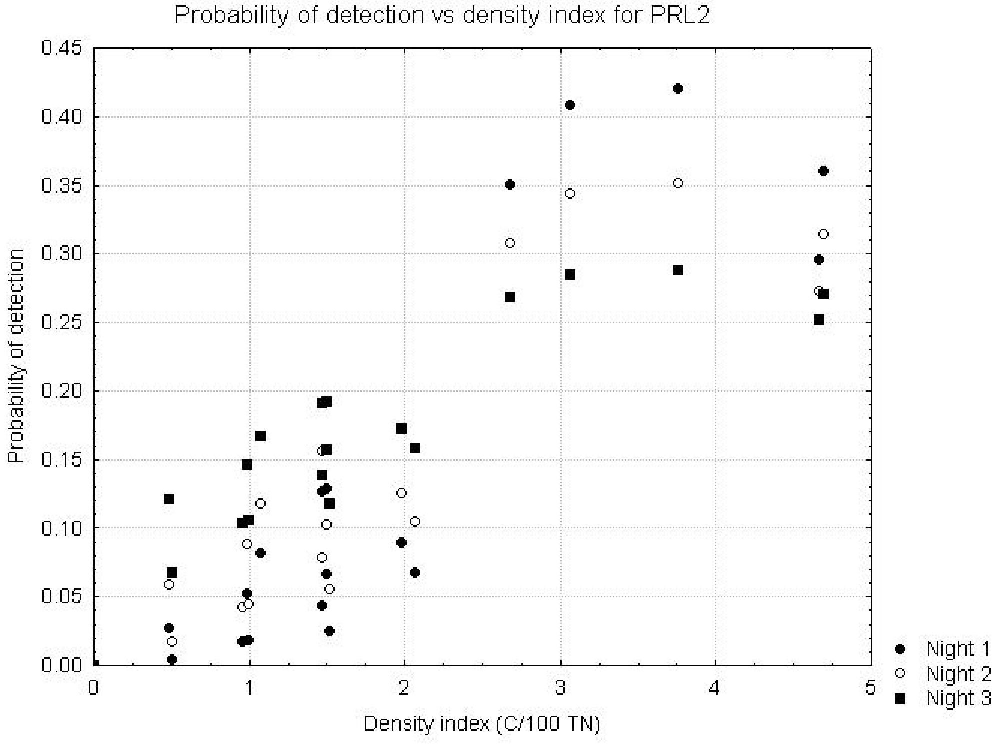

Figure 3.7: Density index and detectability at PRL2 station 2 for the $\psi(.)\gamma(.)p(Tds+DR+CC+GV+DE)$ model

PRU (Pureora unlogged native forest)

The analysis for the PRU line produced three models with ΔAIC values less than two. Average detectability values for the best model were closely correlated with density index (Figure 3.8). The best two models for this trap line were closed to changes in occupancy for the entirety of the five year trapping period. The best fit model (ψ(.)p(t+CC+GV+DE)) describes a situation where the same sites are always occupied, there is no local colonisation or extinction and detectability varies with canopy cover, vascular ground cover and distance to small mammal escape cover.

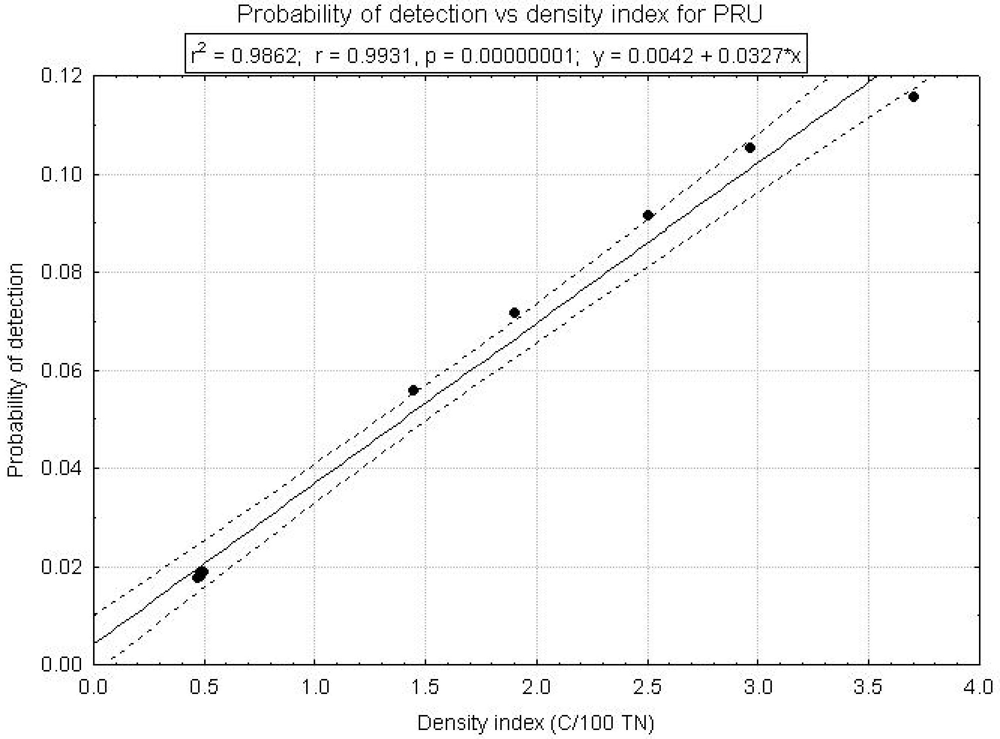

Figure 3.8: Average detectability across all sites against density index on PRU for the ψ(.)p(t+CC+GV+DE) model

SRE (Eglinton Valley)

The best fit model for the SRE line was a constant occupancy model (Figure 3.9). The other model with low ΔAIC was a Markovian model. Like the best fit models for PRE and PRU, the best fit model for the SRE line had a close correlation between density index and detectability (Figure 3.10).

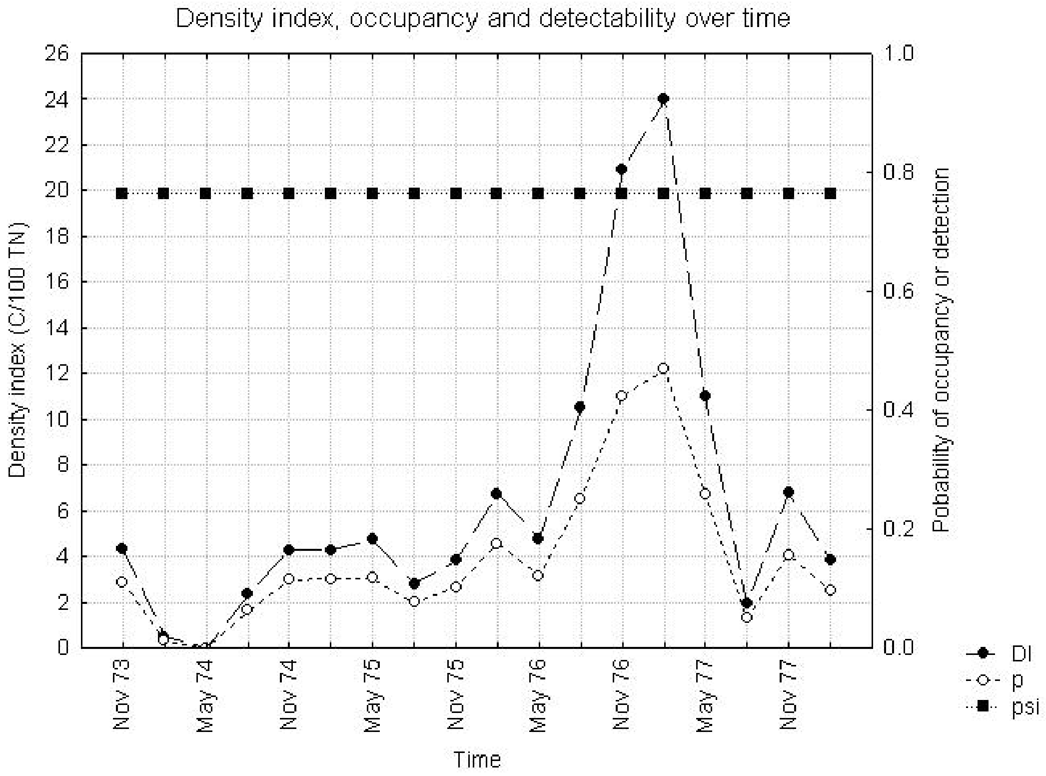

Figure 3.9: Detectability, occupancy and density index on the SRE line for the $\psi(.)\gamma(.)p(t)$ model

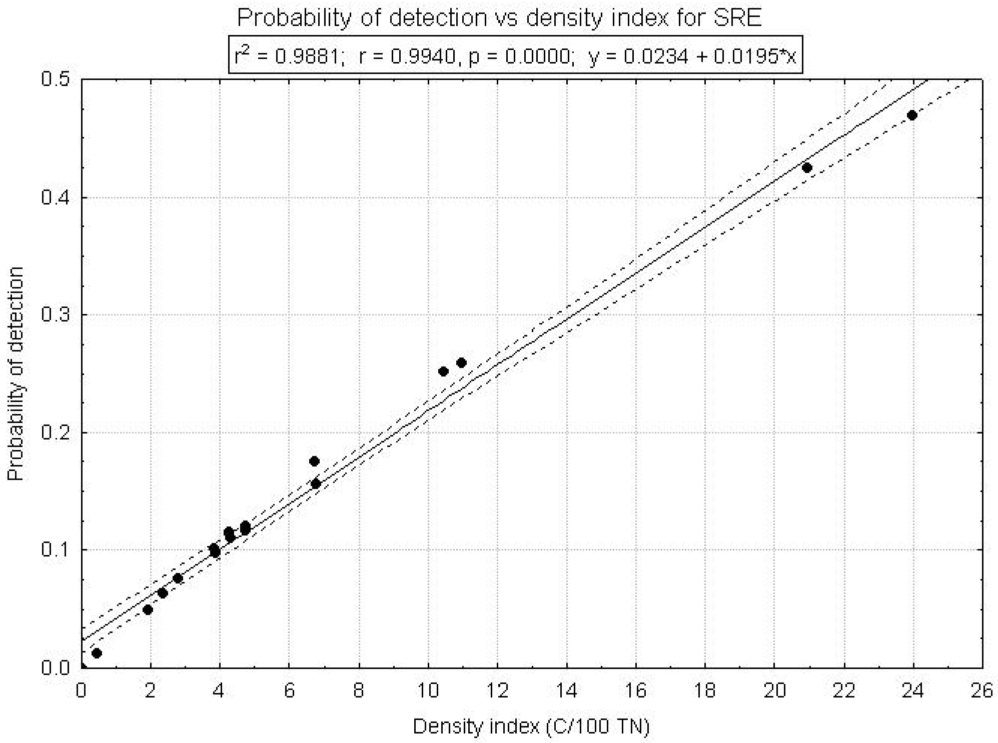

Figure 3.10: Detectability against density index on the SRE line for the $\psi(.)\gamma(.)p(t)$ model

3.5. Discussion

The purpose of this chapter was to use mouse trapping data obtained by conventional methods to evaluate the assumptions made by the density index with respect to detectability and patchiness. In addition this chapter aimed to evaluate the use of the patchiness index and Site Occupancy analysis with these types of mouse data.

This analysis has tested five hypotheses and accepted none in their original form.

3.5.1. Evaluation of hypotheses

First hypothesis: that there are no changes in the detectability of mice at a given trap station within a trapping session

The PRL2 line showed strong support for a decrease in detectability within a trapping session (Table 3.2), line PRU also showed some support (Table A.1). However, a decrease in detectability within a trapping session was not supported by either the PRE or SRE lines, in these areas detectability was constant within a trapping session. Thus I accept this hypothesis in modified form: that there *may or may not* be changes in the detectability of mice at a given station within a trapping session.

Second hypothesis: that there are no changes in the detectability of mice between trap stations within a trapping session.

All three mouse lines at Pureora supported variation in detectability covariates to some extent. The PRL2 line showed strong support for four covariates (distance to the gravel road, canopy cover, vascular ground cover and distance to small mammal escape cover). The PRU line showed some support for three covariates (canopy cover, vascular ground cover and distance to small mammal escape cover). The PRE line showed only a little support for covariates (canopy cover, vascular ground cover and distance to the gravel road were supported in a model with ΔAIC = 2.80, Table A.1)

Because this analysis has shown variation in detectability with covariates in all three testable habitats, detectability must regularly vary between trap stations and thus I reject this hypothesis.

Third hypothesis: that mice are evenly distributed throughout each habitat during given trapping session

Eight of 67 points (12%) from 5 lines were significantly patchy, most from the South Island. This tells us that mice are not always evenly distributed through their habitat, falsifying this hypothesis, though there is variation in the extent of the patchiness over time and between habitats.

This hypothesis could be accepted in a modified form: that mice may be evenly distributed throughout each habitat at a given time. However, this forms one of the main assumptions of the density index. With 19% (6 of 31) of the points from Fiordland found to be significantly patchy, the assumption is obviously being violated on a regular basis in that area. The assumption is much more reasonable in Pureora with 6% (2 of 36) of the points being significantly patchy and with one line (PRU) being completely free from significantly patchy points. However there is also a large body of patchy but not significant (patchiness values 1 to 1.8) observations (see Figure 3.1), some of which will be significant at the 10% level but not at the 5% level considered here.

The degree of variation exhibited by this analysis highlights the importance of testing the assumption of even distribution before it is made. Thus I have chosen not to support the assumption of even distribution by rejecting the original hypothesis without modification.

Brown *et al.* (2004) found that 6 of 19 (32%) possum (*Trichosurus vulpecula*) transects were significantly patchy before control and 1 of 15 (7%) were significantly patchy after control. This indicates that the proportion of lines found to be significant by this study is comparable to the only other study published using this method.

Fourth hypothesis: that the density index for mice is independent of variations in the detectability of mice

The strong linear relationship between detectability and density index on three lines (PRE, PRU and SRE) as shown in Figures 3.6, 3.8 and 3.10, falsifies this hypothesis: the density index and detectability are quite obviously not independent these cases. Even PRL2, where there is no linear relationship, shows higher detectability at higher density index.

Because of the linear relationship between detectability and density index, I reject this hypothesis.

This opens up the possibility that the large density index peak on the PRE line in May of 1984 or the low density index from February 1984 could be the result of altered catchability modifying detection probability as opposed to some constant catchability explanation such as immigration. Buckland *et al.* (2006) point out that samples will be biased if animals close to a trap do not enter it.

King *et al.* (1996b) suggested that this peak in density index in May 1984 could have been due to a temporary flux of insects. That the density index and detectability are not independent and the large change in detectability from February to May (from 0.09 to 0.64, see Figure 3.5) shown by this analysis indicates that the insect hypothesis is possible. This analysis is not able to support this hypothesis, however, it does not contradict it.

It could be argued that because population size is an important component of detectability, density index and detectability would be expected to form a linear relationship. However, these data contain a strong, though unconfirmed, suggestion that the reduction in density index in February 1984, or the peak in density index in May of 1984 were a result of change in catchability not a change in population size.

These data which are suspected to not accurately represent population size still fit closely within the linear relationship between density index and detectability (Figure 3.7). This suggests that some other factor, such as juvenile survival (King 1982), was at work between November and February 1984. King (1982) also describes a decrease in density index in Fiordland around the time that the beech seed began to fall (March 1976).

Fifth hypothesis: that the degree of patchiness in mouse populations is independent of the density index

Only one of the eight significantly patchy samples was collected at a density index greater than 20, which supports this hypothesis. However, one point is insufficient data on which to base a conclusion, thus I accept the hypothesis in modified form: that degree of patchiness in populations of mice *can* be independent of the density index.

It is not possible to draw any conclusions about the patchiness of very high density lines because only two observations were made with density indices above 25 C/100 TN. However, it is worth noting that in order to reach high density indices at least one animal must be caught at almost every station, which makes aggregation less likely.

The data were spread fairly evenly below a density index of 15 regardless of patchiness value, so there was no observable correlation between density index and patchiness index. A series of Kruskal-Wallis ANOVA tests carried out on the results suggested significant differences between both the patchiness index values and the density index values of each trap line ($p = 0.066$ and < 0.001, respectively) and the density index values of seedfall groups ($p = 0.013$).

3.5.2. Evaluation of research questions

First research question: do these data provide any new information regarding the usefulness of the density index as applied to mice?

The first hypothesis was accepted only in modified form and the second hypothesis was rejected reflecting the fact that detectability was not always found to be constant. Nor is detectability independent of the density index, given the rejection of the fourth hypothesis.

The density index is usually considered to lose accuracy above 20-25 captures per 100 trap nights (C/100TN) (Tanaka 1960). Yet this analysis also showed that data collected from index lines may be significantly patchy below this accuracy threshold as shown by the rejection of the third hypothesis. This is somewhat mitigated by the acceptance of the modified fifth hypothesis that patchiness can be independent of the density index.

The fact that this analysis indicates that detectability is not constant, even within a trapping session, and that significant aggregation occurs in mouse populations suggests that the assumptions of even distribution and equal detectability are violated at least some of the time. Without these assumptions, the density index cannot be considered a reliable source of information about mouse populations.

Second research question: do these new techniques provide new information about the processes of change in these populations of mice?

Distance to a road affected models on the two Pureora lines which approached roads (PRL2 and PRE). The PRL2 line was also influenced by distance to escape cover, canopy cover and vascular ground cover. The first trapping session (November 1982) shown on the graph of probability of occupancy against distance to a road from the PRE line (Figure 3.4) resembles a graph of a half-normal model for probability of capture shown by Efford (2004) (this graph shows capture probability against distance from home range centre), indicating that these variables could be important for managers selecting trap sites. Distance to a road was particularly important in determining occupancy on the PRE line and in this type of open habitat I would suggest that traps be placed at least 20m from a road (see Figure 3.4) or not set along roads at all.

King *et al.* (1996b) suggested that mice prefer thick ground cover which is often sparse in forests except close to road margins. If mice do prefer thick ground cover then occupancy would be expected to increase closer to a road. However, on the PRE line, the only line which showed variation in occupancy with distance to a road, probability of occupancy was consistently high only 10 m or more from the road (Figure 3.4). The increase in occupancy with increasing distance from the road could be due to the fact that the canopy was open in this area and dense vegetation was available at some distance from the road (Figures 2.5 and 2.6).

Given that road ways contain neither food nor cover it is logical that an animal would choose a home range with a road at the very edge, not close to the centre, provided that suitable habitat is available further away from the road. However, Martin and Handasyde (2006) found stable bobuck (*Trichosurus cunninghami*) populations in linear strips 10 – 40 m wide along the edges of roads.

In the original analysis conducted by King *et al.* (1996c), distance to a road was found to be an important covariate only for the pooled indigenous forest types. Here, however, distance to escape cover, vascular ground cover and canopy cover were all found to be very significant ($p<0.01$) for the PRL2 line. Apart from the pooled indigenous forest data, few other significant correlations were noted.

The models for PRL2 and PRU lines showed very strong support for variation in detectability with distance to escape cover, vascular ground cover and canopy cover; the original analysis did not detect these covariates as being important on the PRU line. Thus these models support the original covariate analysis and provide a small amount of new information. It is possible that the strong correlations on the PRL2 line are visible there and not in other habitats because of the higher number of ship rats (*Rattus rattus*) in that area which would make access to cover for mice more important for predator and competitor avoidance.

The two patchiest of the three 1975 seedfall peak data points (>20 density index) are from Eglinton, one of these is significantly patchy (Figures 2.3 and 2.4).

The seedfall data collected from the Eglinton Valley at the time suggest that there was no mast event in 1976 (C.M. King unpubl. data; see section 2.1.1.2). It is possible that a small amount of red beech seed, spread unevenly through the valley, could have produced the aggregated population increases observed here, because red beech seed is larger (Wardle 1984) and more nutritious (Beggs 1999).

3.6. Conclusion

My analysis rejects the hypotheses that mice are evenly distributed throughout their habitat and that detectability is independent of the density index. However, I accept the hypotheses that there may be no changes in the detectability of mice at a given station within a trapping session and that degree of patchiness in mouse populations can be independent of the density index.

Chapter Four:

Patchiness and Site Occupancy of ship rats (*Rattus rattus*) and Norway rats (*R. norvegicus*) in five New Zealand forest habitats

4.1. Overview

The purpose of this chapter is to test the two main assumptions of the density index (even distribution, and equal detectability) for rats (ship rats, *Rattus rattus* and Norway rats, *R. norvegicus*) in five types of habitat (pine forest, logged and unlogged mixed podocarp-hardwood forest, homogenous beech forest and heterogeneous beech and podocarp forest) using formal tests of five hypotheses. In addition this chapter aims to investigate the usefulness (or not) of the index of patchiness (Brown *et al.* 2004) and Site Occupancy analysis (MacKenzie *et al.* 2002) in extracting information about rat populations from these data.

In order to assist with visualisation of these data, the raw counts have been graphed in a three-dimensional plot over time. The third dimension is represented by a colour denoting how many animals were caught at that location at that time. These graphs are available in appendix B, Figures B.1 to B.12.

4.2. Patchiness

On the rat trap lines, 36 stations were surveyed for three days, thus each of the 42 samples plotted on the graphs below represents 108 trapnights or one trapping session from one line. Fifty samples (54%) have been discarded from the rat trap analysis because the line caught less than two rats during a trapping session (no line with one capture can be significantly patchy (Brown *et al.* 2004)).

On the Fenn trap lines, both the number of traps and the number of nights over which traps were set varied between trap lines. Each sample from Pureora represents between 320 and 612 trap nights and each sample from Fiordland represents between 400 and 480 trap nights. Of the original 110 samples, 26 (24%) have been discarded from the Fenn trap analysis because the line caught less than two rats during a trapping session.

