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A stochastic computer simulation of island group colonisation by *Rattus norvegicus* in small near shore island systems: specifically Tia Island and the Boat Group.

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Abstract

Rats have a devastating effect of the biota of islands. In New Zealand rats are responsible for the extinction or reduction of many species. In recent times an important conservation strategy in New Zealand has been to clear offshore islands of rats so that they can be used as havens for species vulnerable to rat predation. One of the main limitations in the application of this strategy is our ability to predict how long an island will stay rat free once it is cleared. In this study stochastic simulation models focusing on *Rattus norvegicus* (Norway rat) were developed to help managers better predict the outcome of rat eradications. A sensitivity analysis was carried out to determine what parameters the outcome of the model was most sensitive to. Modelled experiments on Tai Island and the Boat Group were performed. The modelled experiment on Tai Island asked; whether or not Tai Island could be rid of rats either by repeated eradication or permanent poisoning operations, and do age biased mortality rates have an effect on suppressing populations of *R. norvegicus* on islands? The modelled experiment on the Boat Group asked the questions; can stopping the colonisation of one patch in a small metapopulation have consequences for other patches in that metapopulation, is the model strong enough to make precise predictions about how long each island in the group will take to be invaded for the first time, what is the predicted invasion pattern of the Boat Group, and is a ‘rescue effect’ likely to be operating. Parameter and demographic stochasticity were built into the model so that they could affect the amount of uncertainty around the answers to the questions stated above. The demographic part of the model was most sensitive to the juvenile mortality parameter $m_C$ and the adult mortality parameter $M_{1/2}$. The ‘time to invasion’ predicted by the combined model was most sensitive to the distance of the target island, the tendency of migrants to swim straight, and the female fertility.
parameter $B_{nn}$. In the modelled experiment on Tia Island raising both adult and pre-adult mortality significantly reduced the population. Raising pre-adult mortality was more effective at reducing the population than raising adult mortality. Keeping Tia Island rat free by repeated eradication was predicted to be unfeasible because invasion was too frequent. The predictions of the model became less affected by the uncertainty built into the model as mortality rates increased. The modelled experiments on the Boat Group revealed that Kundy Island was the main source of invasion for the whole group, with Rat Island acting as a secondary source. Stopping the invasion of these two islands greatly reduced the chances of invasion for the other islands in the group. There was no indication of islands being used as stepping-stones. The predictions of the model were too imprecise to be useful to managers. The rescue effect occurred on the islets Ka and Ra. Kb showed no effect and Ca showed a large effect but in the opposite direction than predicted by the rescue effect.
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1 Introduction

1.1 Rats in offshore island environments

There are three rat species in New Zealand, *Rattus exulans* (kiore), *Rattus norvegicus* (Norway rat) and *Rattus rattus* (ship rat). All three species of rat were introduced to New Zealand, *R. exulans* by early Polynesian visitors (Holdaway 1996), *R. norvegicus* with early European settlement (Moors 1990), and *R. rattus* by the middle of the nineteenth century (Atkinson 2001). All three species of rat can have a devastating effect on the biota of islands they are introduced to. The local extinctions of large flightless invertebrates, species of nocturnal skink, and the complete disappearance of at least six Passerine species coincided with the introduction of *R. exulans* to the New Zealand archipelago (Towns & Broome 2003).

The best documented example of the effect *R. rattus* has on the biota of offshore islands in New Zealand is the invasion of Taukahepa (Big South Cape Island) in 1962. Prior to the invasion Taukahepa was free of mammalian predators (except for one species of native bat) (Atkinson 2001; Towns & Broome 2003). As a direct result of the rat invasion five of the eighteen bird species present went extinct (Atkinson 2001), including the last population of bush wren (*Xenicus longipes*). The last population of short-tailed bat (*Mystacina robusta*) also went extinct (Towns & Broome 2003).

*R. norvegicus* has a devastating effect on the wildlife of offshore islands it invades (for a few examples see Austin 1948; Moors 1985; Drever & Harestad 1998). The appearance of *Rattus norvegicus* on Langara Island, in the Queen Charlotte group off the coast of British Columbia Canada, coincided with the Ancient Murrelet (*Synthliboramphus antiquus*) population crashing from an estimated 200 000 breeding...
Stochastic computer simulation of island colonisation by *R. norvegicus*.

pairs pre 1971, to $14\ 630 \pm 2\ 060$ breeding pairs in 1993 (Drever & Harestad 1998). There is evidence that Ancient Murrelet adults, chicks, and eggs make up a significant part of the diet of *R. norvegicus* during the nesting season (Drever & Harestad 1998; Hobson, Drever, & Kaiser 1999). As well as the decline in breeding populations of Ancient Murrelet, several other seabird species have disappeared altogether (Drever & Harestad 1998).

*R. norvegicus* also appears responsible for the deaths of several hundred white-faced storm petrels on Maria Island, Hauraki Gulf (Moors 1985), and the local extinction of *Anthus novaezeelandiae* and all small petrels from Campbell Island (Moors 1990). *R. norvegicus* is associated with the decimatation of many native invertebrate populations, for example many of the Large endemic insects on Campbell Island are believed to have been made locally extinct on the main island by *R. norvegicus* (Moors 1990).

Of the three rat species present in New Zealand *R. norvegicus* was chosen as the focus of this study because it is reputed to be a stronger swimmer than the both *R. rattus* and *R. exulans* (Moors 1990) and thus, is more likely to reach islands unaided. It is also known that *R. norvegicus* forages in the inter-tidal zone (Moors 1985; Taylor & Thomas 1993; Hobson *et al.* 1999), bringing it in to close contact with the sea and allowing it to survive on small stepping stone islets. It is believed that *R. norvegicus* has invaded several island systems in New Zealand unaided by humans (Lee 1999; Russell 2002; J. Russell pers. comm.).
1.2 The cost of island eradications and reinvasions

In recent times several offshore islands around New Zealand have been cleared of rats with the intention of using the islands as havens for native fauna threatened by mammalian predators (for a review see Towns & Broome 2003). However, rat eradication is expensive and if rats are able to reinvade an island, extra investment may be needed to clear the island again. If natural reinvasion is frequent, then repeated eradications are neither financially or ecologically feasible. Also non-target species may be adversely affected by poisoning campaigns (Towns & Broome 2003), so repeated eradications could jeopardise other conservation goals. For these reasons it is preferable to carry out eradications as few times as necessary. It is therefore useful to be able to predict how long it might take an island to be reinvaded.