4.2.1. Results

For rats of both species caught in either type of trap, there was significant variation in the patchiness index, but it was not significantly correlated with any other variable (Table 4.1). Thus, the remainder of this section considers only correlations between the density index and other variables.

Table 4.1: p values from Kruskal-Wallis ANOVAs of each grouping for both patchiness and density index values

	Grouping	Patchiness	Density index
Ship rats, rat traps (n = 281)	Patchiness significance	**0.018**	0.4252
	Trap line (PRU and PRL2 only)	0.803	**0.008**
	Season	0.757	0.4786
Ship rats, Fenn traps (n = 1553)	Patchiness significance	**<0.001**	**0.099**
	Trap line	0.237	**0.001**
	Season	0.145	**0.004**
	Seedfall status	0.907	**0.053**
Norway rats (n = 43)	Season (autumn and spring only)	0.439	0.882

4.2.1.1. Ship rats caught in rat traps

Only two samples from Fiordland had a sufficient number of captures to be assessed for aggregation. Thus the significance of seedfall status has not been assessed for ship rats caught in rat traps. At Pureora only PRU and PRL2 were assessed in the trap line ANOVA because the other three lines had only one suitable sample and the Kruskal-Wallis ANOVA requires at least three samples per grouping.

Patchiness values

Two of 42 points (5%) from ship rats caught in rat traps were significantly patchy (Figure 4.1). There were no significant differences between the density indices of the significantly patchy and non-significantly patchy groups (Table 4.1).

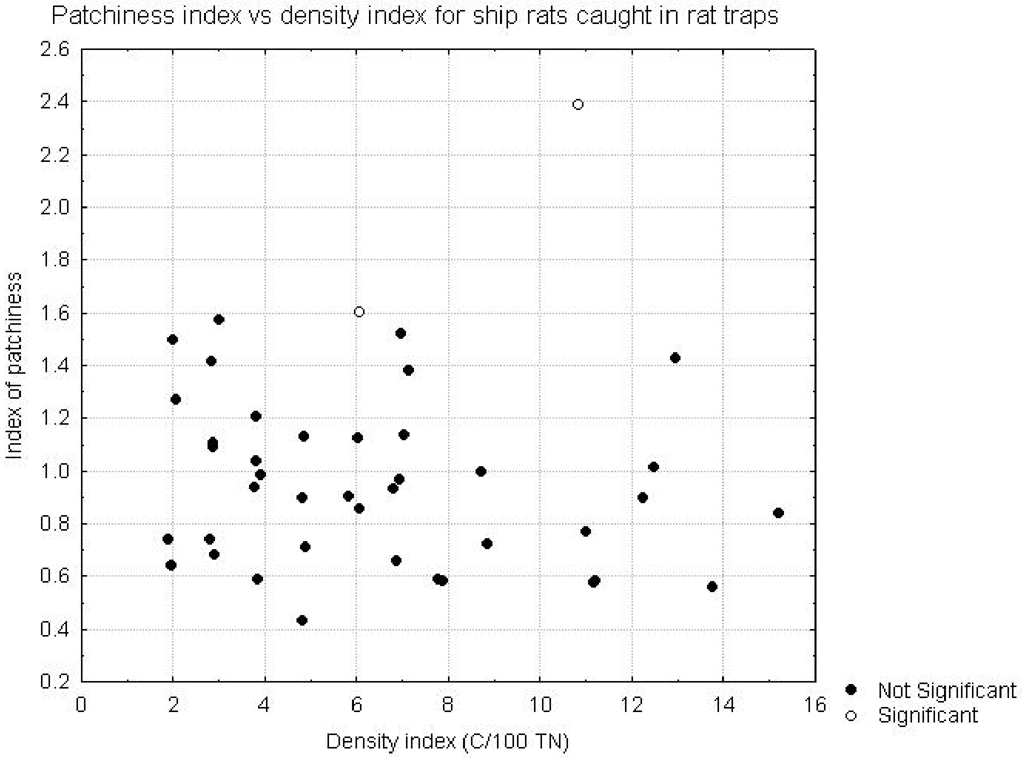

Figure 4.1: Distribution of patchiness and density index values for ship rat captures in rat traps

Trap line

The PRU and PRL2 trap lines were significantly different in terms of density index values (Table 4.1). A larger proportion of the PRU samples were clustered at low density index values whereas the PRL2 samples tended to have higher density index values (Figure 4.2)

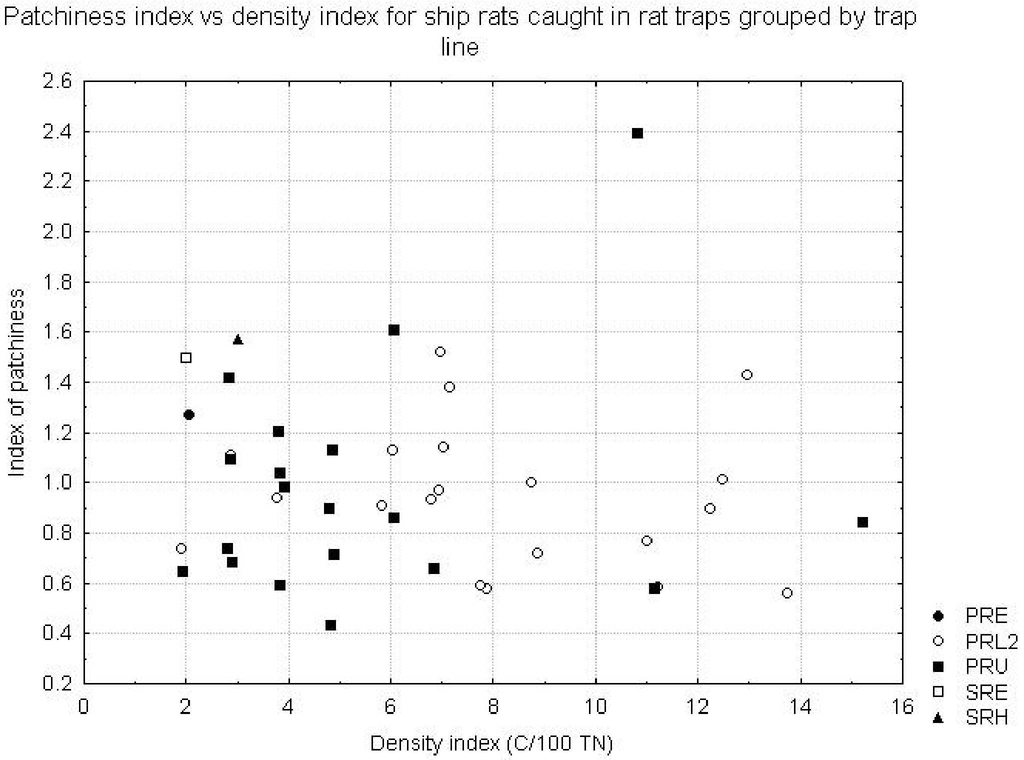

Figure 4.2: Distribution of patchiness and density index values for ship rat captures in rat traps from each trap line

Season

No significant differences in seasonal density indices were found (Table 4.1, Figure B.15).

4.2.1.2. Ship rats caught in Fenn traps

Patchiness significance

Sixteen of 84 samples (19%) from ship rats caught in Fenn traps were significantly patchy, and these significantly patchy samples were spread over a wide range of density index values (Figure 4.3). Significant differences were observed between the density indices of the significant and non significant groups (Table 4.1), probably because the significantly patchy points were not aggregated at low density indices (<2 C/100 TN) as the non-significantly patchy points were.

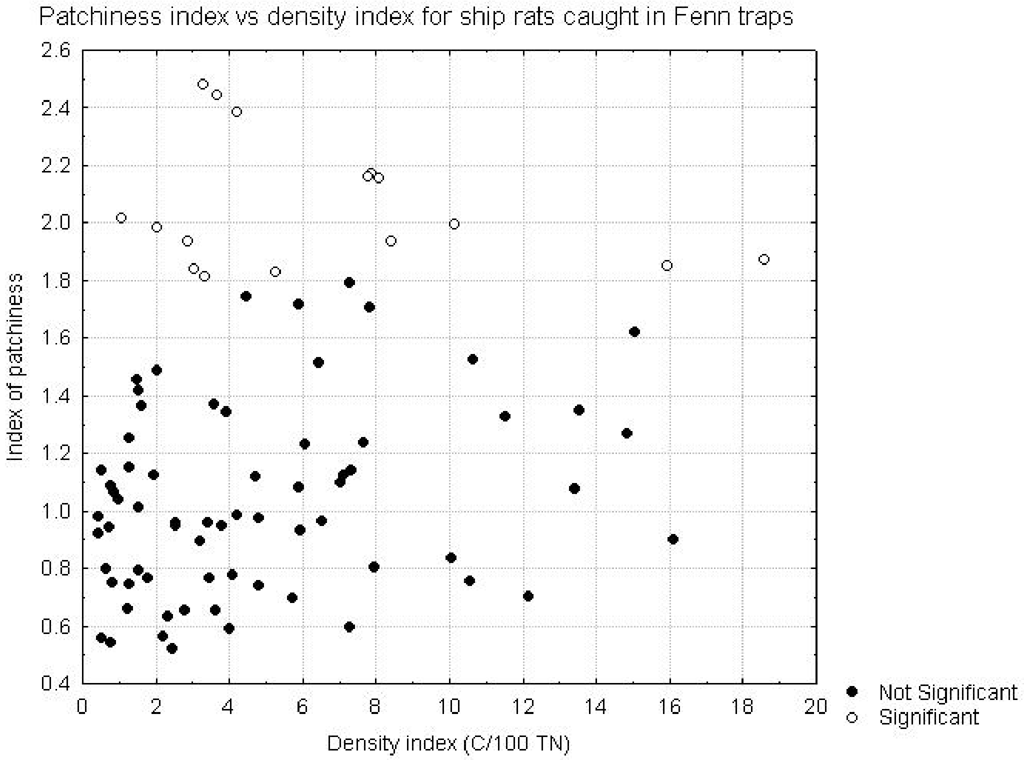

Figure 4.3: Distribution of patchiness and density index values for ship rat captures in Fenn traps

Trap line

Significant differences in density index were observed between trap lines (Table 4.1). Lines PFL and PFU exhibited the largest density index values and the SFE and SFH lines showed the smallest variation in density index values (Figure 4.4).

Season

Significant differences were observed between seasons (Table 4.1). Captures from the summer months showed the least variation in density index values in comparison to other seasons (Figure B.18).

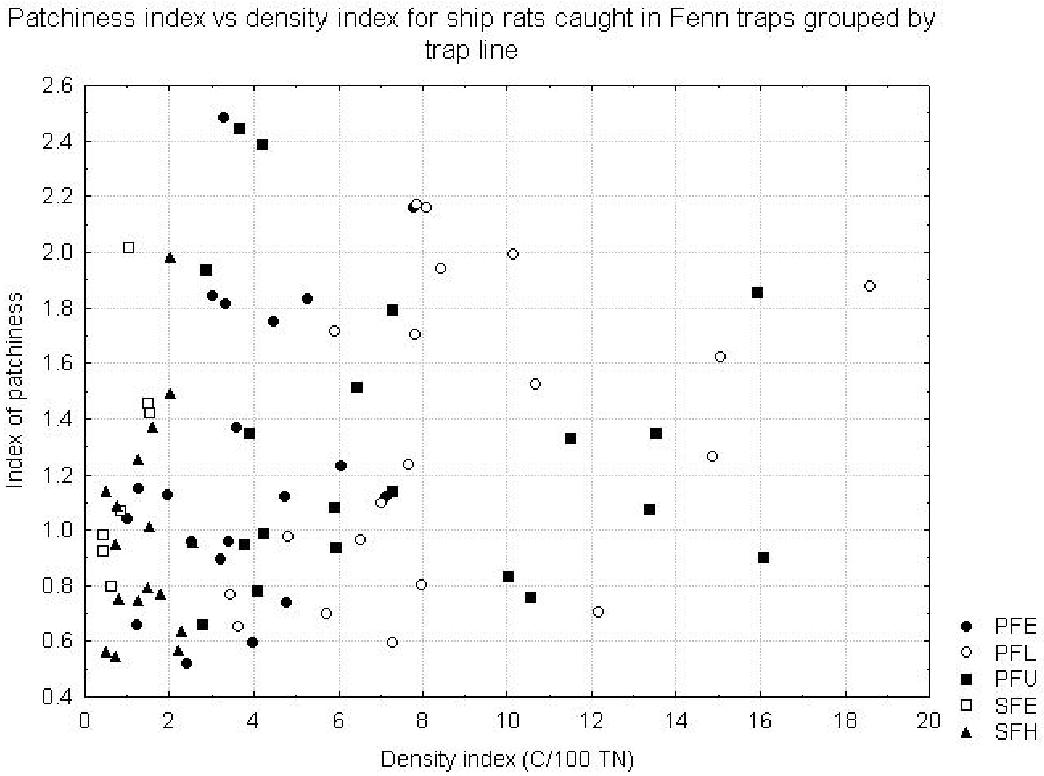

Figure 4.4: Distribution of patchiness and density index values for ship rat captures in Fenn traps from each trap line

Seedfall

Significant differences were observed between the density indices of the two seedfall groups observed (Table 4.1). However, all Fiordland samples had density indices of less than 2.6 C/100 TN (Figure 4.5).

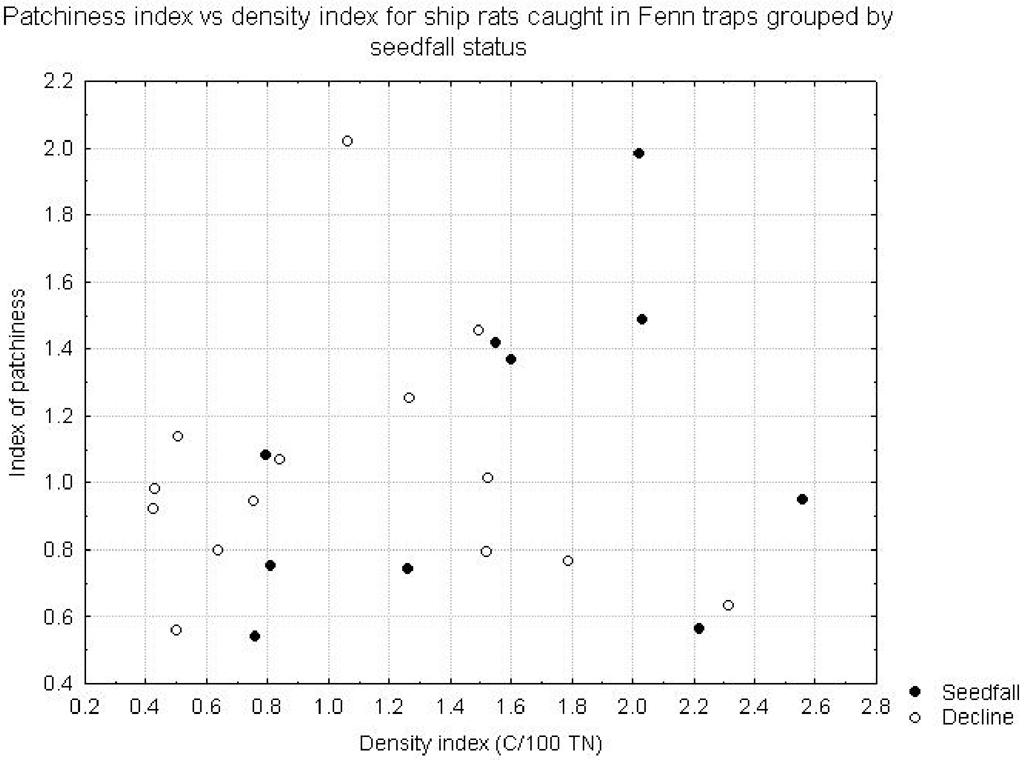

Figure 4.5: Distribution of patchiness and density index values for ship rat captures from Fenn traps from each seedfall phase (Fiordland data only)

4.2.1.3. Norway rats

Patchiness significance

Because all 35 individuals from the PFU line were caught in the same trap (Figure B.12) all samples from this line have the same patchiness value (Figure B.20). This patchiness value is less than one (and thus considered non-significantly patchy) because the trap in which these Norway rats were caught was at the half way point of the trap line, despite being on the very edge of the study area (see Figure 2.4, the trap is marked FU16).

Trap line

Norway rats were captured on two lines, PFL and PFU. However, because the PFL line had only one sample with more than one capture, no ANOVA could be performed.

Season

There were no significant differences in density index values of different seasons (Figure B.21, Table 4.1)

4.3. Site occupancy

The Site Occupancy analysis of ship rats caught in rat traps was confined to the PRL2 and PRU lines because the PRE (n = 2) and SRE (n = 6) trap lines produced insufficient data. All four Fenn trap lines produced sufficient data for the ship rat analyses, though the only the PFU line was adequate for Norway rats.

Definitions for all symbols may be found in the glossary (pages xiv and xv). Tables 4.2 (rat traps) and 4.3 (Fenn traps) show, for each line, all models with ΔAIC values less than two. Additional models with ΔAIC values up to ten can be found in tables B.1, B.2 and B.3.

4.3.1. Results

4.3.1.1. Ship rats caught in rat traps

PRL2 (Pureora logged native forest)

The best fit model for ship rats caught in rat traps on the circular PRL2 line ($\psi(.)p(t+asp+DR+CC+GV+GL)$) had constant probability of occupancy, no colonisation or local extinction, variations in detectability between sessions, and variation in detectability with site aspect, distance to the gravel logging track, canopy cover, vegetative ground cover and cover of forest litter. There was a strong linear relationship between detectability and density index (Figure 4.6).

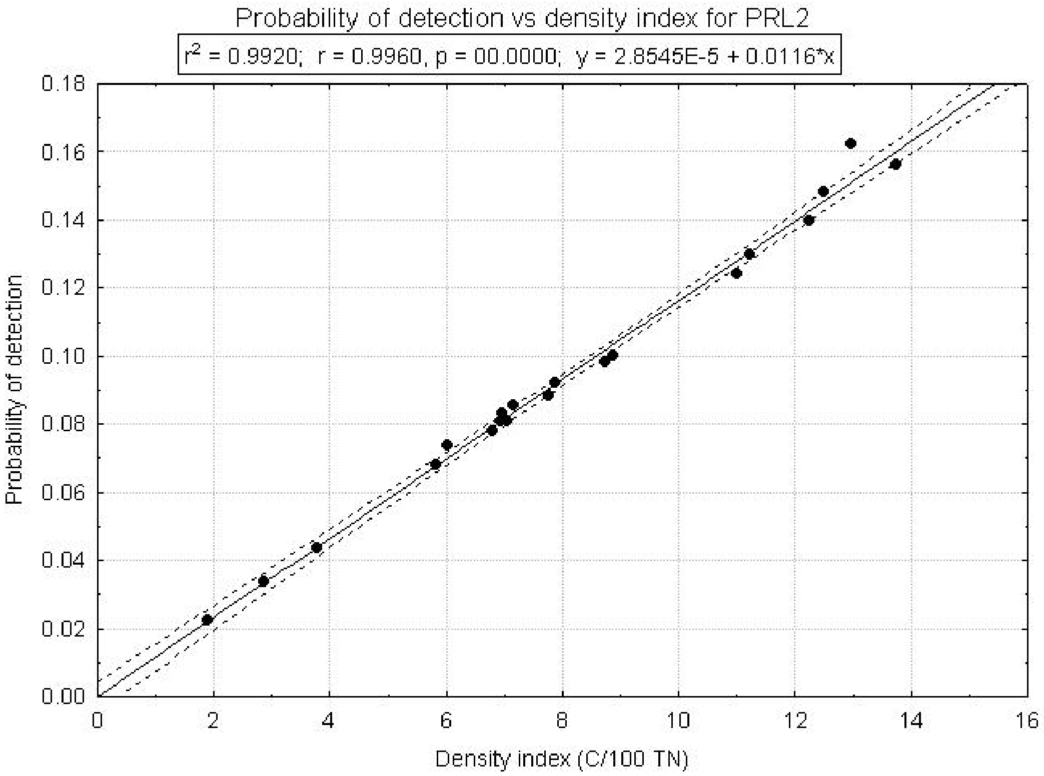

Figure 4.6: Detectability and density index for ship rats on PRL2 using the ψ(.)p(t+asp+DR+CC+GV+GL) model

The best fit model had a probability of occupancy of one – every station caught at least one ship rat – and zero probability of colonisation and local extinction (Table 4.2). Because the analysis supported constant occupancy rather than Markovian changes in occupancy, this indicates that ship rats were present but not necessarily detected at all sites throughout the sampling period, rather than that they were occasionally colonising areas from which they were previously absent. It also implies that sampling with rat traps was light enough not to affect local density.

The analysis strongly supports constant occupancy with variation in detectability with aspect, vascular ground cover and forest litter cover. The analysis also supports variation in colonisation probability with canopy cover and variation in detectability with distance to the logging track, distance to small mammal escape cover and canopy cover. However, the original analyses showed no correlation with these covariates.

PRU (Pureora unlogged native forest)

The best fit model for ship rats caught in rat traps on the PRU line ($\psi(i)\gamma(.)\varepsilon(DE)p(t+alt+CC+DE)$) had variation in probability of occupancy between sessions, constant probability of colonisation, variation in local extinction probability with distance to small mammal escape cover and variation in detectability between sessions, and with altitude, canopy cover and distance to small mammal escape cover. There was a linear relationship between detectability and density index (Figure 4.7)

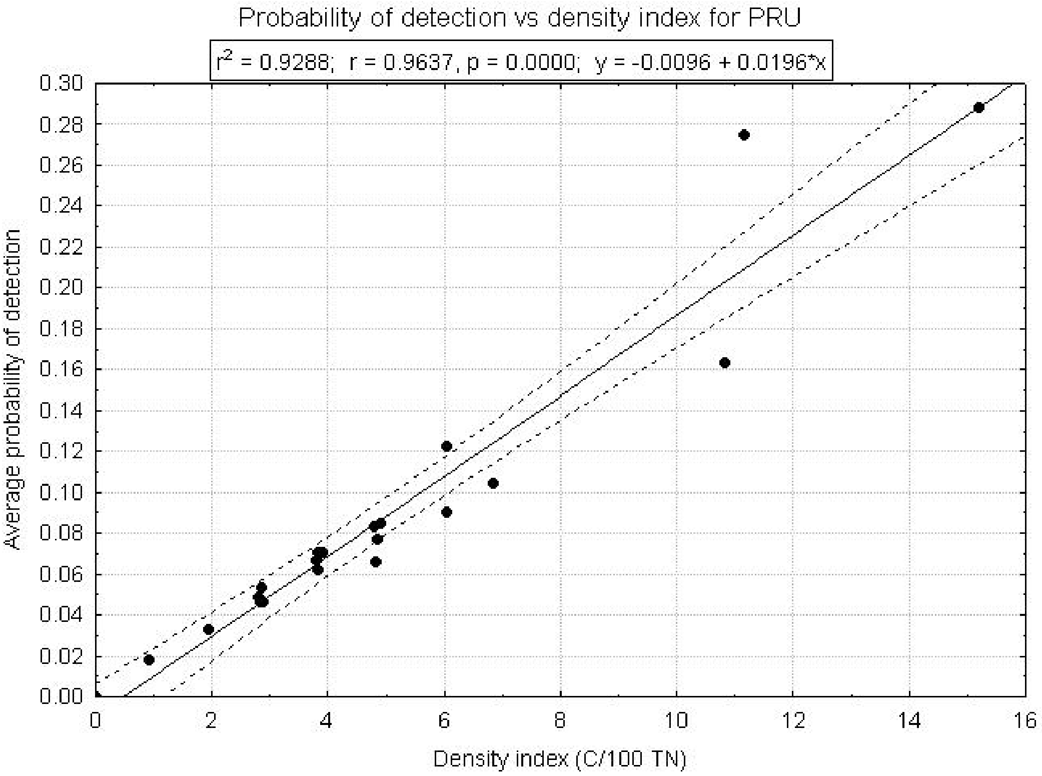

Figure 4.7: Average detectability and density index for ship rats on PRU using the $\psi(i)\gamma(.)\varepsilon(DE)p(t+alt+CC+DE)$ model

The analysis strongly suggests variation in local extinction with distance to small mammal escape cover and variation in detection probability with altitude, canopy cover and distance to small mammal escape cover (Table 4.2).

Neither of the two rodent trap lines which caught ship rats regularly showed any evidence of random occupancy or a decrease in detectability within a three night trapping session.

4.3.1.2. Ship rats caught in Fenn traps

PFE (Pureora exotic forest)

The best fit model (ψ(i)γ(.)ε(H+GV)p(TO*Tds+DR+H+GV)) was a Markovian model with constant probability of colonisation, variation in probability of local extinction with canopy height and ground cover, and variation in detectability and a combination of a decrease in detectability and a trap-out effect as well as variation in detectability with distance to the logging track, canopy height and vascular ground cover. This model shows a weak linear relationship between detectability and density index (Figure 4.8).

The analysis also supports variation in probability of local extinction with distance to the logging track, and variation in detectability with canopy cover, distance to small mammal escape cover, altitude, aspect and drainage, but to a lesser extent.

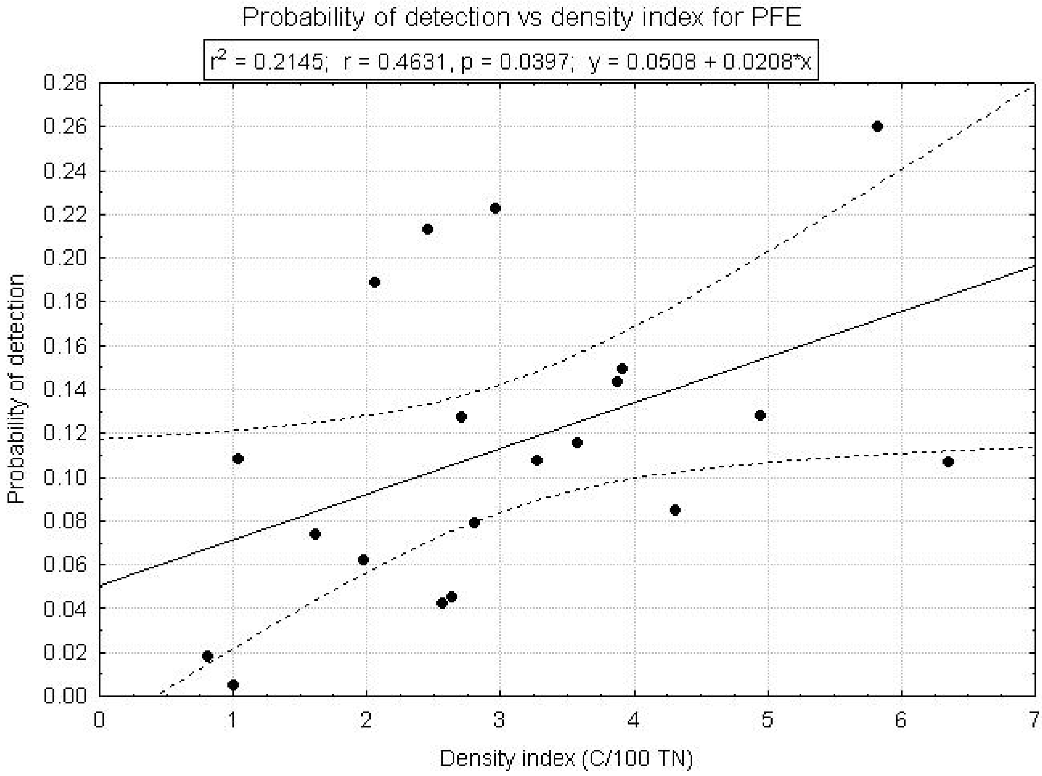

Figure 4.8: Detectability and density index for ship rats on PFE in the first night of each sampling session using the ψ(i)γ(.)ε(H+GV)p(TO*Tds+DR+H+GV) model

PFL (Pureora logged native forest)

The best fit model (ψ(i)γ(.)ε(.)p(TO*Tds+CC)) for ship rats caught in Fenn traps on the PFL line was a Markovian model with constant colonisation and local extinction probabilities and a combination of a decrease in detectability and a trap-out effect as well as variation in detectability with canopy cover. A weak linear relationship between density index and detectability was observed (Figure 4.9, although p = 0.0041).

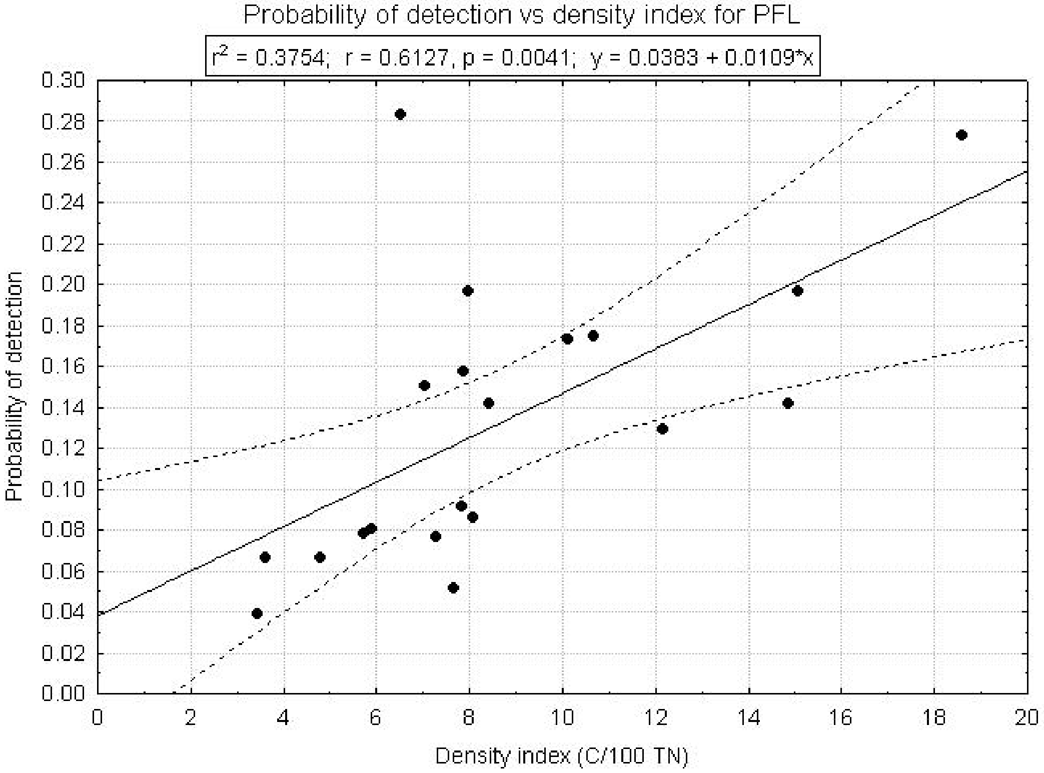

Figure 4.9: Detectability and density index for ship rats on PFL in the first night of each sampling session using the ψ(i)γ(.)ε(.)p(TO*Tds+CC) model

The analysis did not support either random or constant occupancy models suggesting that the occupancy of sites is either at or approaching a dynamic equilibrium.

This is consistent with the PRL2 results, which also showed strong support for variation in detectability with canopy cover. Support for variation with distance to the logging track was weaker but still observed in the PFL analysis. PRL2 did not support canopy height as a covariate and PFL did not show support for variation with aspect, vascular ground cover, or forest litter cover. The PFL analysis showed support for a sessional decrease in detectability and trap-out effect model, where PRL2 did not. This is most likely due to the longer sampling period over longer lines for Fenn traps giving more opportunity to remove individuals from the area.

PFU (Pureora unlogged native forest)

The best fit model ($\psi(i)\gamma(.)\{\varepsilon = 1 - \gamma\}p(TO*Tds+alt)$) for ship rats caught in Fenn traps on the PFU line suggests that stations were occupied at random, with constant colonisation and local extinction probabilities and a combination of a decrease in detectability and a trap-out effect as well as variation in detectability with altitude. This model supported a linear relationship between density index and detectability (Figure 4.10).

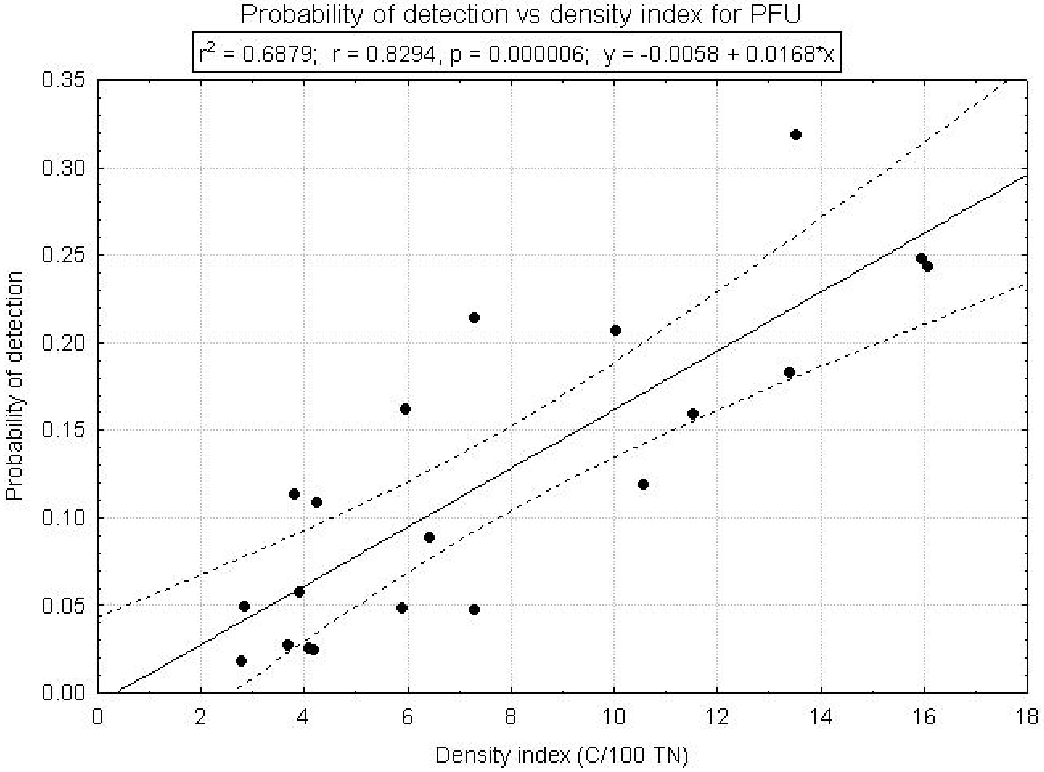

Figure 4.10: Detectability and density index for ship rats on PFU in the first night of each sampling session using the $\psi(i)\gamma(.)\{\varepsilon = 1 - \gamma\}p(TO*Tds+alt)$ model

This analysis also supported variation in probability of occupancy with altitude and Markovian dynamics with constant colonisation and local extinction probabilities, a combination of a decrease in detectability and a trap-out effect as well as variation in detectability with altitude.

SFE (Eglinton Valley, Fiordland)

The best fit model (ψ(.)γ(.)p(t)) suggests dynamic constant occupancy, with constant probability of colonisation, constant (implicit) probability of local extinction and variation in detectability between sessions (Table 4.2). There is a strong linear relationship between density index and detectability (Figure 4.11)

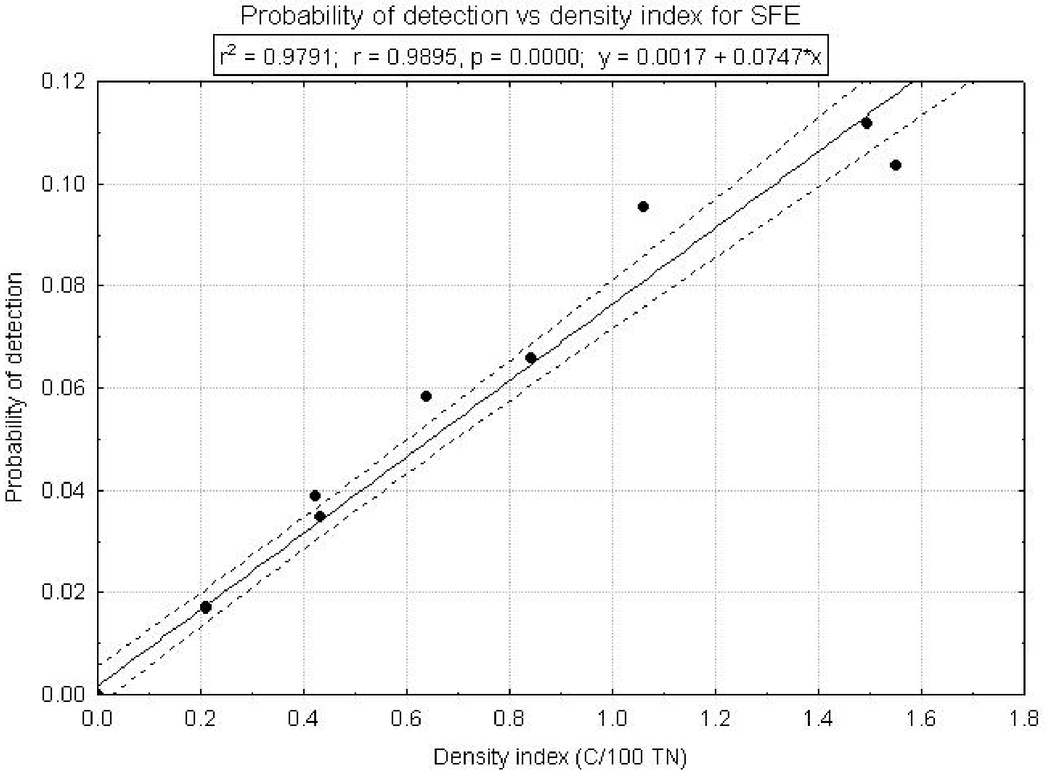

Figure 4.11: Detectability and density index for ship rats on SFE in the first night of each sampling session using the ψ(.)γ(.)p(t) model

4.3.1.3. Norway rats

Norway rats from the PFL trap line (n = 8) have not been analysed using Site Occupancy due to insufficient data.

Only one model was supported by the PFU line, ψ(.)p(t), which indicates that occupancy was constant over time. It implies that the same sites were always occupied, with no colonisation or local extinction. Also, that detectability varied over time, but was constant within a session. Given that all Norway rats observed on this line came from a single trap (FU16 on Figure 2.4), this is an accurate description of these data. A linear relationship between probability of detection and density index was observed (Figure 4.12).

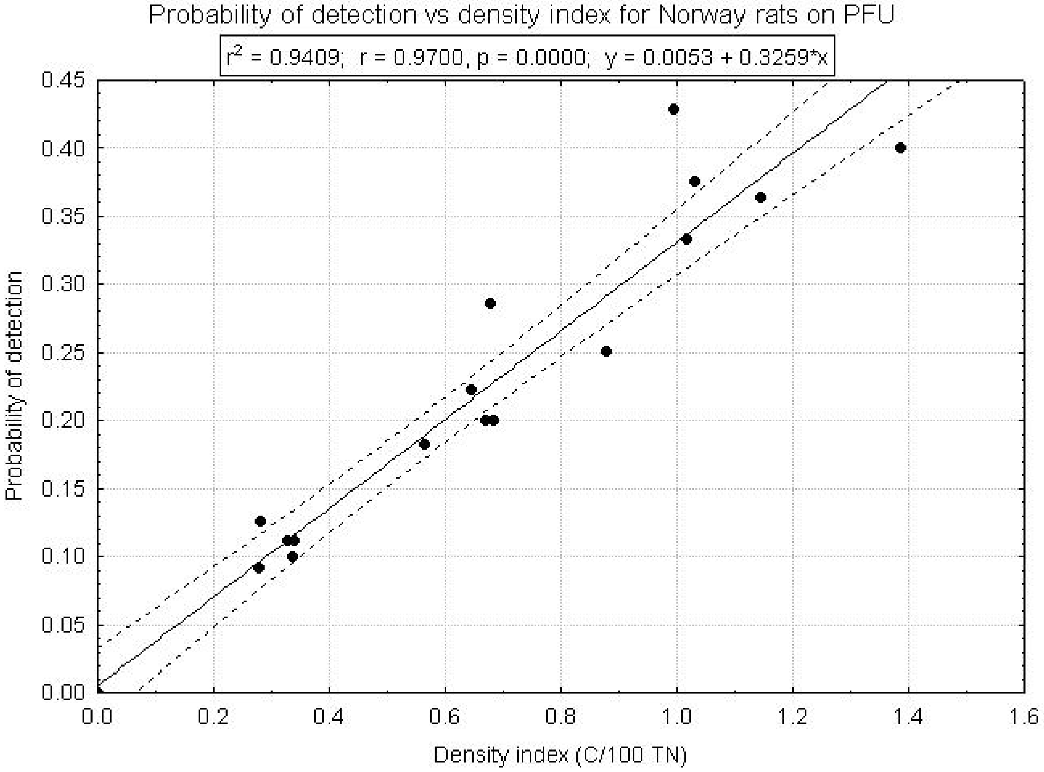

Figure 4.12: Detectability and density index for Norway rats on PFU using the ψ(.)p(t) model

4.4. Discussion

The purpose of this chapter was to test the two main assumptions of the density index for rats: even distribution in space and equal detectability. A second aim was to asses the usefulness of Site Occupancy analysis and the index of patchiness in extracting information from these data. Both techniques were applied successfully, although the usefulness of the patchiness index was limited for ship rats in rat traps, and some data were not suitable for use with one or both of the techniques.

4.4.1. Evaluation of hypotheses

First hypothesis: that there are no changes in the detectability of rats at a given station within a trapping session

This hypothesis was supported by the analysis of Norway rat captures at a single trap on the PFU line; this trap was set beside a small stream at the edge of the forest, most likely near a permanent breeding colony. The lack of variation in occupancy was clearly related to the position of this and surrounding traps in relation to the limited area likely to be occupied by a small breeding colony of Norway rats.

The hypothesis of constant detectability was also supported by the two analyses from ship rats caught in rodent traps at Pureora (PRL2, n = 161 and PRU, n = 106) and from ship rats from Fenn traps in the Eglinton Valley (SFE n = 32). However, it was not supported by the analyses of ship rats caught in Fenn traps from Pureora (PFL = 657, PFU = 467, PFE = 302). Fenn trapped samples of rats from Pureora were much larger than the Fiordland Fenn trap samples. Because ship rats were encountered only occasionally in Fiordland, detectability was relatively constant in comparison to the much larger populations at Pureora where ship rats were rats were detected fairly consistently until all trappable individuals were removed from the area immediately around the traps.

The difference between the detectability of ship rats in the two different trap types at Pureora, both presumably sampling the same population, probably arose because the Fenn traps were set for longer sampling sessions and over longer lines. There is obviously more opportunity to remove all trappable individuals and so create a change in detectability if the population is sampled over a wider area and for a longer period. For example, Shaw (2000) set 815 rat traps (at both 50 and 25 m spacings) continuously for four months in Te Urewera National Park with daily checking of traps in the first one to two weeks after setting. Trap lines totalled approximately 20 km. Shaw found that 50% of the rats he captured were caught in the first week of trapping. He concluded that kill-trapping could be an effective means of reducing rat populations to protect native species. This analysis also supports the idea that kill-trapping of rats over short periods (approximately six days) of intensive trapping may reduce the local population, at least temporarily.