Technical restrictions and a lack of biological knowledge no longer limit large-scale eradication of rats from islands (Simberloff 2003; Towns & Broome 2003). The main factor that now limits which islands can be eradicated is the ability to predict whether an island will be re-invaded, and how long it will take (Towns & Broome 2003).

1.3 Understanding island eradication and invasion in a metapopulation

Understanding the processes that underlie the colonisation of islands by rats could greatly increase our ability to predict how long an island will stay rat free. In order to understand the invasion dynamics of a rat population, potential source populations, the invasion ability of the species, and potential migrant sinks must all be considered. Thus, the rat population of an island must be thought of as just one part of a set of inter-connected sub-populations. With each sub-population unique, and described by a
set of variables such as isolation, contribution to the migrant pool, vulnerability to extinction, and so forth. This sort of population is commonly called a metapopulation (Peltonen & Hanski 1991; Crone, Doak & Pokki 2001). Many metapopulations are composed of a few very large invulnerable 'mainland' populations that are surrounded by 'islands', those populations small enough to go extinct by chance (Peltonen & Hanski 1991). This version of metapopulation probably describes many rat populations on coastal island groups around New Zealand.

Rodent populations on island groups have been found to conform to predictions of metapopulation models (Peltonen & Hanski 1991). Other small mammals have also been found to exist on island groups through a process of repeated extinction and re-invasion (Boyett, Endries and Adler 2000), fulfilling a critical assumption of metapopulation models. This supports the idea that populations of *R. norvegicus* on islands conform to extinction and colonisation patterns envisaged by the metapopulation paradigm.

Most metapopulation studies are concerned with preserving species that exist as a metapopulation (for example Peltonen & Hanski 1991; Gotelli & Kelly 1993; Hanski 1994; Ellner & Fussmann 2003). However, with rat invasions of island groups it is the islands that are the primary concern and not the metapopulation itself. Hence factors such as an islands isolation, relative position within the group, shape, and area should be included in any model, resulting in models that are island, or island group specific.
1.4 The role of modelling in understanding rat invasion of island groups

What factors are most important in predicting re-invasion rate? What effect does an islands isolation or shape have? Are stepping-stone islands important? The ideal way to answer these questions would be to perform empirical studies. However, studying a process that occurs on a large temporal and spatial scale may be prohibitively expensive. Ideally these studies would use rat free islands so that the effect of resident rats could be controlled for. But many rat free islands around New Zealand are of high conservation value. Thus, the decision to allow rats to establish on a rat free island must be weighed very carefully.

Modelling is one way to explore possible consequences without the cost of empirical studies or management interventions such as island eradication. Models are a way to explore the current ‘knowledge state’ and uncover what predictions the ‘knowledge state’ may make about a given problem. Models do not add to the knowledge state (Starfield & Bleloch 1991). The term “knowledge state” is used to refer to all information available that is pertinent to a given problem.

Models can be used to define the problem, organize data, quantify uncertainty, understand the data, test that understanding and make predictions (Starfield & Bleloch 1991). What any one model is used for depends largely on the ‘knowledge state’ for the problem that that model was created to deal with. If there is very little information about the problem then any predictions made by the model will be highly uncertain. In such a case the model will be most useful defining problems and understanding the information available, then tentatively used to test the new understanding (Starfield &
Bleloch 1991). On the other hand if the ‘knowledge state’ for a problem is very large, then an accurate predictive model may be feasible (Starfield & Bleloch 1991).

1.5 The current ‘knowledge state’ relating to rat invasions of islands

The ‘knowledge state’ relating to *R. norvegicus* colonisation of island groups is relatively strong in areas of life history traits and general biological knowledge (see Table 2.1 and section 2.2.3), but is missing key information in relation to migration ability. The average swimming distance of *R. norvegicus* in the open ocean, it’s navigation mechanism or ability, and the willingness of *R. norvegicus* to migrate across water are primary examples of gaps in our existing ‘knowledge state’.

Another weakness in the current ‘knowledge state’ is a lack of pertinent datasets relating to rat metapopulations. Metapopulation datasets should contain the distribution of the species across its metapopulation through time (Gotelli & Kelly 1993). A dataset of this kind does not exist for *R. norvegicus* or any similar species in New Zealand. Although there are good data on the distribution of rodents on New Zealand islands (i.e. the datasets kindly provided to me by J. Parks and J. Russell for the purposes of this study), these datasets lack a time component, which is critical in calculating the rate at which *R. norvegicus* colonises islands. Those data sets that do contain a time component tend to be very small and revolve around re-invasions after successful rat eradication. For example, the dataset kindly provided to me by J. Russell, which documents the repeated re-invasion of the Noises Islands by *R. norvegicus*.

The main consequence of the lack of adequate datasets is that ideas about rat metapopulations, such as their colonisation rate, cannot be tested against the current

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‘knowledge state’. This includes the ideas presented in this study. It will therefore be impossible to know how accurately the models will be able to predict island occupancy or time to occupancy for *R. norvegicus*.

Given the gaps in the current ‘knowledge state’ it is unlikely that the models presented here will have much predictive power. However, examining the precision of the models predictions will indicate how much the weakness in the current ‘knowledge state’ affects our predictive ability. The chance and uncertainty built into each set of simulations will produce a range of predictions. If that range of predictions is tight, we can say that the model outcome is relatively unaffected by the chance mechanism and changes in parameter inputs, which reflect uncertainty in the ‘knowledge state’. On the other hand if the range of predictions is very spread, then we can say that the model outcome is sensitive to the chance mechanism and uncertainty in the ‘knowledge state’.