I therefore accept this hypothesis in modified form: that changes in the detectability of rats at a given station *may* not be detected within a short trapping session but are likely to develop over a longer session.

Second hypothesis: that there are no changes in the detectability of rats between trap stations within a trapping session

The only Pureora analysis which did not support this hypothesis was the PFU Norway rat analysis. Given that Norway rats were caught only in one trap, no covariate (except, perhaps proximity to running water, which was not measured) could be expected to adequately explain this distribution. So, I reject this hypothesis.

Third hypothesis: that rats are evenly distributed throughout each habitat at a given time

There was considerable variation between trap type and rat species. Of 42 samples from ship rats caught in rat traps, 5% were significantly patchy, compared with 19% of 84 samples from ship rats caught in Fenn traps.

The greater aggregation that was observed in ship rats caught in Fenn traps could have been related to the longer sample period, rather than an effect of trap type, trap spacing or bait type. If there is a colony of rats living close to a trap, the more nights the trap is set for, the more opportunity it has to resample individuals from the local population and thus the more likely it is that the distribution will appear aggregated. Likewise, the longer the trap line, the greater the chance that the transect will encounter at least one such colony. The relative importance of the effects of trap type, bait type, scale of sampling effort and sample period would need to be further investigated in order to confirm this interpretation.

All of the 35 Norway rat captures from the PFU line came from the same trap, a distribution which can only be regarded as being highly patchy. Yet because this trap was in the centre of the trap line (trap 16 of 32), this distribution was not considered significantly patchy by the analysis (Figure 2.4, labelled FU16).

Because only a small proportion of the samples from ship rats caught in rat traps were significantly patchy (5%) and because the samples from Fiordland represented only lowest end of the total range of density index values, this hypothesis could be accepted in modified form: that rats *may* be evenly distributed throughout each habitat. Nevertheless, I reject it without modification for the following reasons:

1) The short sampling period for rat traps (three days) specified by the standard rodent monitoring protocol could have reduced the chances of rat traps observing greater aggregation in ship rats in this trap type;
2) A substantial portion of ship rat samples collected from Fenn traps over ten to twelve nights of sampling were significantly patchy (19%);
3) Density index values from Fiordland in both trap types were low, but only two rat trap samples were suitable for analysis and significantly patchy points were found across the whole range of observed density indices in Fenn traps;
4) The Norway rat data from the PFU line were obviously patchy, even though the patchiness index could not detect it.

Fourth hypothesis: that the density index for rats is independent of variations in the detectability of rats

All of these analyses show a linear relationship between detectability and density index, though the relationship for ship rats caught in Fenn traps is weaker (especially in the PFE and PFU analyses) than for ship rats caught in rat traps or

Norway rats. I reject this hypothesis, because the analysis showed that detectability was dependent on density index on all tested lines, despite some weaker relationships.

Fifth hypothesis: that the degree of patchiness in rat populations is independent of the density index

The Norway rat samples were so extremely patchy (collected from only one trap (FU16 on Figure 2.4) and most likely all from one colony) that the patchiness index returned the same patchiness value for every sample. This observable aggregation did not vary with numbers of Norway rats caught (density index) and supports this hypothesis.

Both of the two significant points found for ship rats caught in rat traps were in the mid-range of density index values. However, for ship rats caught in Fenn traps, significantly patchy values were spread over the entire range of density index values.

I therefore accept this hypothesis without modification.

If ship rat populations can be significantly aggregated at the highest density indices observed, what are the implications for conservation programs aimed at controlling rats to improve breeding in native birds? If high density populations of ship rats are aggregated in conservation areas, as observed here, control operations at a wide-scale but at low-levels over short periods may not be the most effective method of protecting breeding birds.

Insufficient data were obtained from Fiordland to comment on aggregation at increased densities during and following a possible seedfall event, although significantly patchy samples were observed during both the seedfall and decline (crash) phases of the beechmast cycle. Only low density populations of ship rats were observed in Fiordland during the 1970s when these data were collected, but population levels over the last few years have reached much higher levels (Dilks *et al.* 2003), most recently in the plague proportions of this summer, following the heavy beech mast in autumn 2006 (NZPA 2006). It is important to investigate the local distribution of rats in beech forest through all stages of the beech mast cycle in order to determine if, where and when rat populations become aggregated and how best to adjust conservation policy in response.

4.4.2. Evaluation of research questions

First research question: do these data provide any new information regarding the usefulness of the density index as applied to rats?

This analysis has shown that rat populations can be patchily distributed and that these local aggregations may be observed across a wide range of density indices. This confirms that the density index calculated from a linear transect is not a good measure of rat populations, because it analyses whole lines together, ignoring the question of whether rat populations from a localised area (or several areas) are in fact distributed evenly along the transect sampled.

Detectability was observed to be constant during short trapping sessions, but in samples collected for longer periods, detectability decreased and a trap-out effect was observed. This indicates that density indices based on removal sampling are more likely to be suitable for describing rat populations monitored over short periods (approximately three days) than longer ones.

Second research question: do these new techniques provide new information about these populations of rats?

The Site Occupancy analysis of ship rats caught in Fenn traps largely supported the original covariate analysis (King *et al.* 1996c). For the PFU line, the Site Occupancy analysis supported the original assessment that altitude was the most important covariate (Table 4.4), despite the fact that all stations were within a 100 m vertical range. The site specific vegetation description analysed by King *et al.* (1996c) suggested that this was due to local ponding of cold air in stream valleys. For the PFL line, my analysis supported the importance of canopy cover more strongly than did the original analysis, as well as supporting variation in detectability with distance to a road (this covariate was not identified as important by the original analysis). However my analysis did not support the importance of altitude or canopy height as strongly as the original analysis did (Table 4.4).

The original analysis identified no covariates as significant in the distribution of captures on any of the rat trap lines. My analysis suggested that aspect, distance to small mammal escape cover, distance to a road, canopy cover, vascular ground cover and forest litter cover were all important covariates on the PRL2 line (Table 4.4). On the PRU line, distance to small mammal escape cover, altitude, canopy cover and canopy height were assessed as important covariates (Table 4.4).

Table 4.4: Comparisons between covariates identified by my analysis and the original analysis (King *et al.* 1996c) for ship rats. Physiography, slope and canopy density were not supported by any analysis.

		My analysis		
		Strongly supported	**Moderately supported**	**Not supported**
Original analysis	**Strongly supported**	*PFU:* alt *PFL:* CC	*PFL:* H	*PFL:* alt
	Moderately supported	*PFE(2):* DR		*PFL:* GV
	Not supported	*PRL2:* asp, DR, CC, GV, GL *PRU:* CC, alt, DE *PFE(2):* GV, H	*PRL2:* DE *PRU:* H *PFL:* DR *PFE(2):* DE, CC, alt, asp, drain	*PRL2:* alt, H, drain *PRU:* asp, DR, GV, GL, drain *PFE(2):* GL *PFL:* asp, DE, GV, GL, drain *PFU:* asp, DR, DE, GV, GL, CC, H, drain

The rejection of hypothesis five suggests that rat populations may be locally aggregated regardless of population size, at least at Pureora. However, the Site Occupancy analysis identified an occupancy (ψ) value of 1 for several models on the PRL2 line and one model on the PFE line. This suggests that all sites may have been occupied regardless of whether or not a rat was detected. It is possible that the patchiness index was detecting a colonial structure in otherwise homogenous ship rat populations, or that ship rat populations tended to aggregate around an unmeasured resource.

The combination of these two, apparently contradictory, analyses indicates that rats may be widespread at Pureora, as originally indicated by Innes *et al.* (2001) but only locally abundant. The bulk of the analyses (PRU, PFE, PFL, PFU) certainly do not support universal occupancy: estimates of initial occupancy were as low as 0.2804 (PFE, Table B.2) and estimates of equilibrium occupancy as low as 0.4672 (PRU, Table B.1). This is not to imply that some stations were never occupied, merely that they were never all occupied at the same time.

The conclusion that rats may be widespread at low levels but only locally abundant challenges the perception from standardised low-level monitoring that rats are widely and evenly distributed throughout North Island mixed forest. Detailed local monitoring with automated devices set for weeks at a time suggests that standard short-term rodent tracking surveys miss a great deal of local heterogeneity in rat distribution (King *et al.* in press).

4.5. Conclusion

My analysis has rejected the hypotheses that rats are evenly distributed throughout each habitat during a given trapping session, that there are no changes in the detectability of rats between trap stations within a trapping session and that the density index is independent of variations in the detectability of rats.

However, I have accepted the hypotheses that degree of patchiness in rat populations is independent of the density index. The question of changes in the detectability of rats at a given trap station within a trapping session depends on the length of the session: it may be negligible in three days but significant after six days.

My analysis has provided new information about these populations and factors affecting the detectability of rats and how they are detected on a trap line.

Chapter Five:

Patchiness and Site Occupancy of stoats (*Mustela erminea*) in five New Zealand forest habitats

5.1. Overview

The purpose of this chapter is to test the two main assumptions of the density index as applied to stoats (*Mustela erminea*) in five different habitats (pine forest, logged and unlogged mixed podocarp-hardwood forest, homogenous beech forest and heterogeneous beech and podocarp forest) using formal tests of five hypotheses. In addition this chapter aims to investigate the potential usefulness (or not) of Brown's index of patchiness (Brown *et al.* 2004) and Site Occupancy analysis (MacKenzie *et al.* 2002) for extracting information about stoat populations from these data.

In order to assist with visualisation of these data and with presentation of the complex variations in sample size, the raw counts have been graphed in a three-dimensional plot over time. The third dimension is represented by a colour denoting how many animals were caught at that location at that time. These graphs are available in appendix C, Figures C.1 to C.6.

At least some samples were available for patchiness analysis from all five habitats and all seasons. But Site Occupancy analysis can not be applied to samples with very low capture rates. Thus, this method was tested on only the summer samples from two habitats: January from Pureora exotic forest over five years, and December, January and February from Eglinton valley beech forest during the peak and decline years following the 1976 seedfall.

5.2. Additional methods

Samples from each summer month in Eglinton had to be analysed separately for the Site Occupancy analysis because the summer is a period of rapid change in stoat populations, so the data from the summer season could not be considered represent a single trapping session with closed occupancy. Nor could these be analysed as six separate samples, because the peak and decline years had such different populations. Splitting the Eglinton samples by month also allows the comparison of results between this area and Pureora, which were sampled only in January.

Data from the whole period of sampling on the Eglinton trap line, including data not used with either the patchiness index or Site Occupancy analysis, were pooled into two night sums and graphed after King (1980). This was done in order to compare the original analysis of trap out effect with this analysis.

5.3. Patchiness

Of the 110 samples collected over all five trap lines during data collection, 62 were discarded from the patchiness analysis because the line caught either no animals or only one animal during a trapping session (no line with one capture can be significantly patchy (Brown *et al.* 2004)). This has left 48 samples in total.

5.3.1. Results

Patchiness values

Four of 48 samples were significantly patchy (Figure 5.1). The differences between the patchiness values of the significantly patchy group and the non-significantly patchy group were, of course, significant, but the associated density indices of these two groups were not (Table 5.1). No samples have been observed for stoats with both high density index and high patchiness values (Figure 5.1) suggesting that aggregation is likely only at low densities.

Trap line

Monthly Fiordland density indices ranged from <1 to 9 C/100 TN however, all of the points from Pureora had density indices below 2 C/100 TN (Figure 5.2). Significantly patchy samples were found on the SFE (2 samples), PFE and SFH lines (Figure 5.2). There were no significant differences between trap line groupings (Table 5.1).

Table 5.1: p values from Kruskal-Wallis ANOVAs of each grouping for both patchiness and density index values

Samples grouped by:	Patchiness	Density index
Patchiness significance	**< 0.001**	0.521
Trap line	0.970	0.463
Season	0.441	**0.044**
Seedfall status	0.813	**0.003**

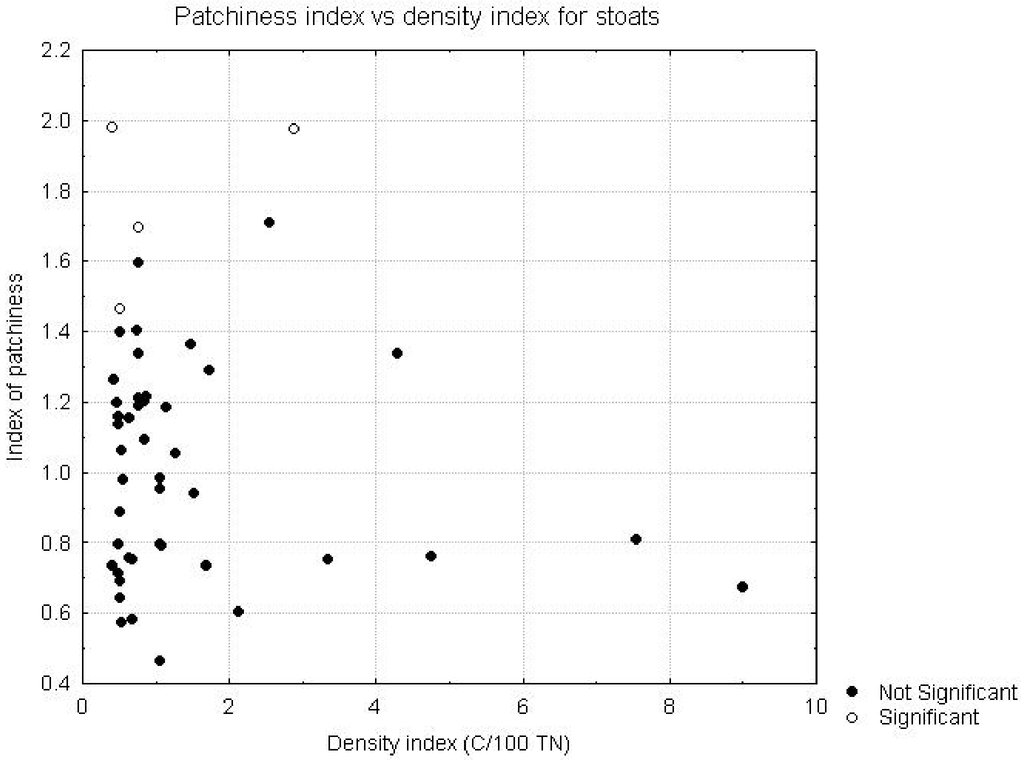

Figure 5.1: Distribution of significantly patchy and non-significantly patchy stoat samples

Season

There were significant differences between density index groupings for season as is expected with the summer population increase due to the dispersal of young stoats. However, there were no significant differences between the associated patchiness index values (Table 5.1).

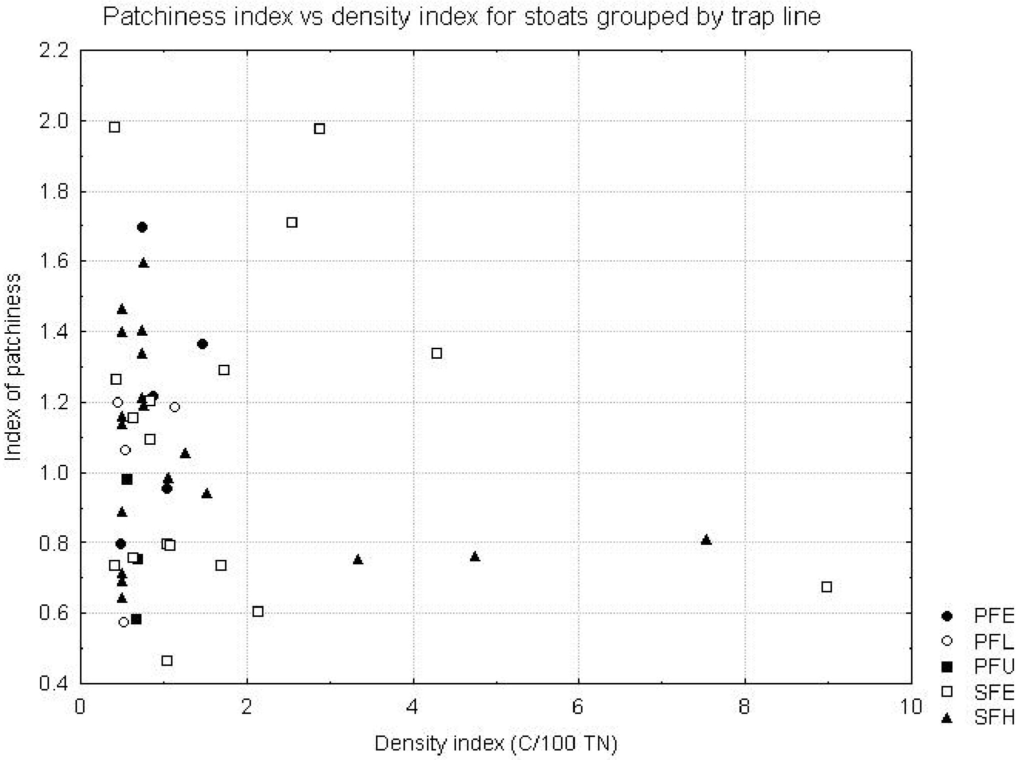

Figure 5.2: Distribution of patchiness and density index values for stoat samples from each trap line

Seedfall status

There were significant differences between density index groupings for seedfall status but not between their associated patchiness index values (Table 5.1). All of the eight points with density index values >2 came from Fiordland. Three of these points came from the decline phase and five from the seedfall phase (Figure 5.3). Of the four points with density index values between 2 and 4, three represented the decline phase and one was from the seedfall phase.

One of the summer seedfall samples from the Eglinton Valley was significantly patchy, but none of those from the Hollyford Valley have patchiness values less than one (Figures C.8-C.10). This probably indicates aggregation near the masting trees and consequently abundant sources of mice (see Chapter two), however the data describing the distribution of trees in this area is insufficiently specific to confirm this.

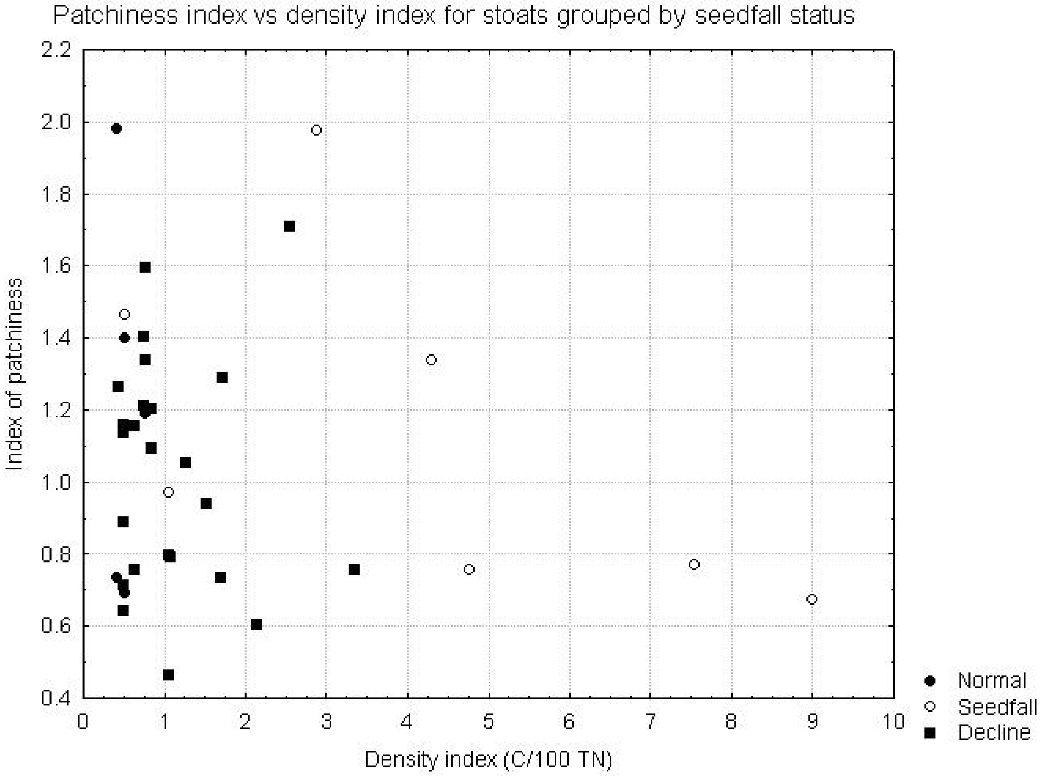

Figure 5.3: Distribution of patchiness and density index values for stoat samples from each seedfall phase (Fiordland only)

Three of those eight points with density index >2 came from the Hollyford Valley and five from the Eglinton Valley (Figure 5.2). All of the Hollyford values had low (<1) patchiness values, whereas three of the Eglinton values had high (greater than 1.3) patchiness index values (one of which was significant) and two had low (<1) patchiness index values.

5.4. Site Occupancy

Definitions for all symbols may be found in the glossary (pages xiv and xv). Table 5.2 shows, for each line, all models with ΔAIC values less than two. Additional models with ΔAIC values up to ten can be found in Table C.1.

5.4.1. Results

PFE (Pureora exotic forest)

All of the models from the PFE line with ΔAIC values less than two supported random changes in occupancy (Table 5.2). There was also some support for trap-out, single-season (constant occupancy) and Markovian models (Table C.1). King *et al.* (1996c) pointed out that more stoats caught at Pureora in the first two trapping sessions (a total of 21 in January and April 1983, compared with 7, 6, 4 and 5 in the same two sessions in the next four years), probably because the area had never been trapped before.

There was no relationship between detectability and density index (Figure 5.4) as the first summer sample, with the highest density index (January 1983) also had a low detectability value in comparison with the second summer sample (January 1984).

There was also support for variation in ψ, γ and p with distance to the gravel road (Table 5.2). The best fit model ($\psi(DR)\gamma(.)\{\varepsilon = 1 - \gamma\}p(t)$) suggested a decrease in occupancy with distance away from the road. This gave occupancy values of one for most (78%) of the line which was originally designated FE1 (King *et al.* 1996a) (Figure 1.1), probably because, for logistic reasons, traps in this area were less than 15 m from the road. However, only one stoat was ever found in this section of the PFE line.

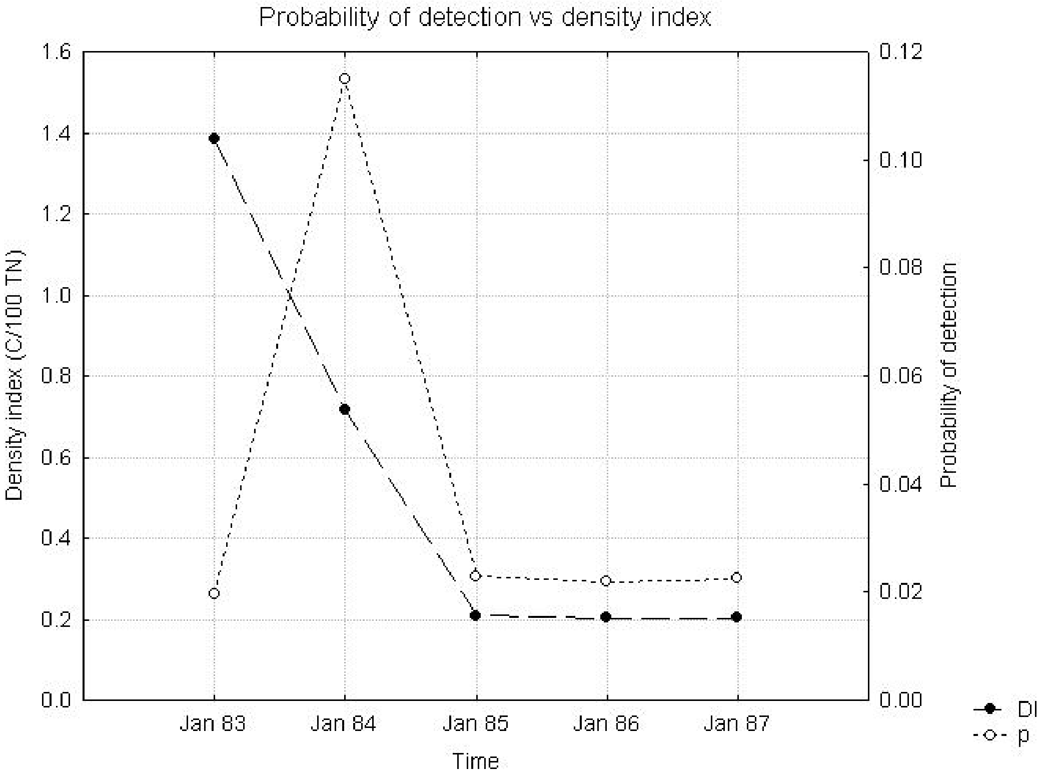

Figure 5.4: Density index and detectability from the PFE line using the $\psi(DR)\gamma(.)\{\varepsilon = 1 - \gamma\}p(t)$ model

SFE (Eglinton Valley)

All three models show a decrease in detectability between the summer of 1976/77 and the summer of 1977/78 (Table 5.3), which is expected, given that these data represent the peak and decline populations.

The December models from the SFE line show strongest support for Markovian models, with some support for random changes in occupancy (Table 5.2) and constant occupancy (Table C.2). The January models show strong support for random changes in occupancy with some support for constant models (Table 5.2). Also strongly supported during these two periods is the p(TO) model, which suggests that stoats were trapped out of the local area in the first six days of trapping (Table 5.2).

The February models from SFE show strong support for constant occupancy (Table 5.2) and some support for the trap-out scenario (Table C.2).

Table 5.3: Density indices, detection probability, initial occupancy, colonisation and local extinction probabilities for the best fit models from three SFE analyses

Model		Density index	p	ψ_i	γ	ε
December $\psi(i)\gamma(.)$ $\{\varepsilon = 1 - \gamma\}p(t)$	76	2.8793	0.0872	0.3252	0.5713	0.4287
	77	1.6967	0.0296			
January $\psi(i)\gamma(.)$ $\{\varepsilon = 1 - \gamma\}p(t)$	77	8.9912	0.1822	0.4816	0.1814	0.8186
	78	1.7260	0.0847			
February $\psi(.)p(t)$	77	4.2965	0.0534	0.7934	N/A	N/A
	78	0.8493	0.0106			

Figure 5.5 has been redrawn from King (1980) and shows the total number of captures for each two night period through the ten to fourteen night trapping session using all data from the Eglinton Valley. It clearly shows a decrease in number of animals caught.

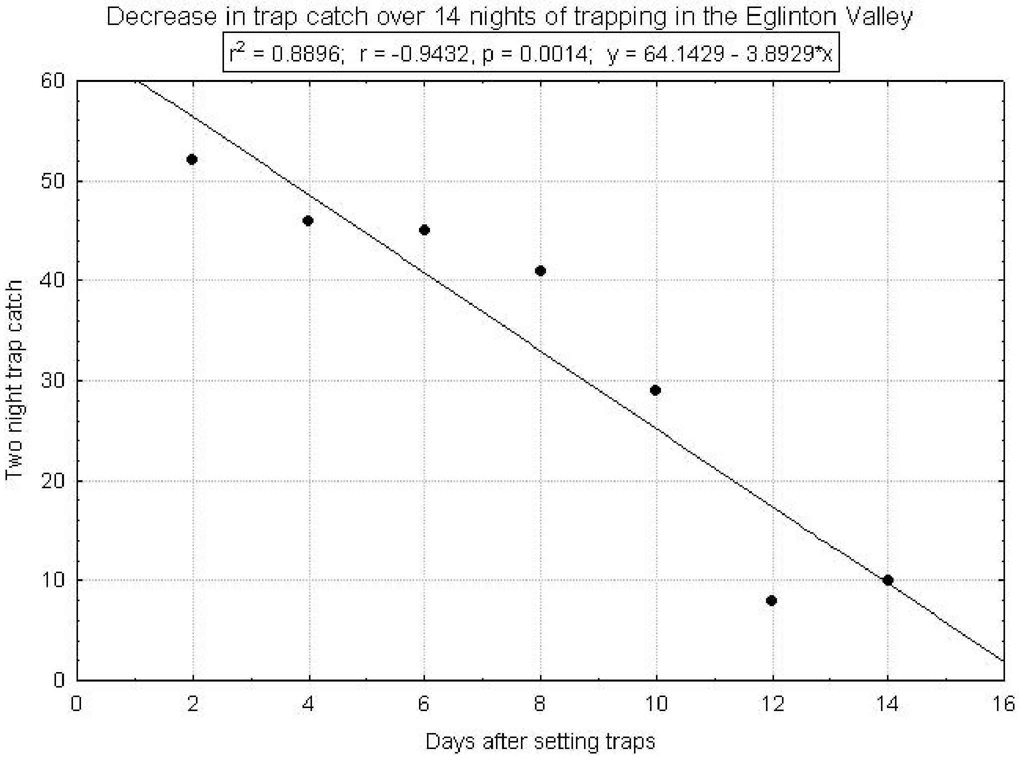

Figure 5.5: Decline in number of stoats captured every two nights, all seasons and all years pooled, recalculated with the data from the Eglinton Valley only (after King 1980).

5.5. Discussion

The purpose of this chapter was to test the two main assumptions of the density index using formal tests of four hypotheses. I have accepted one of these hypotheses in its original form, two in modified form and rejected one altogether.

Site Occupancy analysis could not be applied to two trap lines (PFL and PFU) due to lack of data. The results that have been presented should be regarded with caution because of the extreme zero inflation of the data, however, the results are internally consistent. For example, similar results were obtained from samples taken in January in both Eglinton and the Pureora exotic forest.

5.5.1. Evaluation of hypotheses

First hypothesis: that there were no changes in the detectability of stoats at a given trap station within a trapping session.

None of the p(Tds) models that were tested had ΔAIC values less than 10, showing that detectability did not trend down within a session. However, there was strong support for a p(TO) model in December and January on the SFE line (Table 5.2) and some support on the PFE line and in February from the SFE line (see Table C.1). These models imply a trap-out effect: most animals available to be caught were removed during the first six days of trapping. This conclusion confirms the suggestion of King (1980) based on much simpler methods that capture rate declined during each trapping session.

There are indications that this trap-out effect was present in all four analyses reported in Table 5.2 and C.1, violating the assumption of constant detectability through a trapping session. Thus, I reject my first hypothesis.

Second hypothesis: that there are no changes in the detectability of stoats between trap stations within a trapping session

There is only mild support for this hypothesis from one model on the PFE line with a ΔAIC value of 4.60. This model supports variation in probability of detection with the distance to a logging track.

Because there is little evidence to either support or falsify this hypothesis, I accept it in modified form: that there *may or may not* be changes in the detectability of stoats between trap stations within a trapping session.

Third hypothesis: that stoats are evenly distributed throughout each habitat during a given trapping session.

Four of the 48 points from the five trap lines were significantly patchy (one of twelve from Pureora and three of 36 from Fiordland). Hence, stoats are not always evenly distributed throughout the habitat, so this hypothesis is falsified.

However, the patchy lines represent only 8% of the data which had the potential to be significantly patchy (two or more captures within a session). Because the majority of the data were relatively evenly distributed, violations of the assumption of even distribution were detected only occasionally in this data set.

It seems more reasonable to accept this hypothesis in modified form: that stoats *may or may not* be evenly distributed throughout the habitat.

Purdey *et al.* (2004) found that most of the live stoat visits recorded, and dead stoats collected, in the Grebe Valley during the decline phase of the 1999/2000 seedfall event, were observed in only 9 of their 30 traps. This distribution appears patchy even to casual inspection (Purdey *et al.* 2004). A cursory analysis of the data provided in Purdey's (2004) paper gives a significantly patchiness value of 2.1 ($p = 0.014$).

My analysis showed that all of the significantly patchy points from the Eglinton (SFE) and Hollyford (SFH) Valleys during the 1976/77 seedfall were detected during the seedfall phase. This is what would be expected if the distribution of seeding trees was patchy causing locally high mouse populations.

This analysis indicated that probability of occupancy increased with proximity to a road on the PFE line (Table 5.2), suggesting that stoats may use roads through mature exotic forest as movement corridors or to hunt prey (such as rabbits) which may prefer the grassy road margin habitat.

Only one trap line (PFU) was not set along a road. Unfortunately, the PFU line caught an insufficient number of stoats to make Site Occupancy analysis viable and it thus cannot be used as a comparison with PFE. However, radio tracking data from the Eglinton Valley suggested that stoats may use the road to scavenge food from road kills (Murphy and Dowding 1995).

Fourth hypothesis: that the density index for stoats is independent of variations in the detectability of stoats.

This analysis found no relationship between density index and detectability of stoats on the PFE line (Figure 5.4). However, all three models from the SFE line show a decrease in detectability with the decrease in density index from the summer of 1976/77 to 1977/78. This decrease is expected, given that these data represent a seedfall peak and crash year. It is possible that density index is dependent on the detectability of stoats only at this time of the beech mast cycle; this idea may be worth testing further.

Because one trap line tested showed independence between density index and detectability while the other did not, I accept this hypothesis with modification: the density index *can* be independent of variations in the detectability of stoats.

Fifth hypothesis: that the degree of patchiness in stoat populations is independent of the density index.

This data set included too few significantly patchy samples on which to base a firm conclusion. Only one of these was associated with a density index value greater than two, and Figures 5.1, 5.2 and 5.3 show a conspicuous lack of points in the upper right hand corner (high patchiness and high density). However, the

Kruskal-Wallis ANOVA indicated that there were no significant differences in the density index values of the significant and non-significant groups (Table 5.1).

Thus, I accept this hypothesis in modified form: that the degree of patchiness in stoat populations *may* be independent of the density index.

5.5.2. Evaluation of research questions

First research question: do these data provide any new information regarding the usefulness of the density index as applied to stoats?

This analysis indicates that stoat populations are usually evenly spread through all forest habitats, without significant patchiness. If correct, this vindicates the randomly placed index line method used by DOC to monitor stoats (C. Gillies & D Williams, unpubl.), which assumes that stoats are evenly spread across the landscape.

Perhaps more importantly however, this analysis suggests that routine trapping with traps reset daily over a short period may be an effective method of stoat control, if only briefly. Many of the models suggested a trap-out effect, indicating that most individuals are removed from the trapping area in the first six nights of trapping. Longer trapping periods therefore do not meet the constant detectability assumptions of the density index (captures per unit effort). I suggest that, in order to use removal trapping data to calculate a density index for stoats, it is necessary to use shorter periods of trapping than the 10-12 nights used in this analysis.

It is possible that daily checking of traps may be more cost-effective at reducing local populations of stoats than current DOC practice of checking traps only once per week (Lawrence and O'Donnell 1999). Further testing would be required to confirm this.

Second research question: do these new techniques provide new information about the processes of change in these populations of stoats?

Stoat populations were significantly patchy during the seedfall phase in both Eglinton (SFE, two (12%) of 17 samples) and Hollyford (SFH, one (5%) of 19 samples) Valleys (Figures 5.2, 5.3 and 5.4). The significantly patchy samples from Eglinton have higher patchiness values and one has a higher density index value than the Hollyford samples do. A likely explanation for this is that stoats aggregate near prey sources (rodents), which would probably be aggregated around masting trees.

The seedfall data collected from the Eglinton Valley at the time suggest that there was no mast event in 1976 (C.M. King unpubl. data; see section 2.1.1.2). It is possible that a small amount of red beech seed, spread unevenly through the valley, could have produced the aggregated peak mouse populations observed here (see Chapter three, p. 57) and consequently aggregated peak stoat populations. The difference in the degree of patchiness in stoat captures between the two valleys was consistent with the variation in mouse aggregation (Figure 3.2).

This analysis suggested some support for random changes in occupancy in the Pureora exotic forest and the Eglinton Valley. Random occupancy refers to the fact that there is no consistency in occupancy, it makes no predictions about which traps are occupied and how frequently.

I suggest two potential explanations for the observation of random occupancy: juvenile dispersal (King and McMillan 1982) or large home range size (Murphy and Dowding 1995, Cuthbert and Sommer 2002). Both of these factors would cause violations of the assumptions of independence and closure had these data been collected using live trapping rather than kill trapping methods. This needs to be taken into consideration in any future use of the Site Occupancy method for monitoring stoats. The juvenile dispersal hypothesis is supported by the fact that, of the three months analysed from Eglinton (SFE) it was the January sample which supported random occupancy as strongly as did the Pureora (PFE, January) sample. Both of these would have been collected during the peak time for juvenile dispersal (King and McMillan 1982).

5.6. Conclusion

My analysis has accepted three of the four hypotheses, all in modified form. Stoats may be evenly distributed throughout each habitat; the density index can be independent of variations in the detectability of stoats; and the degree of patchiness in stoat populations may be independent of the density index. However, while detectability of stoats is initially constant, it declines rapidly after approximately six days as the few available (or the most highly trappable) individuals are caught.

Chapter Six:

General discussion and conclusion

6.1. Overview

The most widely used method of monitoring small mammals (mice (*Mus musculus*), rats (*Rattus rattus* and *R. norvegicus*) and stoats *(Mustela erminea*)) in New Zealand, is based on regular removal trapping along fixed transect lines and the subsequent calculation of the number of captures per unit effort. This density index assumes that animals are evenly distributed along the transect line and that all animals are equally catchable. The objectives of this thesis were (1) to evaluate the assumptions made by the density index with respect to detectability and patchiness of small mammals, and (2) to evaluate the whether the patchiness index and Site Occupancy analysis methods might contribute to improved protocols for monitoring small mammal populations in the future.

This analysis suggests that neither of the two assumptions of the density index (even distribution and equal detectability) are met with any regularity.

This analysis also suggests that both the patchiness index and Site Occupancy analysis methods may be suitable for evaluating small mammal populations in the future, provided that samples are large enough and the sampling design is appropriate. Site Occupancy analysis was difficult to apply to removal data when capture records were few, this was particularly true in the stoat data sets. However, both techniques proved internally consistent (if not always in agreement), and both extracted useful new information out of existing monitoring data for small mammals.

6.2. Application of new techniques

Both techniques were unsuitable for use where the data were very sparse, for example when animals were caught at only one station on a trap line. Where data were more abundant, the index of patchiness was entirely suitable for use with stoat or standard rodent monitoring data because these are very similar to the data for which the patchiness analysis was originally designed. This index suggested that most natural populations are normally well dispersed, and occasionally significantly aggregated. Only rarely did the patchiness analysis return a significantly patchy value of <1.8 for any species on any trap line. Only three exceptions to this were found: PRU ship rats (patchiness value 1.60, February 1985); PFE stoats (patchiness value 1.70, October 1987); and SFH stoats (patchiness value 1.46, during seedfall, November 1976)

Site Occupancy analyses are best applied to repeated counts of live animals with good information on potential sources of heterogeneity, so were more often derailed by the problem of inadequate data than were the patchiness indices. The stoat data sets were unsuitable for Site Occupancy analysis most often. However, when the data were adequate, this method did provide useful information, because it is not always necessary to know precisely how many animals are present in an area (indeed, a density index does not answer this question). Site Occupancy would work even better with data collected with this analysis technique specifically in mind, including all necessary covariate information and attention to the serious issue of independence of samples.

6.2.1. Usefulness of Site Occupancy and the index of patchiness in evaluating the hypotheses

The assumptions of the density index have often been questioned but rarely tested, even though it has been the main tool of routine monitoring since the early 1970s. A cost-efficient first step towards addressing this problem is to evaluate a set of hypotheses using re-analyses of existing data. The main problems encountered in using this approach were due to deficiencies in the data sets (such as lack of covariates, insufficient sample sizes etc), because they were collected for other purposes. The compensating advantage of using existing data was that samples representing a very wide range of locations, habitats and years, consistently collected by identical or nearly identical methods, were available without the cost of undertaking new field work. The conclusions of the re-analysis are robust enough to contribute useful information to the debate on future monitoring methods but cannot give a decisive answer. They are potentially important because they show that the assumptions of the density index are often violated.

The new methods were useful in showing that: (1) Small mammals were not always evenly distributed along a trap line, although in many cases aggregation was minimal. The Fiordland analysis showed concurrent aggregation of mice and stoats during a partial seedfall. (2) Detectability in all species estimated from removal data varied either between stations with covariates, or at the same station as individuals were removed, though this was not the case for every trap line. Given sufficient data, Site Occupancy analysis was able to control for these variations in detectability.

6.3. Pureora

Useful results were obtained for three of the four species recorded (mice, ship rats and stoats). The total number of capture records analysed was 496, 1695 and 57 respectively. The fourth species, the Norway rat, has been excluded from the evaluation of hypotheses because the 43 capture records were, paradoxically, too extremely patchy to produce useful results with either method (Chapter four).

6.3.1. Evaluation of hypotheses: Pureora

First hypothesis: that there are no changes in the detectability of small mammals at a given trap station within a trapping session.

This hypothesis was falsified by the analyses of two of the four species (mice and ship rats) studied, although there were variations between habitat types and between trap types for ship rats.

The models showed strong support for a decrease in detectability of mice through each trapping session in logged native (PRL2) but not exotic or unlogged native forests (PRE or PRU). Models for ship rats caught in Fenn traps showed strong support for a decrease in detectability and a trap out effect over a ten to twelve night trapping session: models for ship rats caught in rat traps supported neither. Stoat data could be analysed only from the exotic forest (PRE) and these data showed no support for a decrease in detectability during the ten to twelve night Fenn trapping session.

Thus I accept this hypothesis in modified form: that there *may or may not* be changes in the detectability of small mammals at a given trap station within a trapping session.

Second hypothesis: that there are no changes in the detectability of small mammals between trap stations within a trapping session

All mice, stoat and ship rat samples were affected by habitat covariates to varying degrees, indicating that detectability varied between trap stations within a trapping session.

Thus I reject this hypothesis.

Third hypothesis: that small mammals are evenly distributed along each Pureora trap line during a given trapping session.

One (8%) of 12 samples of stoats, two (6%) of 36 samples of mice and two (5%) of 40 samples of ship rats caught in rat traps were significantly patchy. The number of patchy points in each of these three data sets was insufficient to falsify this hypothesis conclusively, but for ship rats caught in Fenn traps, the result was very clear; 14 (23%) of 60 samples were significantly patchy.

Thus I reject this hypothesis.

Fourth hypothesis: that the density index is independent of variations in the detectability of small mammals at Pureora.

There was a strong linear relationship between density index and detectability along two (both $p < 0.001$) of three mouse and all five ship rat (p values from <0.001 to 0.040) analyses show a strong linear relationship between density index and detectability. For ship rats caught in Fenn traps, this is correlation was weaker ($r^2 = 0.215, 0.375, 0.688$ for PFE, PFL and PFU respectively) and absent for stoats.

Thus I accept this hypothesis in modified form: that the density index *may or may not* be independent of variations in the detectability of small mammals. I note with this modified hypothesis that the stoat was the only species at Pureora for which detectability and density index were found to be independent.

Fifth hypothesis: that the degree of patchiness in small mammal populations is independent of the density index at Pureora.

The few significantly patchy samples were of stoats (one of twelve, 8%) and mice (two of 36, 6%) were collected at low density index values. Data points were conspicuously absent from the upper right area of Figure 5.1 and less clearly, Figure 3.1 (high density index and high patchiness index).