1.6 Model formation

Stochastic simulation models have been used to model rodent populations (Blackwell, Potter & Minot 2001), and models incorporating a random movement component have been widely used (Starfield & Bleloch 1991; Ollason, Bryant, Davis, Scott & Tasker 1997; Lande, Engen & Sæther 1998; Keeling 2002; Ellner & Fussmann 2003). Stochastic simulations are well suited to modelling metapopulations because the pattern of occupancy in metapopulations is determined by chance. stochastic models are therefore well represented in metapopulation literature (for example; Gotelli & Kelly 1993; Hanski 1998; Lande *et al*. 1998; Sæther, Engen, Swenson, Bakke & Sandegren 1998; Sæther, Engen & Lande 1999; Keeling 2002).

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The problem of island colonisation in a multi-island system is potentially very complex. There are multiple invasion pathways, with some pathways being more likely than others. Also invasion pathways may change with time as source populations go extinct and others establish. Stochastic simulations can deal with complexity because they do not explore every possible outcome. Rather, stochastic simulations incorporate random numbers into an algorithm, resulting in a model outcome that is determined partly by chance. One outcome determined by chance is not very useful by itself, as it gives no indication of how likely or unlikely that outcome was. To overcome this, many simulations must be run, with each simulation recording a measurable outcome. In this way each set of simulations does not produce just one answer, but rather a distribution of possible answers, with some answers being more likely to occur than others. Thus, stochastic simulation models do not tell us every possible outcome, but they can tell use how likely a particular outcome is, given the assumptions made by the model.

1.7 The sensitivity analysis

Given the sparseness of the ‘knowledge state’ surrounding island colonisation by rats, one of the main outcomes of this study will be the sensitivity analysis. Previous sensitivity analyses that have been applied to population models of rodents have been concerned with the population growth rate (Oli, Slade & Dobson 2001; Oli & Dobson 2003) rather than the colonisation rate.

Broadly, sensitivity analyses tell us the degree that any outcome of the model is affected by changes in the values of its parameters. This information can then be used
to set research priorities (Hunter, Moller & Fletcher 2000). Parameters that the model is most sensitive to are those that warrant the most research attention, as these parameters potentially have the most effect on the system (Oli et al. 2001; Yearsley Fletcher & Hunter 2003).

Sensitivity analyses only produce information about processes that are modelled. For example a simple colonisation model would be rats leaving a source island and arriving on the nearest target island, the only variable is the number of rats that leave the source island. The only variable this simplified model could be sensitive to is the number of rats that leave the source island. The model would tell us nothing about the way rats navigate while swimming or how far they can swim, and nothing of the relative importance of these variables. This is the price of simplicity. Models should strive to be as simple as possible so that the processes within them are understandable and the outcomes are easier to interpret (Starfield & Bleloch 1991). But the simpler the model the less informative it is about key determinates of the outcome. Because an important part of the sensitivity analysis will be discerning those parameters that best describe the system as many logical parameters as possible have been included in the model.

1.8 Modelled experiments on Tia Island and the Boat Group

1.8.1 Background on the Titi Islands and the island groups used as the focus for the modelled experiments

The Titi Islands or mutton bird islands, are a group of approximately 30 coastal islands around Rakiura Island (Fig.1.1). The Titi Islands exist primarily in four main groups: the widely spaced north-eastern group (not used in this study); the Breaksea
group and Tia Island (Fig. 1.2); the Boat Group (Fig. 1.3); and the Taukahepa group (not used in this study).

Figure 1.1 The position of the two island groups (Tia Island and the Boat group) used in the modelled experiments relative to Rakiura Island.

The Titi islands are of importance to Rakiura Maori, who harvest titi (Sooty Shearwaters, *Puffinus griseus*) on many of the islands. There is a will among the birding community (in this context Rakiura Maori who harvest titi) to preserve harvestable populations of titi on these islands for cultural and economic reasons. Given the destructive impact rats may have on seabird colonies (Austin 1948; Moors 1985; Moors 1990; Drever & Harestad 1998; Hobson et al. 1999) and the birders own experience with rats (Drummond 1910; Atkinson 2001), the birding community is justifiably concerned about rat invasions of the Titi Islands and have initiated a plan to eradicate rats (*R. rattus*) from four of the islands (Moller, Nevins & Adam 2003). Also The Titi Islands are of high conservation value, having nesting colonies of

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several species of Procellariids, Yellow-eyed penguins (*Megadyptes antipodes*), and threatened land birds such as fernbirds (*Megalurus punctatus punctatus*), saddleback (*Philesturnus carunculatus carunculatus*) and robins (*Petroica australis*).

This study contributes to the Kia Mau Te Tīti Mo Ake Tōnu Atu ("Keep the Titi forever") research project. This is a collaboration between Rakiura Maori and the University of Otago that aims to provide information to help manage the titi populations that nest on the Titi Islands.

Modelled experiments were carried out using two island groups from the Titi Islands. These were Tia Island and its surrounding islands and source populations (Fig. 1.2) and the Boat Group (Fig 1.3). Tia Island was used firstly because it is very near to shore, being only 660m from the nearest headland. This made it useful for exploring the possibilities of keeping islands at high risk of rat invasion rat free. Secondly Tia Island already supports a population of *R. norvegicus* and the population of titi has been greatly reduced by the arrival of *R. norvegicus* on both Tia Island and Weka Island (a neighbouring island) (Drummond 1910). For this reason it has long been a goal of the birders (bird harvesters) on Tia Island to rid the island of rats (H. Moller pers. comm.). A primary aim of this project is to assess the feasibility of keeping Tia Island rat free if it was ever cleared of rats.
Stochastic computer simulation of island colonisation by *R. norvegicus*.

![Diagram of island colonisation](image)

Figure 1.2 Tia Island and its neighbour Weka Island. The black boxes show the relative positions of the mainland sources and islands as they were entered into the model.