The two (5% of 40 samples) significantly patchy samples for ship rats caught in rat traps were confined to the mid range of density indices (around 6 and 11 C/100

TN, see Figure 4.1). However, significantly patchy values for ship rats caught in Fenn traps fell across the entire range of density indices (Figure 4.3).

There are too few significantly patchy samples from mice, stoats and ship rats caught in rat traps to justify a conclusive rejection of this hypothesis, so I accept it in modified form: that the degree of patchiness in small mammal populations *can* be independent of the density index.

6.3.2. Evaluation of research questions: Pureora

First research question: do these data provide any new information regarding the usefulness of the density index as applied to rodents and stoats at Pureora?

This analysis suggests that the density index is not a reliable measure of small mammal populations, particularly not for ship rat populations sampled for longer periods with Fenn traps. Ship rats caught in Fenn traps varied in detectability at a given trap station within a session as well as between trap stations within a session. In addition, average detectability per session depended on the density index, and the degree of patchiness depended on the survey method: 23% of samples were significantly patchy regardless of density index in comparison to 5% from rodent trap lines.

Mice varied in detectability at a given trap station within a trapping session and between trap stations within a trapping session, but were not often (6% of 36 samples) significantly patchy, and then only at low density index values.

Stoats varied in detectability between trap stations within a trapping session, but the density index was independent of detectability. Only a small (8%) proportion of 12 samples were significantly patchy, and all of these were at low density index values.

Second research question: do these techniques provide new information about the processes of change in these populations of rodents and stoats?

This analysis does not contradict, but cannot specifically support the insect hypothesis put forward by King *et al.* (1996b) to explain the density index peak of mice May 1984 (Figure 3.1) in the young exotic forest. The strong linear relationship between density index and detectability (Figure 3.6) indicates that probability of detection was very low in February 1984, immediately before the peak, and very high in May 1984 during the peak. However, these analyses cannot separate the independent effect of population size on detectability from the effect of catchability on detectability.

The results of the analysis from the Eglinton Valley during the 1976 seedfall event were similar in some respects to those from the young exotic forest at Pureora (compare Figures 3.5 and 3.9). This supports King *et al.*'s (1996b) original suggestion that the cause may be related to food supply, as the post-seedfall peaks are known to be the result of an increased supply of both insects and beech seed (Fitzgerald *et al.* 2004). However, the mouse population increases during a different season and over a longer period of time during a seedfall than was observed at Pureora.

There was no rodent line sampling the older exotic forest, and though this analysis showed that mice were more abundant further from the road through the young plantation the older exotic forest is a quite different habitat (see Chapter two). An alternative explanation is that stoat home ranges in older exotic forest are large, and that the trap line caught stoats wandering from one part of their range to another along or across the road.

The local trap out effect detect detected in ship rats in this study suggests an explanation for the observation that 50% of rats were captured in the first week of sampling (Shaw 2000) in Te Urewera National Park. A marked difference between the samples of ship rats collected by rat traps and by Fenn traps was probably a consequence of a difference in sampling period used with each trap. Both were sub-optimal. The three night sample provided by the rat traps was insufficient, particularly when rats were abundant, and the 10-14 night Fenn trap sample wasted effort because detectability greatly decreased after six nights.

6.3.3. Conclusions regarding Pureora data

This analysis has accepted three of five hypotheses, all in modified form. There *may or may not* be no changes in the detectability of small mammals at a given trap station within a trapping session; the density index for rodents *may or may not* be independent of variations in the detectability, but detectability probably is independent of the density index in stoats; and the degree of patchiness in small mammal populations *can* be independent of the density index.

6.4. Fiordland

Of the three species recorded in Fiordland, the best data were for mice and stoats. Comparatively few ship rats were caught, especially in rat traps, but there were enough data from rats caught in Fenn traps to include them in the evaluation.

6.4.1. Evaluation of hypotheses: Fiordland

First hypothesis: that there are no changes in the detectability of small mammals at a given trap station within a trapping session.

For both ship rats and mice, detectability was constant at each trap station within each trapping session. However, stoats showed a trap-out effect (detectability was constant for the first six days of trapping and very low following this period).

Thus I accept this hypothesis in modified form for rodents, but reject it for stoats.

Second hypothesis: that small mammals are evenly distributed throughout each habitat during a given trapping session.

This hypothesis could not be tested for the Fiordland data because the only habitat description of the two valleys (Johnson in King 1982) was not sufficiently site-specific to construct habitat covariates for analysis.

Third hypothesis: that small mammals are evenly distributed along each Fiordland trap line during a given trapping session.

Two of 24 samples for ship rats (8%) and three of 36 for stoats (8%) but six (19%) of 31 mouse samples were significantly patchy.

I reject this hypothesis, definitely for mice and tentatively for rats and stoats. The analysis suggests that mouse populations were often significantly aggregated.

Fourth hypothesis: that the density index is independent of variations in the detectability of small mammals in Fiordland.

For mice and rats there was a strong linear relationship between density index and detectability (both $p < 0.001$). For stoats, the decrease in density index from the seedfall to the decline phase was accompanied by a decrease in detectability, in both valleys and in all three monthly groupings.

Therefore, I reject this hypothesis.

Fifth hypothesis: that the degree of patchiness in small mammal populations is independent of the density index in Fiordland.

All three species produced at least some significantly patchy samples, but they were distributed across different ranges of the density index values for each species. For stoats, the significantly patchy samples were all in the lower range of density index values (below 3 C/100 TN, compared with the maximum value per month of around 9 C/100 TN). For ship rats, the density indices were very low and the significantly patchy samples were in the mid range (around 1 and 2 C/100 TN). Mice had significantly patchy samples across the whole range of density index values (significant samples between 2 and 24 C/100 TN, compared with the maximum value around 25 C/100 TN).

Thus I accept this hypothesis with modification: that the degree of patchiness in small mammals *can* be independent of variations in the density index.

6.4.2. Evaluation of research questions: Fiordland

First research question: do these data provide any new information regarding the usefulness of the density index as applied to rodents and stoats in Fiordland?

This analysis has shown that mice are not evenly distributed along a trap line and that this aggregation is independent of the density index. Ship rats and stoats showed some tendency towards aggregation, although for stoats this was restricted to lower density index values.

Other work in this area has already shown that indices of abundance and population size are related (Ruscoe *et al.* 2001) and this analysis confirms that relationship. Even though we are now able to estimate detectability using sophisticated new methods, this still cannot separate catchability and population size, leaving the results open to questions; would variation in catchability result in a curved relationship between density index and detectability?

Second research question: do these techniques provide new information about the processes of change in these populations of rodents and stoats?

This analysis showed aggregation in both mice and stoats in both valleys in Fiordland. Mice showed slightly more aggregation in the Hollyford Valley and stoats slightly more in the Eglinton Valley. Both mice and stoats showed both high density index values and high (though not necessarily significant) patchiness values during the seedfall phase in the Eglinton Valley (Figures 3.2, 3.3, 5.2 and

5.3). Samples from the Hollyford Valley had either high density index or high patchiness index during the seedfall phase, but not both together. This observation, together with the continued aggregation of both species in the decline phase, confirms Purdey *et al.*'s (2004) suggestion that mice may survive in scattered patches of forest and that stoats may aggregate in these areas to take advantage of them.

Unfortunately, it is impossible to tell which species of beech masted in the Eglinton Valley in 1976 (Figure 2.10) either because the seed trays were placed in an unrepresentative area or because the mast event was in silver beech and not red beech (which dominated the canopy near the seed trays). This, together with the results of the patchiness analysis and the near complete failure of Purdey *et al.*'s (2004) rodent trap lines to detect a remnant population of mice in the Grebe Valley highlight the dangers of sampling small areas of forest habitat.

6.4.3. Conclusions regarding Fiordland data

This analysis has accepted two of four testable hypothesis in modified form: there *may or may not* be changes in the detectability in small mammals at a given trap station within a trapping session; the degree of patchiness in small mammals *can* be independent of variations in the density index.

6.5. Consequences for small mammal monitoring and control

Ship rats caught in Fenn traps at Pureora (Figure 4.3) and mice in Fiordland (Figures 3.1 and 3.3) were significantly aggregated at high density index values. This may have implications for monitoring, control or eradication measures used on these species. Where animals are aggregated, control or monitoring measures are more likely to be confounded by local trap saturation or an insufficient supply of bait in high density areas.

In contrast, stoats were usually relatively evenly spread along the trap line in both areas, exhibiting aggregation only at low (<3 C/100 TN, Figure 5.1) density index values. This suggests that large scale, low density control is the best strategy for keeping stoat numbers low.

Site Occupancy models for Fenn trap lines sampling stoats in the Eglinton valley and both stoats and ship rats at Pureora, suggest a frequent local and temporary trap out effect. King (1980) drew a similar conclusion from the pooled Eglinton and Hollyford data using much simpler analysis methods confirmed here (Figure 5.5). Other models confirm a decreasing trend in detectability during the trapping session, even for mice (as in Pureora logged forest). These results suggest several things:

The modelling emphasises the importance of controlling for the decrease in detectability expected with removal sampling, whether it is a downwards trend or a trap-out effect. A change in detectability (either up or down) will affect the results of any method of analysis unless the variation is controlled. This analysis found changes in detectability in all three species wherever suitable samples were available, indicating that any analysis of data collected from these species should check for changes in detectability and control for these changes if present. The conventional density index is unable to do this.

If the aim of the operation is to collect research data, the modelling suggests that sampling for ship rats and stoats may be ineffective, or at least inefficient, after the first six nights. Sampling beyond six nights for either of these species may be wasted effort and risks diluting the data set with immigrants. Importantly, the optimum sampling period for stoats and ship rats may be different, and further investigation is required to determine what this is.

On the other hand, if the aim of the operation is to reduce the local population to protect native fauna, the modelling suggests that daily checking of traps for around six consecutive nights at a time may be a more effective method of reducing local populations than weekly checking of traps left permanently set.

Both stoats and ship rats exhibited evidence of a trap-out effect, suggesting that six nights of sampling may reduce the local population to close to undetectable levels (Figure 4.5). New individuals will immigrate once local individuals have been removed, but this effect is not instantaneous. This is especially true when either target or non-target populations are aggregated due to the trap saturation effect. Intermittent versus continuous trapping regimes should be tested in a concurrent study to determine which is more effective.

6.6. General conclusion

This analysis has accepted three of five hypotheses, all in modified form. There *may or may not* be no changes in the detectability of small mammals at a given trap station within a trapping session; the density index *may or may not* be independent of variations in the detectability of small mammals (detectability and density index were independent only for stoats in the Pureora exotic forest); the degree of patchiness in small mammal populations *can* be independent of the density index.

This analysis concludes that in most cases, the density index is not a rigorous measure of small mammal populations, as its assumptions are regularly violated. On the other hand, the same types of data used for density indices can be validly examined using the index of patchiness. These historical data sets were not ideal material for use with Site Occupancy analysis, but it provided some useful information despite this, and would be very suitable to analyse detectability and distribution of small mammals from data collected with this technique in mind.

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Appendix A

Block area graphs

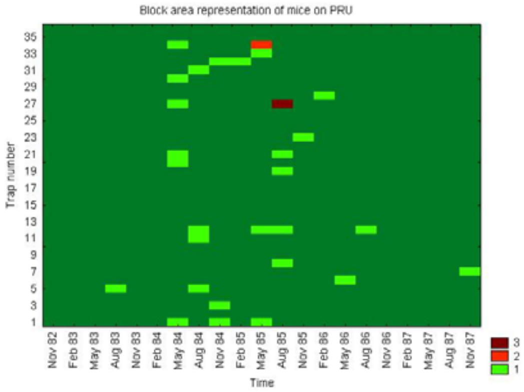

Figure A.1 sample size and distribution of mice on PRU

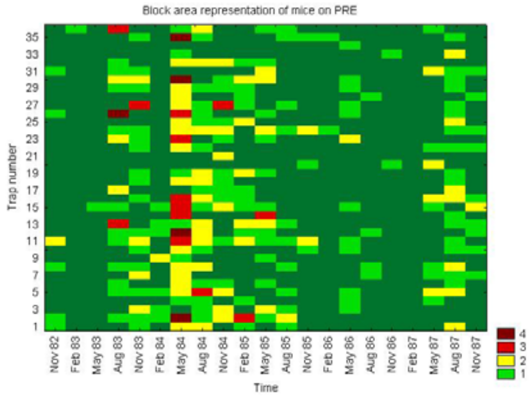

Figure A.2 sample size and distribution of mice on PRE

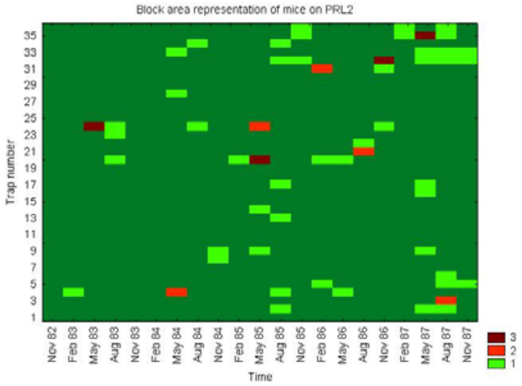

Figure A.3 sample size and distribution of mice on PRL2

Figure A.4: Sample size and distribution of mice on SRE

Figure A.5: Sample size and distribution of mice on SRH

Patchiness

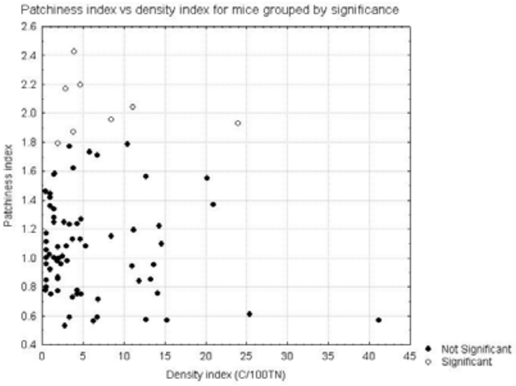

Figure A.6: Scatter plot of mice showing density index graphed against patchiness index

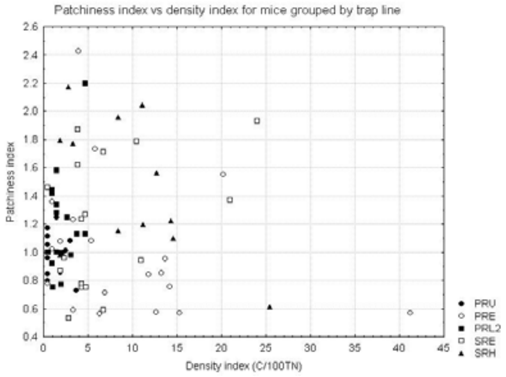

Figure A.7: Scatter plot of mice showing data separated by trap line

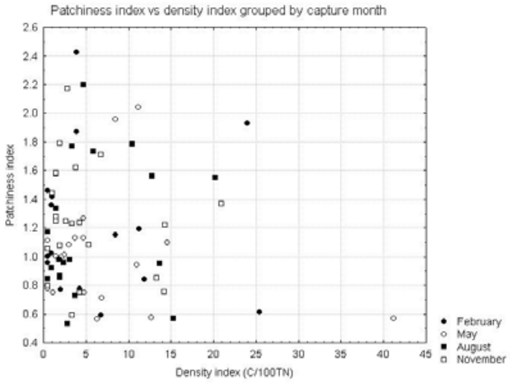

Figure A.8: Scatter plot of mice showing data separated by season

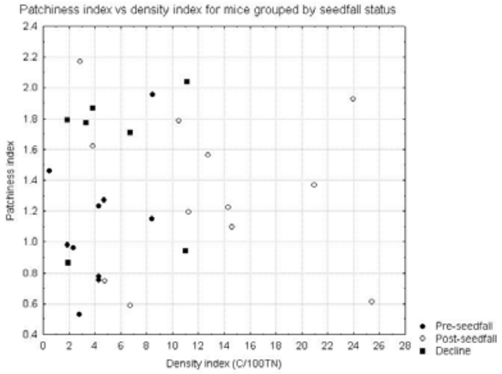

Figure A.9: Scatter plot of mice showing data separated by seedfall status

Site Occupancy

Table A.1 following.

Table A.1: Top ranking models for mice from each trap line. Numbers in brackets are implicit, not explicit in these models, thus have been calculated (using Equation 2.1 or 2.2) in order to display them here.

Model	**ΔAIC**	*w*	*L*	*-2logL*	ψ_i	γ	ε	ψ_{eq}
PRE								
ψ(DR)γ(.)ε(.)p(t)	0	0.3107	0.0965	1501.66	varies	0.2719	0.0291	(0.9033)
ψ(DR)γ(DR)ε(.)p(t)	0.56	0.2348	0.0729	1500.22	varies	varies	0.0426	varies
ψ(i)γ(.)ε(.)p(t)	1.20	0.1705	0.0530	1504.86	0.3739	0.3138	0.0381	(0.8917)
ψ(.)γ(.)p(t)	1.55	0.1431	0.0445	1507.21	0.8517	0.2932	(0.0511)	N/A
ψ(.)γ(.)ε(.)p(t+DR+CC+GV)	2.80	0.0766	0.0238	1500.46	0.3959	0.3302	0.0387	(0.8951)
ψ(CC)γ(.)ε(.)p(t)	3.16	0.0640	0.0199	1504.82	varies	0.3129	0.0381	(0.8915)
PRL2								
ψ(i)γ(.)p(Tds+DR+CC+GV+DE)	0	0.2917	0.0851	472.69	0.4433	0.3178	(0.3991)	N/A
ψ(i)γ(.)ε(GV)p(Tds+DR+CC+GV+DE)	0.21	0.2626	0.0766	468.90	0.1187	0.2447	varies	varies
ψ(i)γ(.)ε(.)p(Tds+DR+CC+GV+DE)	0.34	0.2461	0.0718	471.03	0.1178	0.3034	0.3411	(0.4708)
ψ(i)γ(.){ε = 1 – γ}p(Tds+DR+CC+GV+DE)	0.76	0.1995	0.0582	475.45	0.1525	0.4245	(0.5755)	N/A
ψ(i)γ(GV)p(Tds+DR+CC+GV+DE)	1.57	0.1524	0.0583	264.715	0.4563	varies	varies	N/A
PRU								
ψ(.)p(t+CC+GV+DE)	0	0.3743	0.1401	238.7	0.6836	N/A	N/A	N/A
ψ(.)p(t)	1.03	0.2297	0.0528	245.73	0.7415	N/A	N/A	N/A
ψ(.)γ(.),p(t)	2.61	0.1325	0.0648	245.31	0.5956	0.1027	(0.0415)	N/A
ψ(.)p(Tds+CC+GV+DE)	4.83	0.0437	0.0213	241.53	0.6863	N/A	N/A	N/A
ψ(.)p(t+GV+CC)	4.87	0.0428	0.0209	245.57	0.7364	N/A	N/A	N/A
SRE								
ψ(.)γ(.)p(t)	0	0.5697	0.3245	1206.06	0.7644	0.4189	(0.1291)	N/A
ψ(i)γ(.)ε(.)p(t)	1.91	0.2192	0.1249	1205.97	0.6091	0.3987	0.1194	(0.7695)
ψ(i)γ(.)ε(t),p(t)	3.09	0.1232	0.0712	1175.15	0.8419	0.1000	varies	varies
ψ(i)γ(.){ε =1 – γ}p(t)	4.36	0.0653	0.0377	1210.42	0.7340	0.8040	(0.1960)	N/A
ψ(.)p(t)	7.83	0.0115	0.0067	1215.89	1.0000	N/A	N/A	N/A