Although most islands in the Boat Group have never supported populations of *R. norvegicus* (the exception being Kundy Island) (Moller et al. 1999), this group was used to model complex rat invasion patterns in an archipelago of many islands. The Boat Group contains enough islands that multiple invasion pathways are possible for each island, but is not so large that computation is too complex for the model deal with. Also all the islands in the Boat Group are relatively small (< 30 ha). This is an important reason for choosing the Boat Group over other island groups, because the amount of time the model takes to complete each simulation is dependant on the number of migrants in the system, thus, the smaller the populations involved the better the model ran.

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1.8.2 Aims of the Modelled experiments on Tia Island

Does the current “knowledge state” allow us to ask questions about;

a) whether or not near shore islands like Tia Island can be rid of rats either by repeated eradication or permanent poisoning operations, and what sort of answers might we expect from these enquiries?

b) does the “knowledge state” contain enough information to determine the effect age biased mortality rates have on suppressing populations of \( R. \textit{norvegicus} \) on islands?
Modelled experiments in which adult and pre-adult mortality rates are varied on Tia Island will help to answer these important questions.

1.8.3 Aims of the modelled experiments on the Boat Group

Modelled experiments on the Boat Group aim to question our current 'knowledge state' about the effect keeping some islands in the Boat Group rat free will have on other islands in the Boat Group;

a) Can stopping the colonisation of one patch in a small metapopulation have consequences for other patches in that metapopulation? A consequence that will interest wildlife managers is whether or not protecting a few islands from rat invasion will reduce the chances of invasion for the other islands in the system?

b) Is the model strong enough to make precise predictions about how long each island in the group will take to be invaded for the first time?

c) Is the invasion pattern produced by the modelled experiment on the Boat Group a stepping stone type pattern, where each colonised island is used to invade the next island in line? Or does a single point pattern apply, where all invasions are sourced from just one or two colonised islands, or the mainland itself?

d) Is a 'rescue effect' likely to be operating? The 'rescue effect' is a metapopulation process where a patch or island is saved from extinction by continued subsidisation from immigration (Gotelli & Kelly 1993; Lande et al. 1998). It was tested whether or not the rescue effect might be occurring on the small islets of the Boat Group (Fig. 1.3) by measuring the average time to extinction. If the 'rescue effect' is occurring on these islets then it is expected...
that the average time to extinction will tend to be shorter (i.e. the population is
less persistent) when the main source of immigration is cut off.

Empirical evidence that the rescue effect occurs in small mammal metapopulations is
lacking (Boyett et al. 2000). The ‘rescue effect’ is of particular interest to managers
because if it is occurring then it means that it may make island populations that are
less isolated harder to eradicate because their populations will be supplemented by
immigration. The ‘rescue effect’ would also mean that if a main island population was
eradicated then surrounding rat populations might be more likely to go extinct
naturally, or easier to eradicate.

The modelled experiments presented here are developed primarily to help managers
decide about which islands are most suitable for rat eradication. Is the current
‘knowledge state’ strong enough to make predictions that are accurate and precise
enough to be useful? If the models presented here find that the ‘knowledge state’ is
not strong enough then, an attempt will be made to show how much uncertainty exists
and what areas of the ‘knowledge state’ need to be improved to reduce that
uncertainty.
2 Methods, model structure, and parameterisation

Following the approach of Keeling (2002) I establish a model composed of two sub-models:

1. A swimming model that determines how many migrants survive the journey from any island to every other island in the archipelago.

2. A demographic model that incorporates births, deaths, emigration and gender of neonates. The demographic model affects colonisation rate by determining the number of migrants entering the migrant pool. The higher the model population the more migrants attempt to disperse to new patches, which increases the colonisation rate (Keeling 2002).

The modelled experiments were composed of either 300 (the Boat Group experiments) or 500 (the Tia Island experiment) simulations. Each simulation was run for 100 turns in the case of the modelled experiment on the Boat Group and 12 turns after Tia Island was invaded.

2.1 What was included and what was left out of the model

Stochasticity

Three types of stochasticity were built into the model: demographic stochasticity; migration stochasticity; and parameter stochasticity. Demographic stochasticity was included in the model by making the processes of death, sex allocation of births, and age class and sex of emigrates stochastic. Demographic processes were made stochastic because at low populations, such as when a population is first established, chance events can have a large effect on weather or not a population becomes established.

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Migration stochasticity was incorporated by modelling the process of swimming as a series of random directional decisions and jumps. Modelling swimming as a series of random directional jumps assumes that migrants have no knowledge about the island system they live in or the capacity to respond to any such knowledge. Thus, in the model, islands do not attract migrants and migrants cannot orientate while swimming to travel directly towards the nearest island. In reality however, those islands that are detectable from across water may attract migrants and the probabilities allocated to random direction movements will not reflect these associations. For example an island may have a large, noisy, smelly, highly detectable colony of seabirds. If rats detect the seabirds from another island they may try to swim there in search of food. In reality it is unknown if rats can see target islands or maintain a direction when swimming.

Swimming is modelled as a stochastic process for two reasons. Firstly, it is unknown how rats swim or how frequently they colonise islands, and current data are insufficient to create a function between distance of the target island and the rate at which it is colonised. It has been suggested that the rate of island colonisation declines exponentially with distance (Hanski 1998). Deterministic functions such as these assume that there are a large number of migrants in the migrant pool. Some of the islands in this study will have <100 migrants in their pool of potential colonisers. At these low numbers, stochastic effects become important. Secondly, turning frequency of a swimming rat was made stochastic because the relationship between an islands position in relation to another island and its rate of colonisation is not known. If there is a large island in the vicinity of a smaller island the larger island may absorb many migrants before they reach the smaller island. This may result in the situation where raising the mortality rate on the larger island by trapping or poisoning protects the smaller island from colonisation. The extent of these hypothesised effects will depend
on the orientations of the relevant islands, the comparative size of the small island to the large island, and the area of water explored by a swimming rat before it finds an island. This last factor will depend on the turning frequency of a swimming rat. In the model, swimming turning frequency is determined by the two parameters $P_s$ and $P_P$ (see section 2.6.1 for an explanation of these parameters).

Another stochastic effect related to the swimming process is which side of the island migrants leave from. In this model for simplicity every migrant had an equal chance of leaving from any side. In reality this may not be the case. One side of an island may be more heavily populated than the other, leading to more migrants leaving from the populous side. Also rodents are more likely to enter the water from the end of a peninsula (Hanski & Peltonen 1988). Thus, if an island has a uniform coastline on one side and lots of headlands and peninsular on another more migrants will leave the island from the convoluted side.

Parameter stochasticity was built into the model so that the strength of the 'knowledge state' (in this case represented by parameter uncertainty) could affect the precision of the predictions produced by the model. Parameter uncertainty was incorporated into the model in the following way. At the start of each simulation the value for every parameter was drawn at random from a uniform distribution, whose upper and lower bounds were determined (where possible) by the amount of uncertainty surrounding the estimate. Where possible the upper and lower bounds were determined using a 95 percent confidence interval based on several studies (see Table 2.1 for studies used). If this was not possible then a maximum likelihood test was used (for more detailed discussion of this test see page 47). For some parameters these two methods were not possible and uncertainty was effectively infinite. Where this was the case the upper
and lower bounds were set at the arbitrary values of the estimate plus or minus 30 percent.

For simplicity environmental stochasticity was not included in the model. This means that events like mast years and particularly wet or dry years are ignored. There are two likely biases caused by the omission of environmental stochasticity. Firstly populations are less likely to go extinct because there are no bad years to reduce the population. Secondly colonisation rates are likely to be more stable, because the number of migrants will not drop in bad years or explode in good years.

**Density Dependence**

Density dependence was included in the demographic model by making female fertility and pre-adult mortality density dependent. There have been several studies that address whether density dependence works in populations of small rodents. One recurrent finding from these studies is that female reproduction reduces with increasing density (Craig & Bunn 1989; Montgomery, Wilson & Elwood 1997; Lewellen & Vessey 1998; Prevot-Julliard, Henttonen, Yoccoz & Stenseth 1999; Liam, Julliard, Stenseth & Jaksic 2001). In the model this is represented by the density dependent relationship FBF (female breeding factor). Intuitively it would be expected that the relationship between the FBF and density would be curved. Up to a point individuals have enough food to maintain their body condition and density can rise to this point with little effect. But once food per-individual drops below maintenance level females will start to lose reproductive condition. The shape of this relationship is affected by altering the parameter $a$ (see Fig. 2.4). Pre-adult mortality was also modelled as density dependent. That pre-adult mortality is density dependent is supported by empirical studies (Lewellen & Vessey 1998; Oli et al. 2001).
mortality rate was modelled as increasing with increasing density. A curved relationship of the same form as FBF was used to model the relationship between pre-adult mortality rate and density.

Emigration was also made density dependent. Studies on density dependent migration across water for rats are lacking, although there is some literature on the subject for rodents in general (Hansi, Peltonen & Kaski 1991). Hanski et al. (1991) found that shrew (Sorex araneus) dispersal from a mainland to islands increased significantly during years of high density. However despite having five continuous years of data, Hanski et al. (1991) had only two years when population densities were markedly higher than the other years. It is only these two years that the conclusions above were based on. As far as these data go they suggest that shrews migrate to islands at “usual” densities, but migration rate increases significantly when density increases significantly. This suggests that migration across large bodies of water is density dependent.

Making emigration density dependent had two main effects on the model. Firstly it meant that there was no migration between islands when populations were low, such as in the non-breeding period or in the turn of the model directly after the non-breeding period, when the population was still low. Secondly it put a cap on population size for any one island, because when the population reached Mt all subsequent individuals became migrants.

A special case of density dependence is the Allee effect. The Allee effect is a type of inverse density dependence where at very low densities each individual has a decreased chance of survival and/or reproduction. The Allee effect is potentially

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important on large islands where rats may have trouble finding mates when density is extremely low. For simplicity this model does not include the Allee effect. This condition is unlikely to affect the model because only small islands (< 30 ha) were used for modelled experiments and sensitivity analyses.

Adult mortality was made density independent. This is because none of the studies above (Craig & Bunn 1989; Montgomery et al. 1997; Lewellen & Vessey 1998; Prevot-Julliard et al. 1999; Liam et al. 2001) could demonstrate that high densities lead to high adult mortality. This indicates, either, mortality is density independent, or, the raise in mortality only occurs at very high densities, densities not achieved in these studies because reduced breeding lowered the population before it reached that point.

The effects of currents are ignored
The effects of ocean currents are ignored in the stochastic swimming model. This is clearly not true of many stretches of costal ocean. Ocean currents could increase the chances that an island will be invaded if that island is down current from a potential source. Ocean currents could also protect an island from invasion. If a strong current lies between two islands, then it may be very difficult for a rat to swim the strait without being swept away.

Equal Habitat quality
For simplicity, in each simulation all islands are assumed to be of equal quality in terms of rat habitat. This assumption may be violated because some islands and islets included in the modelled experiments may have larger food and water sources than others.
It is also assumed that all islands produce migrants of equal quality in terms of navigation ability and swimming distance. This assumption may be violated if some islands have a more reliable, or a higher quality food source than others.

The potential effects of predation are also ignored. If an island supports a population of potential predators then it may have higher mortality rates. Some islands included in this study are predator free, while others support populations of weka (*Gallirallus australis*), which is a potential predator of *R. norvegicus* (pers. obs.). Harrier hawks (*Circus approximans*) are known predators of rat species in general (Moors 1990; Moller & Craig 1987) and can easily fly from Stewart Island to the island systems included in this study. The effect of predation from harrier hawks may not be evenly spread, with more remote islands being visited less often.