Appendix B

Block area graphs

Figure B.1: Sample size and distribution of ship rats on PFE2

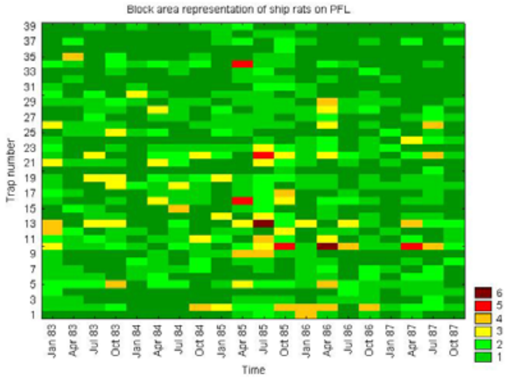

Figure B.2: Sample size and distribution of ship rats on PFL

Figure B.3: Sample size and distribution of ship rats on PFU

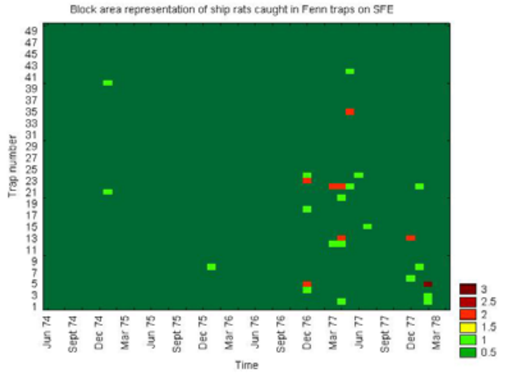

Figure B.4: sample size and distribution of ship rats on SFE

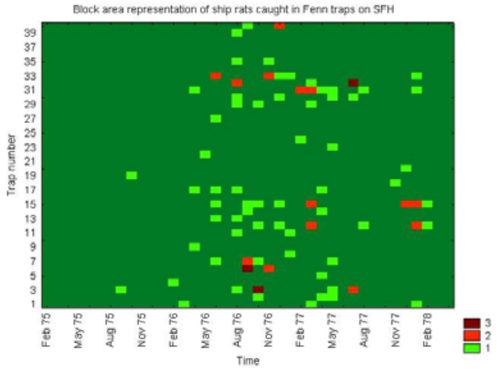

Figure B.5: sample size and distribution of ship rats on SFH

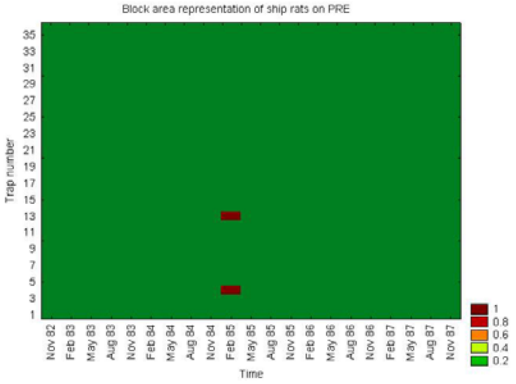

Figure B.6: Sample size and distribution of ship rats on PRE

Figure B.7: sample size and distribution of ship rats on PRL2

Figure B.8: sample size and distribution of ship rats on PRU

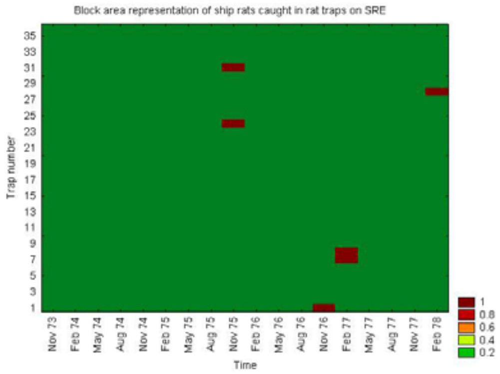

Figure B.9: sample size and distribution of ship rats on SRE

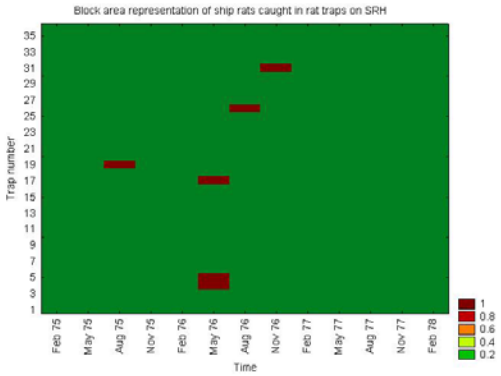

Figure B.10: sample size and distribution of ship rats on SRH

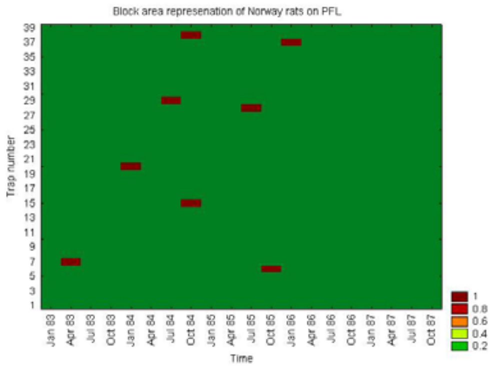

Figure B.11: Sample size and distribution of Norway rats on PFL

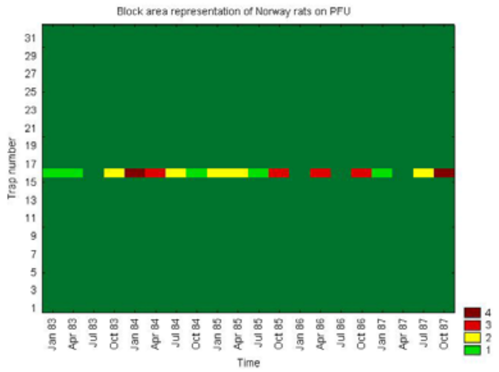

Figure B.12: Sample size and distribution of Norway rats on PFU

Patchiness

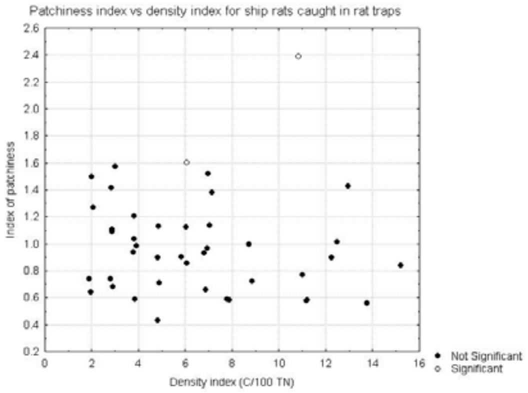

Figure B.13: Scatter plot of ship rats from rat traps showing density index graphed against patchiness index

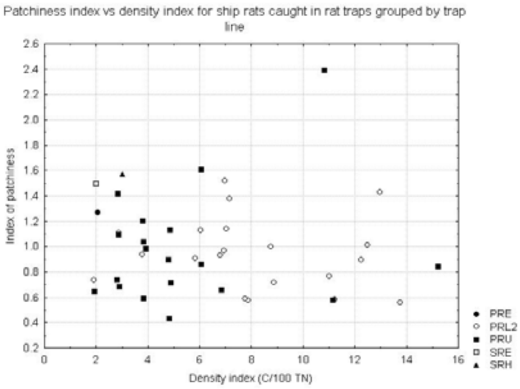

Figure B.14: Scatter plot of ship rats from rat traps showing data separated by trap line

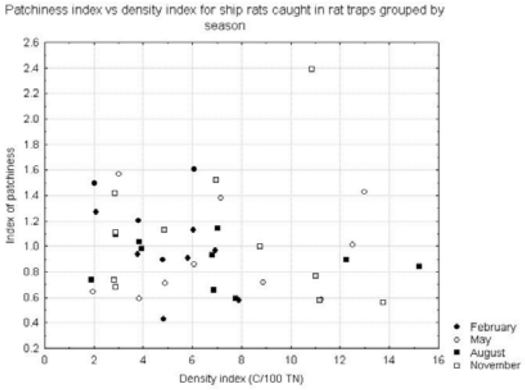

Figure B.15: Scatter plot of ship rats from rat traps showing data separated by season

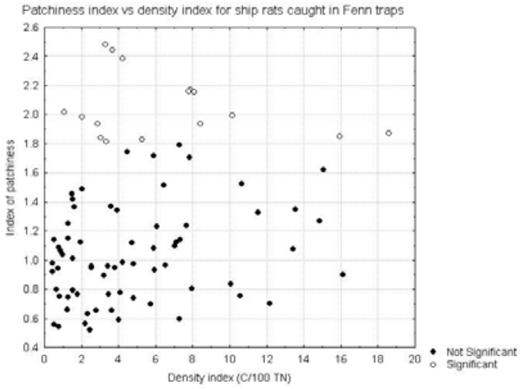

Figure B.16: Scatter plot of ship rats from Fenn traps showing density index graphed against patchiness index

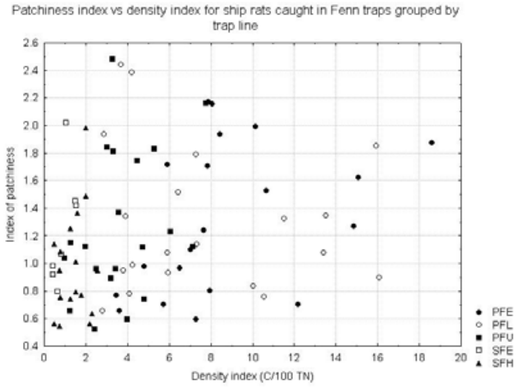

Figure B.17: Scatter plot of ship rats from Fenn traps showing data separated by trap line

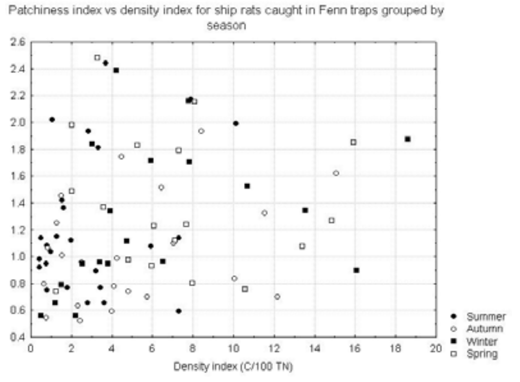

Figure B.18: Scatter plot of ship rats from Fenn traps showing data separated by season

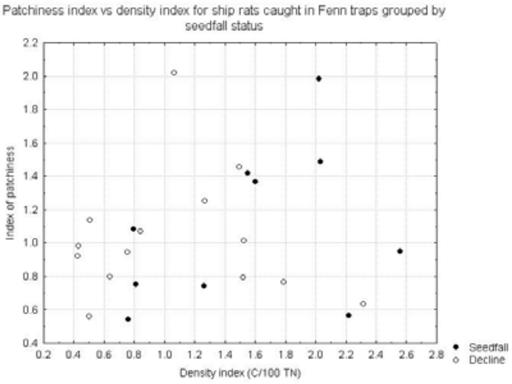

Figure B.19: Scatter plot of ship rats from Fenn traps showing data separated by seedfall status

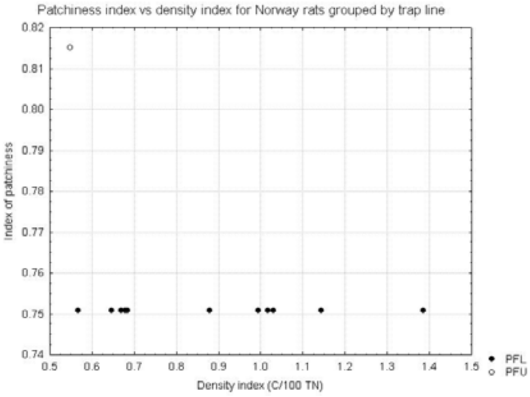

Figure B.20: Scatter plot of Norway rats showing data separated by trap line

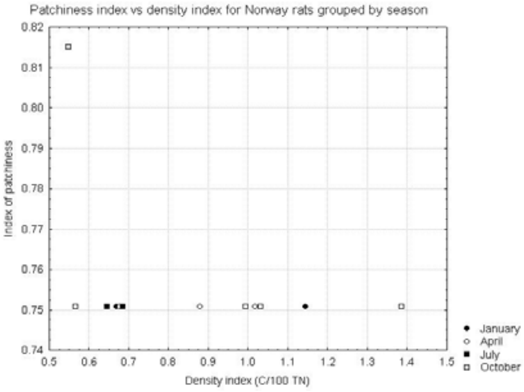

Figure B.21: Scatter plot of Norway rats showing data separated by season

Site Occupancy

Tables B.1 to B.3 following.

Table B.1: Top ranking models for ship rats caught in rat traps from each trap line. Numbers in brackets are implicit, not explicit in these models, thus have been calculated (using Equation 2.1 or 2.2) in order to display them here.

Model	ΔAIC	*w*	*L*	*-2logL*	ψ_i	γ	ε	ψ_{eq}
PRL2								
ψ(.)p(t+asp+DR+CC+GV+GL)	0	0.5207	0.2711	1061.38	1.0000	N/A	N/A	N/A
ψ(.)p(t+asp+DR+CC+GV+GL+DE)	1.97	0.1944	0.1012	1061.35	1.0000	N/A	N/A	N/A
ψ(.)γ(.)p(t+asp+DR+GV+GL)	3.67	0.0831	0.0433	1065.05	0.6907	0.5991	(0.2683)	N/A
ψ(.)γ(CC)p(t+asp+DR+CC+GV+GL)	4.00	0.0705	0.0367	1061.38	1.0000	varies	varies	N/A
ψ(.)p(t+asp+CC+GV+GL)	4.18	0.0644	0.0335	1067.56	1.0000	N/A	N/A	N/A
ψ(.)γ(.)p(t+asp+DR+CC+GL)	6.17	0.0238	0.0124	1067.55	0.6906	0.5900	(0.2643)	N/A
ψ(GL)γ(.)p(t+asp+DR+CC+GV+GL)	6.47	0.0205	0.0107	1063.85	varies	0.5346	varies	N/A
ψ(asp)γ(.)p(t+asp+DR+CC+GV+GL)	9.39	0.0048	0.0025	1066.77	varies	0.5247	varies	N/A
ψ(GV)γ(.)p(t+asp+DR+CC+GV+GL)	9.90	0.0037	0.0019	1067.28	varies	0.4919	varies	N/A
PRU								
ψ(i)γ(.)ε(DE)p(t+alt+CC+DE)	0	0.3851	0.1483	765.87	0.4115	0.9332	varies	N/A
ψ(i)γ(.)ε(DE)p(t+alt+DR+CC+DE)	1.78	0.1582	0.0609	765.65	0.4180	0.9988	varies	N/A
ψ(i)γ(.)ε(DE)p(t+alt+DR+CC+DE)	3.26	0.0755	0.0291	767.13	0.3548	0.8621	varies	N/A
ψ(DE)γ(.)ε(DE)p(t+alt+DR+CC+DE)	3.44	0.0690	0.0266	765.31	Varies	1.0000	varies	N/A
ψ(i)γ(CC)ε(DE)p(t+alt+DR+CC+DE)	3.47	0.0679	0.0262	765.34	0.3932	varies	varies	N/A
ψ(i)γ(.)ε(DE)p(t+alt+DR+CC+DE)	3.59	0.0640	0.0246	769.46	0.4038	1.0000	0.6815	(0.5947)
ψ(DR)γ(.)ε(DR)p(t+alt+DR+CC+DE)	3.67	0.0615	0.0237	765.54	Varies	0.8570	varies	N/A
ψ(i)DR)ε(.)p(t+alt+DR+CC+DE)	5.13	0.0296	0.0114	769.00	0.3822	varies	0.6637	N/A
ψ(i)γ(.)ε(CC)p(t+alt+DR+CC+DE)	5.33	0.0268	0.0103	769.20	0.4045	1.0000	varies	N/A
ψ(i)γ(DE)ε(.)p(t+alt+DR+CC+DE)	5.59	0.0235	0.0091	769.46	0.4038	varies	0.6815	N/A
ψ(i)γ(.)ε(DE)p(Tds+alt+DR+CC+DE)	7.13	0.0109	0.0042	771.00	0.4117	0.9279	varies	N/A
ψ(i)γ(.)ε(.)p(t+alt+DR+CC+GV)	7.45	0.0093	0.0036	773.32	0.3825	1.0000	0.6801	(0.5952)
ψ(i)γ(.)ε(.)p(t)	8.31	0.0060	0.0023	782.18	0.3231	0.5193	0.5921	(0.4672)
ψ(i)γ(.)ε(.)p(t+DR+CC)	8.40	0.0058	0.0022	778.27	0.3541	0.5275	0.6002	(0.4678)
ψ(CC)γ(.)ε(.)p(t+alt+GV+D+DE+DR+CC)	9.58	0.0032	0.0012	769.45	Varies	1.0000	0.6712	(0.5984)

Table B.2: Top ranking models for ship rats caught in Fenn traps from each trap line at Pureora. Numbers in brackets are implicit, not explicit in these models, thus have been calculated (using Equation 2.1 or 2.2) in order to display them here.

Model	**ΔAIC**	*w*	*L*	*-2logL*	ψ_i	γ	ε	ψ_{eq}
PFE (ship rats)								
ψ(i)γ(.)ε(H+GV)p(TO*Tds+DR+H+GV)	0	0.4584	0.2101	2444.73	0.3083	0.0833	varies	varies
ψ(i)γ(.)ε(H+GV)p(TO*Tds+DR+H+CC+GV)	1.25	0.2454	0.1125	2443.98	1.0000	0.0000	varies	varies
ψ(i)γ(.)ε(H+GV+DR)p(TO*Tds+DR+H+GV)	2.02	0.1670	0.0765	2444.75	0.3080	0.0835	varies	varies
ψ(i)γ(.)ε(H)p(TO*Tds+DR+H+GV)	3.88	0.0659	0.0302	2450.61	0.3046	0.0824	varies	varies
ψ(i)γ(.)ε(H)p(TO*Tds+DR+H)	6.53	0.0175	0.008	2455.26	0.3125	0.0795	varies	varies
ψ(i)γ(.)ε(.)p(TO*Tds+DR+DE)	6.74	0.0158	0.0072	2457.47	0.2804	0.0715	0.0281	(0.7179)
ψ(i)γ(.)ε(GV)p(TO*Tds+DR+H)	8.24	0.0074	0.0034	2456.97	0.3273	0.0775	varies	varies
ψ(.)γ(.)p(t+alt+asp+drain+D+D+DE+DR)	8.68	0.0060	0.0027	2455.42	0.6593	0.0483	(0.0250)	N/A
ψ(i)γ(.)ε(DR)p(TO*Tds+DR+H)	9.64	0.0037	0.0017	2458.37	0.2877	0.0893	varies	varies
PFL (ship rats)								
ψ(i)γ(.)ε(.)p(TO*Tds+CC)	0	0.2396	0.0574	4170.08	0.9084	0.2404	0.0662	(0.7841)
ψ(CC)γ(.)ε(t+CC),p(TO*Tds+CC)	0.53	0.1838	0.0440	4130.61	varies	0.3690	varies	varies
ψ(i)γ(.)ε(.)p(TO*Tds+CC+DR)	0.71	0.1680	0.0402	4168.79	0.9043	0.2396	0.0659	(0.7843)
ψ(i)γ(.)ε(t+CC)p(TO*Tds+CC)	1.60	0.1076	0.0258	4133.68	0.9936	0.3681	varies	varies
ψ(i)γ(.)ε(.)p(TO*Tds+CC+H)	1.69	0.1029	0.0247	4169.77	0.9068	0.2415	0.0670	(0.7828)
ψ(CC)γ(CC)ε(t+CC)p(TO*Tds+CC)	2.01	0.0877	0.0210	4130.09	varies	varies	varies	varies
ψ(i)γ(CC)ε(t+CC)p(TO*Tds+CC)	3.48	0.0420	0.0101	4133.56	0.9642	varies	varies	varies
ψ(DR)γ(.)ε(t+CC)p(TO*Tds+CC)	3.61	0.3940	0.0094	4133.69	1.0000	0.3669	varies	varies
ψ(i)γ(.)ε(t)p(TO*Tds+CC)	4.89	0.0208	0.0050	4138.97	0.9631	0.4213	varies	varies
ψ(i)γ(.)ε(t+DR)p(TO*Tds+CC)	6.74	0.0082	0.0020	4138.82	0.9613	0.4320	varies	varies
PFU (ship rats)								
ψ(i)γ(.){ε = 1 – γ}p(TO*Tds+alt)	0	0.4812	0.2316	3067.54	0.6297	0.7315	(0.2685)	N/A
ψ(alt)γ(.){ε = 1 – γ}p(TO*Tds+alt)	1.43	0.2354	0.1133	3066.97	varies	0.7320	(0.2680)	N/A
ψ(i)γ(.)ε(.)p(TO*Tds+alt)	1.89	0.1870	0.0900	3067.43	0.6311	0.7026	0.2576	(0.7317)
ψ(alt)γ(.)ε(.)p(TO*Tds+alt)	3.31	0.0920	0.0443	3066.85	varies	0.7035	0.2573	(0.7322)
ψ(i)γ(t){ε = 1 – γ}p(TO*Tds+alt)	9.91	0.0034	0.0016	3041.45	0.6172	varies	varies	N/A

Table B.3: Top ranking models for ship rats caught in Fenn traps in the Eglinton Valley and Norway rats caught in Fenn traps on the PFU line at Pureora. Numbers in brackets are implicit, not explicit in these models, thus have been calculated (using Equation 2.1 or 2.2) in order to display them here.