*Seasonal fluctuation*

This model includes breeding and non-breeding seasons. The breeding season for many populations of *R. norvegicus* in New Zealand starts in spring and continuing through autumn, although the exact start and end months of breeding are variable across the country (Moors 1985; Taylor 1986; Moors 1990; Taylor & Thomas 1993).

No other form of season effect was included in the model. In the demographic model this was expressed by making the carrying capacity the same in every turn. In the stochastic swimming model dispersal ability is held constant throughout the year. It is likely that the drop in ocean temperature that occurs during winter makes this simplification unrealistic. Also if there are periods of limited food availability migrants may be in poorer condition in some parts of the year, which will reduce their swimming distance. If in reality dispersal ability is variable throughout the year, the
model will overestimate the dispersal ability of migrants during winter and times of limited food availability.

**Individual based model**

This model was based on individuals rather than populations. Modelling at the individual level allowed the outcomes of the model to be more influenced by stochastic events as the number of individuals decreased. Also, modelling at the individual level provides information on which processes of rats swimming need to be studied more closely and how the parameters in the demographic model affect the colonisation rate of islands. For example, is a rats propensity to turn while swimming more important than the overall distance it can swim? And is the number of migrants more important than how well those migrants swim? Another possibility is that there are interaction effects between some of the factors.

**Inbreeding depression**

For simplicity, no inbreeding depression was included in the demographic model. If only a single pregnant female reaches an island it is possible that she could found a population, however for this to happen rats from the same litter would have to mate. If inbreeding depression does occur in *R. norvegicus*, this simplification will cause the model to overestimate the effect pregnant female migrants have on the colonisation rate of islands.

**2.2 The order in which processes were carried out in the combined model**

At the beginning of each simulation the value for each parameter was chosen as detailed above and initial population sizes were set; empty islands were set to zero.

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The model then cycled through a specified number of turns. In each turn, first the stochastic swimming model calculated emigration and then immigration for every island; immigrants were introduced to the population at this point. The demographic model was then used to calculate mortality. Then the number of individuals in every age class was calculated for the next turn; it was at this point that births from immigrants were introduced into the population.

The length of one turn is three months. This was chosen because most females start breeding at around three months of age (Greenman & Duhring 1923; Innes, King, Flux & Kimberley 2001).

2.3 Stochastic Swimming Model

The stochastic swimming model connects populations through emigration and immigration. General structure of the stochastic swimming model is shown in Fig. 2.1. An emigrant leaves island A (flow $E_{a.s.it}$ where $a$ is age class, $s$ is sex, $i$ is the island being left, and $t$ is time) and becomes part of the migrant pool for island A. If the migrants in migrant pool A survive to find island B then they become part of immigration for island B (flow $I_{a.s.it}$ where $a$ is age class, $s$ is sex, $i$ is island arrived at, and $t$ is time).
Figure 2.1 Structure of connection between island models. Age class $a$ can be 0, 1, 2 or 3; sex $s$ can be male or female; $i$ refers to the island that the rat is coming from for $E$, and the island that the rat is going to for $I$; $t$ is the time step.
2.3.1 Calculating the number of emigrants

Emigration (Eq. 2.1, where \( a \) is age class, \( s \) is sex and \( t \) is time: Fig. 2.1) is the number of individuals that leave the population. The number of emigrants is calculated using a migration threshold (Mt). Mt is the density beyond which all surplus individuals migrate. Mt is assumed to be greater than \( K \) (defined in Eq. 2.1), and is expressed as a percentage of \( K \). Consider a hypothetical example where: \( K = 5 \) rats per ha and \( Mt = 1.1 \). The density at which migration occurs would be \( 5 \times 1.1 = 5.5 \) rats per ha. In this example, if the density on the island were below 5.5 rats per ha then no rats would emigrate. If the density went above 5.5 rats per ha then the number of emigrants would be:

\[
\text{Number of emigrants} = N_{\text{total}} - (Mt \times K \times \text{area})
\]

Where: \( N_{\text{total}} \) is the total number of individuals on an island in all age classes.

Mt: is Migration threshold, and is explained above.

\( K \): is Carrying capacity, and is the density at above which mortality and birth rates cease to change with increasing density.

Area: is the area of the island in ha.

Eq. 2.1 is only calculated if \( N_{\text{total}} > (Mt \times K \times \text{area}) \), so that there cannot be a negative number of emigrants. The number of emigrants was rounded to a whole number. The number of emigrants is then distributed among the age and sex classes at random. Mt envisions a situation where an individual will only move if the island it is on is 'full'.

Mt is a crude approximation of the relationship between emigration and density, and was used because the lack of quality data caused problems in parameterising the...
stochastic swimming model. The threshold form of the relationship between Mt and density means that there is only one parameter to estimate in regard to this relationship. With spare data and for reasons explained in section 2.6.2 minimising the number of parameters in the stochastic swimming model was more important than adding greater detail to the model.

Once the number of emigrants has been calculated, the required number of ‘virtual rats’ leave their populations and are passed to the stochastic swimming simulation. The stochastic swimming simulation then calculates how many of the migrating ‘virtual rats’ survive, and which islands the survivors arrive on.

2.3.2 Stochastic swimming simulation

In the stochastic swimming model maps of the island systems were first translated into grid co-ordinates. Each grid co-ordinate is composed of two numbers, a row position and a column position. The row numbers increase from south to north and the column numbers increase from west to east. Grid position row 1, column 1 (GP(1, 1)) is taken as the south-western corner of the most western island. Island systems are translated into grid co-ordinates by assuming each island is represented by a rectangle that lies north/south or east/west across the grid (an island cannot lie diagonally across the grid). This means that each island is represented by four GP’s, the south-western corner, the south-eastern corner, the north-eastern corner and the north-western corner. A hypothetical island may be described by the points, GP(1, 1) (south-western corner), GP(10, 1) (north-western corner), GP(1, 5) (south-eastern corner) and GP(10, 5) (north-eastern corner). This island would be 10 pixels along its north/south axis and 5 pixels along its east/west axis. A migrant is said to have arrived at the above hypothetical island if the migrants row position is greater than or equal to 1 but less than 10.
than or equal to 10, and the migrants column position is greater than or equal to 1 but less than or equal to 5.