Model	**ΔAIC**	w	L	$-2logL$	ψ_i	γ	ε	ψ_{eq}
SFE (ship rats)								
$\psi(.)\gamma(.)p(t)$	0	1.0000	1.0000	333.65	0.1260	0.0852	(0.5910)	N/A
PFU (Norway rats)								
$\psi(.)p(t)$	0	1.0000	1.0000	162.03	0.0312	N/A	N/A	N/A

Appendix C

Block area graphs

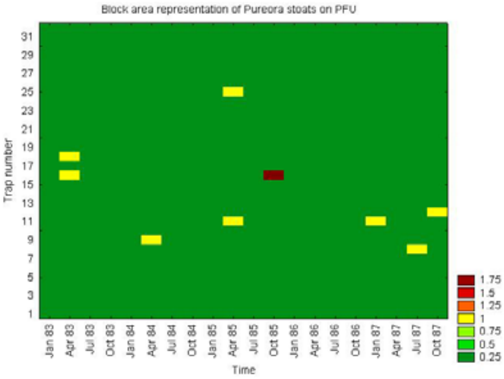

Figure C.1: Sample size and distribution of stoats on PFU

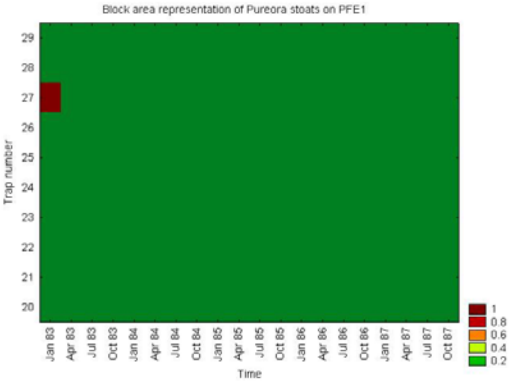

Figure C.2: Sample size and distribution of stoats on PFE1

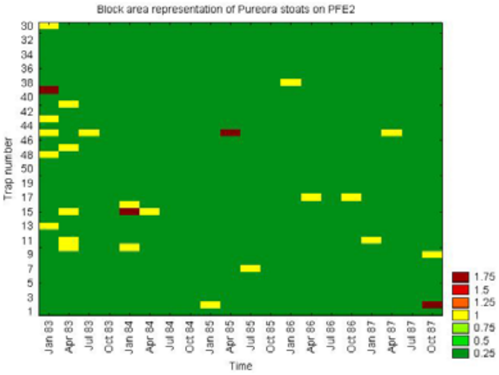

Figure C.3: Sample size and distribution of stoats on PFE2

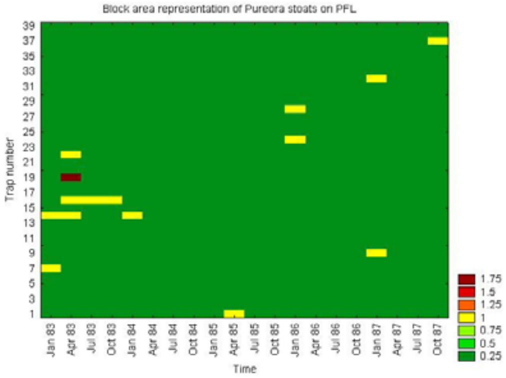

Figure C.4: Sample size and distribution of stoats on PFL

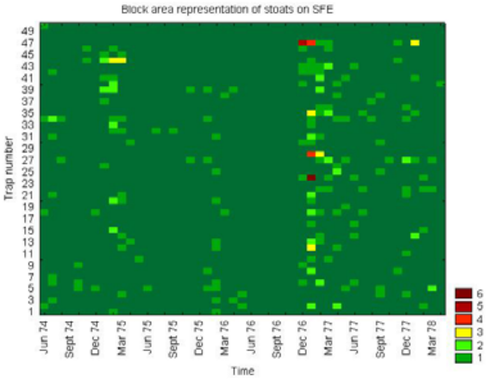

Figure C.5: sample size and distribution of stoats on SFE

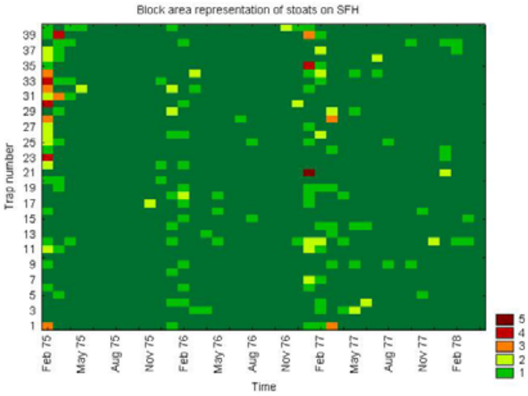

Figure C.6: sample size and distribution of stoats on SFH

Patchiness

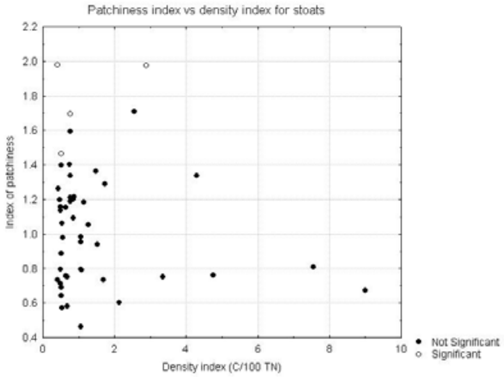

Figure C.7: Scatter plot of stoats showing density index graphed against patchiness index

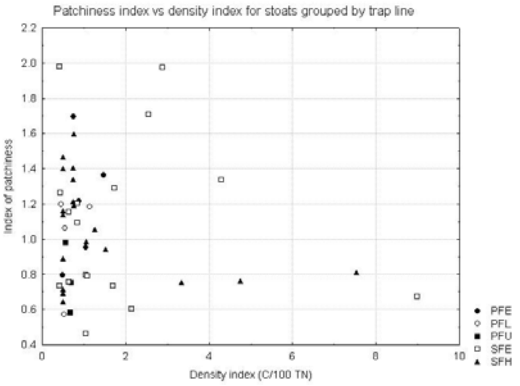

Figure C.8: Scatter plot of stoats showing data separated by trap line

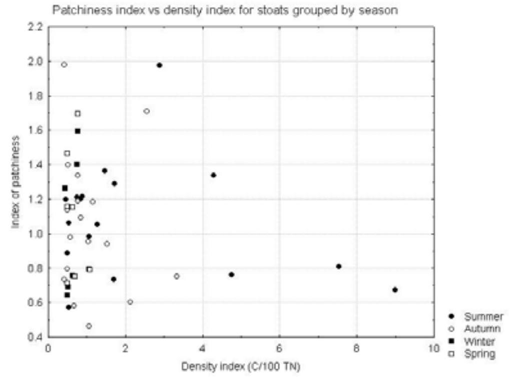

Figure C.9: Scatter plot of stoats showing data separated by season

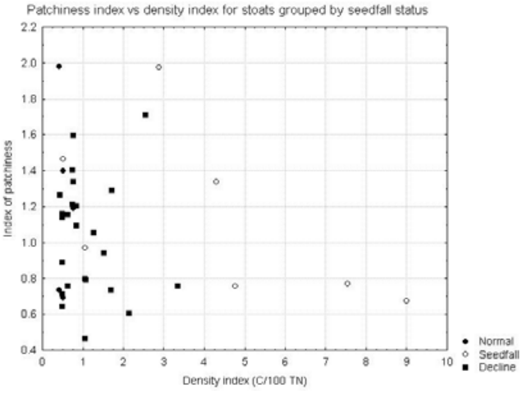

Figure C.10: Scatter plot of stoats showing data separated by seedfall status

Site Occupancy

Table C.1 following.

Table C.1: Top ranking models for each trap line. Numbers in brackets are implicit, not explicit in these models, thus have been calculated (using Equation 2.1 or 2.2) in order to display them here.

Model	**ΔAIC**	*w*	*L*	*-2logL*	ψ_i	γ	ε	ψ_{eq}
PFE - January								
$\psi(DR)\gamma(.)\{\varepsilon = 1-\gamma\}p(t)$	0	0.3152	0.0993	164.37	varies	0.0927	(0.9073)	N/A
$\psi(i)\gamma(.)\{\varepsilon = 1-\gamma\}p(t)$	0.86	0.2050	0.0646	167.23	0.4929	0.0927	(0.9073)	N/A
$\psi(.)\gamma(DR)\ \{\varepsilon = 1-\gamma\}p(t)$	1.17	0.1756	0.0553	165.54	0.4929	varies	varies	N/A
$\psi(.)\gamma(.)\{\varepsilon = 1-\gamma\}p(t+DR)$	1.75	0.1314	0.0414	166.12	0.2975	0.1526	(0.8474)	N/A
$\psi(.)p(t)$	3.17	0.0646	0.0204	171.54	0.8741	N/A	N/A	N/A
$\psi(.)p(t+DR)$	3.5	0.0548	0.0173	169.87	0.7819	N/A	N/A	N/A
$\psi(.)\gamma(.)\{\varepsilon = 1-\gamma\}p(TO)$	3.56	0.0531	0.0168	167.93	0.5612	0.0693	(0.9307)	N/A
SFE - December								
$\psi(i)\gamma(.)\{\varepsilon = 1-\gamma\}p(t)$	0	0.7440	0.5535	194.14	0.3252	0.5713	(0.4287)	N/A
$\psi(.)p(t)$	2.44	0.2197	0.1634	198.582	0.7372	N/A	N/A	N/A
$\psi(t)\gamma(.)p(t)$	6.04	0.0363	0.0270	198.18	varies	0.3757	varies	N/A
SFE – January								
$\psi(i)\gamma(.)\{\varepsilon = 1-\gamma\}p(t)$	0	0.4271	0.1824	328.75	0.4816	0.1814	0.8186	N/A
$\psi(i)\gamma(.)\{\varepsilon = 1-\gamma\}p(TO)$	1.41	0.2110	0.0901	328.16	0.4861	0.1523	(0.8477)	N/A
$\psi(.)\gamma(.)p(t)$	1.80	0.1736	0.0742	330.55	0.4565	0.4716	(0.5615)	N/A
$\psi(i)\gamma(.)\varepsilon(.)p(t)$	1.99	0.1579	0.0674	328.74	0.4816	0.1868	0.8245	(0.1847)
$\psi(.)p(t)$	5.29	0.0303	0.0130	336.04	0.5565	N/A	N/A	N/A
SFE - February								
$\psi(.)p(t)$	0	0.5763	0.3321	211.24	0.7934	N/A	N/A	N/A
$\psi(.)\gamma(.)p(t)$	1.30	0.3008	0.1734	210.54	0.6666	0.9643	(0.4823)	N/A
$\psi(.)p(TO)$	3.09	0.1229	0.0708	212.33	0.7871	N/A	N/A	N/A

Appendix D

Brief description of the IOPUT (Uznanski and Watkins 2006) program

IOPUT (Index Of Patchiness with Unavailable Traps) was designed to calculate the index of patchiness described by Brown *et al.* (2004) when some trap stations are unavailable.

The original method developed by Brown *et al*. (2004) requires the status of every trap to be recorded as occupied or not on every possible trapping occasion. Brown's method does not allow for unavailable traps (for example where a trap was sprung but no animal caught, or only a non-target animal was caught). When the IOPUT program encounters an unavailable trap, it treats the data as if the trap was not there in the field; the distance between the neighbouring stations is doubled but the unavailable station cannot be randomised nor does it receive part of the redistributed catch when calculating the average distance as an empty trap would.

For three captures over ten stations the captures are broken into segments (tenths) and split among bins as follows (numbers represent different captures):

111 111 111 122 222 222 223 333 333 333

This will always be the most efficient way of distributing the captures even if the captures are clustered at one end (eg: 1,1,1,0,0,0,0,0,0,0)

Source code for the program follows, released under the GPL public licence.

```
#the \ symbol causes the python interpreter to ignore the following new line.
#!/usr/bin/python
#################################################
#IOPUT v 1.0 Date last modified: 18/2/2007
#distributions.py
#################################################

#################################################
#This program 'IOPUT' (Index Of Patchiness with Unavailable Traps), was designed
# to calculate the index of patchiness described by Brown et al. (2004) when some
#trap stations are unavailable.
#
#The algorithm spreads out captures evenly over the total available number
#of bins (traps/stations) calculating the weighted sum of the movements made
#
#For three captures over ten bins the captures are broken into segments (tenths)
#and split among bins as follows (numbers represent different captures):
#111 111 111 122 222 222 223 333 333 333
#This will always be the most efficient way of distributing the captures even if
# the captures are clustered at one end (eg: 1,1,1,0,0,0,0,0,0,0)
#################################################


import sys
import csv
import permutations
import random

### generateWeights
# returns the index of patchiness value as described above
# requires  filled_bins      (list) number of bins with objects (ie in a line of 10
#                                with 2 captures, 2)
#           bin_locations    (list) the index value that will call each bin that is
#                                not unavailable from the data list
# returns                    (floating point value) the index of patchiness

def generateWeights(filled_bins, bin_locations):
  weight = 0
  bin_count = len(bin_locations)
  if bin_count == 0:
    return 0
  segment_count = len(filled_bins)
  for segment, bin in enumerate(filled_bins): # each segment corresponds to a\
                   single filled bin
    low, low_fill = divmod(bin_count * segment, segment_count)
    high, high_fill = divmod(bin_count * (segment + 1), segment_count)
    if high_fill >= bin_count: # if this is true, the segment fits into a single\
                   bin with room to spare.
      weight += abs(bin - bin_locations[high]) * bin_count
    else:
      weight += abs(bin - bin_locations[low]) * (segment_count - low_fill) #\
                   count the start of the segment in its bin
      if high < bin_count:
        weight += abs(bin - bin_locations[high]) * high_fill
      for k in range(low + 1, high):
        weight += abs(bin - bin_locations[k]) * segment_count
  return float(weight)/bin_count

### findLiveBins
# requires  bin_list         (list) the data
# returns   a tuple containing:
#           live_bins        (list) contains the contents of each available bin
#           bin_locations    (list) the index value that will call each bin that is
#                                not unavailable from the data list

def findLiveBins(bin_list):
  live_bins = []
  bin_locations = []
  for index, item in enumerate(bin_list):
    if item is not None: # if it's a live bin...
      live_bins.append(item) # add the item in it to the list of live bins...
      bin_locations.append(index) # and add its location to the locations list
  return live_bins, bin_locations

### findFilledBins
# requires  live_bins        (list) contains the contents of each available bin
#           bin_locations    (list) the index value that will call each bin that is
```

```
#                               not unavailable from the data list (defaults to
#                               None if not specified)
# returns   filled_bins     (list) returns a paired list of the contents of each
#                               available bin and the index value that will call
#                               it

def findFilledBins(live_bins, bin_locations = None):
  filled_bins = []
  if bin_locations is None:
    bin_locations = range(len(live_bins))
  for item, location in zip(live_bins, bin_locations):
    filled_bins.extend([location] * item) # add as many filled bins to the list as
                    there are catches in each bin.
  return filled_bins

### getScatterCots
# requires  bin_list        (list) the data
# returns   scatter_cost    (floating point value) the index of patchiness (via
#                                 generateWeights)

def getScatterCost(bin_list):
  live_bins, bin_locations = findLiveBins(bin_list)
  filled_bins = findFilledBins(live_bins, bin_locations)
  scatter_cost = generateWeights(filled_bins, bin_locations)
  return scatter_cost

### skipFirstIterations
# requires  iterator    (integer) starting point in the data
#           count       (integer) count value (defaults to 1)

def skipFirstIterations(iterator, count = 1):
  for item in iterator:
    if count > 0:
      count -= 1 # count down until I don't have to skip any more
    else:
      yield item # then produce iterator items after that.

### convertToNumbers
# requires  line    (list) a line from the data file

def convertToNumbers(line):
  return [safeRun(int, None, k) for k in line]

### safeRun
# converts '-'s from the data file to None
# requires  _func           (int) line number for the data being parsed in
#           _failure        catches failures (defaults to None)
#           *args           (list) all unnammed optional arguments in the list
#           **named_args    (list) all nammed optional arguments in the list
# returns the data or None

def safeRun(_func, _failure = None, *args, **named_args):
  try:
    return _func(*args, **named_args) # this might fail...
  except:
    return _failure # but if it does, just give me the argument I passed in; I\
                    don't really care how it failed.

### runDataFile
# requires  filename    (str) the name of the file
# prints the output (data + results)

def runDataFile(filename):
  families = {}
  for line in skipFirstIterations(csv.reader(file(filename))):
    name, family, data = line[0], line[1], convertToNumbers(line[2:])
    analysis_output = getPatchinessStuff(data)
    print ",".join([str(k) for k in [name, family] + data +
                    list(analysis_output)])
```

```
### getPatchinessStuff
# Computes all required values for patchiness calculations
# requires  data    (list) list of data from the CSV
# returns           (list) the results of the analysis

def getPatchinessStuff(data):
  live_bins, bin_locations = findLiveBins(data)
  filled_bins = findFilledBins(live_bins, bin_locations)
  scatter_cost = generateWeights(filled_bins, bin_locations)
  min_scatter = scatter_cost
  max_scatter = scatter_cost
  scatter_sum = 0
  scatters_above = 0
  scatters_below = 0
  scatter_count = 0
  if permutations.countPermutations(live_bins) < 1000000: # this is the maximum\
                    number of permutations permitted before the data are\
                    randomised
    is_random = False
    for permuted_live_bins in permutations.permutations(live_bins):
      permuted_filled_bins = findFilledBins(permuted_live_bins, bin_locations)
      permuted_scatter_cost = generateWeights(permuted_filled_bins, bin_locations)
      if permuted_scatter_cost < min_scatter:
        min_scatter = permuted_scatter_cost
      if permuted_scatter_cost > max_scatter:
        max_scatter = permuted_scatter_cost
      scatter_sum += permuted_scatter_cost
      scatter_count += 1
      if permuted_scatter_cost < scatter_cost:
        scatters_below += 1
      else:
        scatters_above  += 1
  else:
    is_random = True
    permuted_live_bins = live_bins[:]
    for k in range(50000): # if the data are randomised, only 50000 permutations\
                    are calculated as this is much more time consuming
      random.shuffle(permuted_live_bins)
      permuted_filled_bins = findFilledBins(permuted_live_bins, bin_locations)
      permuted_scatter_cost = generateWeights(permuted_filled_bins, bin_locations)
      if min_scatter is None or permuted_scatter_cost < min_scatter:
        min_scatter = permuted_scatter_cost
      if max_scatter is None or permuted_scatter_cost > max_scatter:
        max_scatter = permuted_scatter_cost
      scatter_sum += permuted_scatter_cost
      scatter_count += 1
      if permuted_scatter_cost < scatter_cost:
        scatters_below += 1
      else:
        scatters_above  += 1
  average_scatter = scatter_sum / scatter_count
  if average_scatter == 0:
    patchiness_index = 0
  else:
    patchiness_index = scatter_cost / average_scatter
  return scatter_cost, is_random, average_scatter, max_scatter, min_scatter,
                    patchiness_index, scatters_above, scatters_below

### Self test code
# if called in IDLE outputs tests below
# if program is run from comand line, this is not used

if __name__ == "__main__":
  if len(sys.argv) == 1:
    print "Self testing.  If anything prints False, something has broken."
    print findFilledBins([0,1,1,0,0,0,1,0,0,0]) == [1, 2, 6]
    print findFilledBins([2,2,3,1,1,2,0,2,1,1,0,2,1,0,1,0,1,2,1,1]) == [0, 0, 1,\
                    1, 2, 2, 2, 3, 4, 5, 5, 7, 7, 8, 9, 11, 11, 12, 14, 16, 17,\
                    17, 18, 19]

    print findLiveBins([1,0,0, None,2]) == ([1,0,0,2],[0,1,2,4])

    print getScatterCost([0,1,1,0,0,0,1,0,0,0]) == 5.1
    print getScatterCost([0,1,0,0,1,1,0,0,1,0]) == 2.8
    print getScatterCost([1,1,0,0,0,0,0,0,0,0]) == 8.0
    print getScatterCost([1,0,0,0,0,0,0,0,0,1]) == 4.0
```

```
  print getScatterCost([0,1,1,0,1,1,1,1,0,0,0,1,1,0,1,1,0,1,1,1,1,1,1,1,0,\
                  1,1,1,1,1,1,0,1,1,0,0,0,1,1,1]) == 29.8
  print getScatterCost([2,2,3,1,1,2,0,2,1,1,0,2,1,0,1,0,1,2,1,1]) == 38.2
  print getScatterCost([3,1,3,0,3]) == 3.0
  print getScatterCost([2,2,1,1]) == 2.0
  print getScatterCost([None, None, None, None, None]) == 0.0
  print getScatterCost([1,0,0, None,2]) == 3.25

  print convertToNumbers(['0','1','2','3','4','-'])

  runDataFile("shortsample.csv")
else:
  runDataFile(sys.argv[1])
```

```
#the \ symbol causes the python interpreter to ignore the following new line.
#!/usr/bin/python

################################################
#IOPUT v 1.0 Date last modified: 18/2/2007
#permutations.py
################################################

################################################
#This program 'IOPUT' (Index Of Patchiness with Unavailable Traps), was designed to
#calculate the index of patchiness described by Brown et al. (2004) when some
#trap stations are unavailable.
#
#This section of the algorithm calculates the permutations, essentially every possible
#ordering of a list of numbers.
################################################

import time

### permutations
# requires  d   (list) the list of data

def permutations(d):
  data = d[:]
  data.sort()
  n = len(data) - 1
  while 1:
    yield data
    j = n - 1
    while j >= 0 and data[j] >= data[j + 1]: # find the first data point that isn't\
                 in descending order from the end
      j -= 1
    if j < 0:
      break
    l = n
    while data[j] >= data[l]: # find the smallest point in the descending section\
                 that is bigger than point found earlier
      l -= 1
    swap(data, l, j)
    reverse_slice(data, j + 1)

### swap
# requires  data    (list) the list of data
#           first   (int) the index of the first point to be swapped
#           second  (int) the index of the second point to be swapped

def swap(data, first, second): # swap two things in a list
  temp = data[first] # create a copy of the first item
  data[first] = data[second] # make the first item equal to the second
  data[second] = temp #make the second item equal to the copy of the first one (items\
                 are now swapped)

### reverse_slice
# requires  data    (list)          the list of data to have a piece reversed
#           start   (int)           the start of the section to be reversed (defaults\
                    to 0)
#           end     (int or None)   the end of the section to be reversed (defaults\
                    to None)

def reverse_slice(data, start = 0, end = None):
  if start < 0:
    first = start + len(data)
  else:
    first = start
  if end is None:
    second = len(data) - 1
  elif end < 0:
    second = end + len(data) - 1
  else:
    second = end - 1
  while first < second:
    swap(data, first, second)
    first += 1
    second -= 1

### countPermutations
# requires  d           (list) the list of data
```

```
# returns   numerator   (int) the number of permutations required

def countPermutations(d):
  item_counts = {}
  for item in d:
    item_counts[item] = item_counts.get(item, 0) + 1
  n = len(d)
  numerator = 1
  denominator = 1
  for value in item_counts.itervalues():
    for k in range(value, 0, -1):
      numerator *= n
      denominator *= k
      gcd = greatestCommonDenominator(numerator, denominator)
      numerator /= gcd
      denominator /= gcd
      n -= 1
  return numerator

### greatestCommonDenominator
# requires  a   (int) first number greatest common denominator required for
#           b   (int) second number greatest common denominator required for
# returns   a   (int) the greatest common denominator

def greatestCommonDenominator(a, b):
  while b:
    n = a % b
    a = b
    b = n
  return a

### Time to generate items
# if called in IDLE outputs the time from below
# if program is run from comand line, this is not used

if __name__ == "__main__": # this section estimates the time needed to run the module
  data = [0,0,1,1,0]
  t = time.time()
  x = 0
  for p in permutations([0,0,1,1,0]):
    #print p
    x += 1
  total_time = time.time() - t
  print '%i items in %0.6f seconds: %0.6f seconds per item' % (x, total_time,\
                   total_time/x)
  #print data
```