The algorithm in appendix 1 is used for each migrant from each island at each turn to determine which island, if any, the migrant reached.

In plain English, appendix 1 says that a side or corner of the island that the migrant is on is randomly chosen. The migrant then leaves from a random point on that side of the island or if a corner is chosen the migrant leaves from that corner. The migrant leaves the island by jumping a distance of five pixels directly away from the island.

The migrant then starts to ‘swim’. The process of ‘swimming’ involves choosing a direction for the migrant to jump. The direction of the jump is determined by first choosing a random number between zero and one, if the random number is below the value $P_s$ (defined in section 2.6.1 and appendix 1) then the migrant jumps in the same direction as the previous jump (it “swims” straight). If the random number is above the value $P_s$ then one of eight directions is randomly chosen. After the direction of the jump is determined the migrant jumps a specified number of pixels (PPJ) in the chosen direction. After each jump the position of the migrant is evaluated to see if it has reached an island. If an island is reached one is added to the number of individuals in the age and sex class of the migrant, for the island that was reached. If the migrant was pregnant, as determined by a random binary switch that is 1 $P_p$ (defined in section 2.6.1 and appendix 1) proportion of the time, then the value “litter size” (defined in appendix 3, Eq. 16) was also added to age class 0 of the island that was reached. Only females in age classes 1, 2, or 3 could be pregnant. If a migrant reached an island then that migrant stopped “swimming” and the process started again for a
new migrant. If an island was not reached the migrant makes another directional
decision and jump. This process continues until the migrant reaches an island or has
made MD jumps, at which point the process starts again for another migrant.

Any ‘virtual rats’ that reach an island are passed to the demographic model, which
integrates them into the new population.

2.4 Demographic model

2.4.1 Population simulation

The population was simulated as a pair of stochastic demographic models. Each pair
of models represents an island. One of the models in a pair represents the female
population; the other model represents the male population (denoted by the subscript $f$
or $m$ in Fig. 2.2). Female and male populations are modelled separately because at low
populations, as when populations are first establishing, a sex ratio imbalance will
affect the chances that a population will establish.

The demographic models are age structured, having four age classes.

a) Pre-adult (0) which is defined as any individual that is below the potential
   breeding age.

b) Age class 1 (1) is one turn older than a pre-adult.

c) Age class 2 (2) is two turns older than pre-adult; and

d) Age class 3 (3) is greater than or equal to three turns older than pre-adult.

An individual stays in each age class for one turn. This means that it takes one year
for an individual to go from birth to the end of age class 3.

The overall structure of the demographic model is shown in Fig 2.2.
Figure 2.2 Structure of the island population models. Life stages are in boxes while rates are open text.
Before the population simulation started adult immigrants were introduced into the population, the population simulation was then run.

2.4.2 Calculating mortality rates

Mortality was the first process calculated. The mortality rate for age class 0 ($M_{0,s,t}$ in Fig. 2.2; where 0 is the age class, s is sex and t is time) is modelled as a density dependent relationship of the form:

$$M_{0,s,t} = A^a((N_{\text{total,}t} / \text{area})^a) + M_{0}$$  \hspace{1cm} \text{Eq. 2.2}

Where:

$$N_{\text{total,}t} = 0f_t + 1f_t + 2f_t + 3f_t + 0m_t + 1m_t + 2m_t + 3m_t$$  \hspace{1cm} \text{Eq. 2.3}

Area: is the area of the island in hectares.

$a$: is a parameter that as it increases in value causes the curve describing the relationship between $M_{0,s,t}$ and density to begin rising later but more steeply (see Figure 2.4 for how $a$ affects the shape of the curve).

$M_{0}$: is the value of $M_{0,s,t}$ when $N_{\text{total,}t} = 0$.

$A$: is a scaling parameter which ensures $M_{0}\text{st} = mC$ when $(N_{\text{total,}t}/\text{area}) = K$ for any given value of $a$, and is given by:

$$A = (mC - M_{0})/K^a$$  \hspace{1cm} \text{Eq. 2.4}

Where: $mC$ is the value of $M_{0,s,t}$ when $(N_{\text{total,}t}/\text{area}) = K$. $mC$ is the highest mortality rate that pre-adults experience.
Mortality rates for age classes 1, 2 and 3 are assumed to be density independent. The average relationship between \( M_{a,s,t} \) and density is shown in Fig. 2.3. The algorithm shown in appendix 2 used a binomial mortality switch (MS) to translate mortality rates \( M_{a,s,t} \) into number of individuals dying. The algorithm in appendix 2 was used to convert the rates \( M_{a,s,t} \) into a real number of individuals because it introduces stochasticity to the model.

### 2.4.3 Calculating the number of individuals in the next turn

After mortality rates were converted into the number of individuals dying for each age class, the number of individuals moving into the next age class for the next turn was calculated. The number of individuals in age classes 1 and 2 in the next turn is given by:

\[
N_{a+1,s,t+1} = (N_{a,s,t} - E_{a,s,t}) + I_{a,s,t} \cdot \text{Number dying}_{a,s,t}
\]

And the number of individuals in age class 3 in the next turn is given by:

\[
N_{3,s,t+1} = (N_{3,s,t} - E_{3,s,t}) + I_{3,s,t} \cdot \text{Number dying}_{3,s,t} + (N_{2,s,t} - E_{2,s,t}) + I_{2,s,t} \cdot \text{Number dying}_{2,s,t}
\]

Where: \( N_{a+1,s,t+1} \) is the number of individuals in the next age class of sex \( s \) at the next turn.

\( N_{a,s,t} \) is the number of individuals in age class \( a \) of sex \( s \) at time \( t \).

\( E_{a,s,t} \) is the number of emigrants leaving from age class \( a \) of sex \( s \) at time \( t \).
The method for calculating the number of emigrants is discussed above in section 2.3.1.

$I_{a,s,t}$ is the number of immigrants coming into age class $a$ of sex $s$ at time $t$.

The method used to calculate the number of immigrants is discussed in section 2.3.2.

Number dying $a,s,t$ is defined above and in appendix 2.

As shown in Eq. 2.6 the number of individuals in age class 3 in the next turn is calculated using inputs from both age class 3 and age class 2. This was done so that individuals did not die automatically when they reached age class 3. The brackets are included in Eq. 2.5 and Eq. 2.6 to denote the order in which the terms were calculated. First emigration is removed from the population then immigrants were included in the population, and finally mortality was removed from the population.

Eq. 2.5 and 2.6 mean that the 'virtual rats' in age class 3 are taken from age class 2 and the surviving members of age class 3 for the previous turn. Those in age class 2 are taken from age class 1, and those in age class 1 are taken from age class 0. This leaves age class 0 empty.

2.4.4 Calculating the number of Births

Once the number of individuals in the adult age classes was calculated, 'virtual rats' in age class 0 were created using the reproduction algorithm in appendix 3. The reproduction algorithm first determines if males are present in the population and whether or not it is the breeding season. If no males are present, or it is the non-
breeding season then no births are produced. If males are present, and it is the breeding season then the total number of breeding aged females in the population is multiplied by the constant 'Litter size' and the density dependant factor FBF, to give the total number of births. The births are then distributed randomly between the sexes.

The reproduction algorithm links male and female populations in two ways. Firstly only females create births; those births go into the offspring pool and are divided stochastically between males and females. Secondly males must be present for females to create births (through MI).

2.4.5 The relationship between adult mortality, pre-adult mortality, FBF and density in the demographic model

The adult mortality is modeled as a density independent relationship (straight line in Fig. 2.3). Both $M_0$ and FBF are modeled as density dependent relationships (curved lines in Fig. 2.3).

In Fig 2.3 the curves describing FBF and $M_0$ bend in the opposite direction, even though Eq. 2.2 and Eq. 2.17 in appendix 3 are identical in form. The reason can be found in Eq. 2.4 and Eq. 2.19 in appendix 3. When FBF is being calculated $B_{ns}$ is always greater than $b_C$, thus, the scaling factor $A$ is a negative number which causes the curve to descend as density gets higher. In biological terms this means that at lower densities more offspring are produced than at higher densities. When mortality for age class 0 is being calculated $M_{n0}$ is less than $m_C$, thus, the scaling factor $A$ is always positive and causes the curve to rise as density gets higher. In biological terms this means that as density increases so does the mortality rate.
Stochastic computer simulation of island colonisation by *R. norvegicus*.

Figure 2.3 The average values of mortality for age class 0 (open squares), mortality for age classes 1, 2 and 3 (closed triangles), and FBF (closed squares), against density. For both $M_0$ and FBF is 2. $M_{00} = 0.17$, $mC = 0.622$; $Bn_0 = 0.66$, and $bC = 0.1$. Mortality rate for age classes 1, 2, and 3 is 0.329.
It must be kept in mind that values used in Fig 2.3 are only average values. Because the parameters that describe each curve in Fig. 2.3 are determined by randomly selecting a value from a uniform distribution before each simulation they will have a different shape in each simulation. But if many simulations are run the average value for each parameter in Fig. 2.3 will be the roughly what is shown Fig. 2.3 because those values are the centre of the uniform distribution.

The parameter $a$ can cause the curves $M_0$ and FBF to vary from a straight line ($a = 1$) to a threshold relationship ($a > 60$). Fig. 2.4 shows an example of how $a$ affects FBF, $a$ has the same effect on the shape of $M_0$. 
Figure 2.4 Hypothetical density dependant relationship between FBF and density. In this example $B_{n_0} = 0.9$, $C = 0.4$ and $k = 4$. The effect of varying $a$ can be seen in the difference between the three curves. In the straight line (closed squares) $a = 1$, while in the middle line (open circles) $a = 10$, and in the most steeply curved line (closed triangles) $a = 60$. 

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2.5 Assumptions and biases in the model

Assumptions implicit in the order of calculation

Because a computer program can only calculate one thing at once, the order in which the model calculates processes creates assumptions. By removing emigrants from the population before mortality is calculated it assumes that rats will rather leave a crowded island than stay on the island and risk being attacked or starving to death. Introducing immigrants before mortality and births are calculated assumes that immigrants have the same mortality and fertility rates as residents.

The point births from immigrants are introduced into the population

The point at which births from immigrants are introduced into a population causes a bias in this model. Because immigration is calculated before mortality in this model, if immigrant births are introduced into the population during the immigration phase then pre-adults from immigrants go through the higher pre-adult mortality rate twice, compared to only once for pre-adults from residents. This bias would lead the model to underestimate the role pregnant female migrants have in colonising islands. The alternative, and the approach that was used, is to hold immigrant births out of the population until after mortality is calculated. Because immigrant births are introduced into the population after the first mortality phase, the situation arises where a parent may die but its litter still survives (because the litter misses the first mortality phase but the parent does not). This is clearly not a realistic situation because in reality if a mother dies her litter will also die unless they are very near independence. This bias will make the model overestimate the importance pregnant female migrants have in colonising islands. This problem gets worse as adult mortality rates become higher relative to pre-adult mortality rates, because more immigrant mothers are killed relative to the number of immigrant births that survive.

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Colonisation behaviour of individuals is as for the Noises Islands

By calibrating four parameters against the invasion history of only one island system, the Noises Islands (Table 2.1, section 2.6.1, and section 2.6.2), the model assumes that rats display the same colonisation behaviour as those in the Noises Islands regardless of the location of the islands system. This assumption may be false in the case of the two island systems modelled in this study. Both Tia Island and the Boat Group are located off the coast of Stewart Island, much further south than the Noises Islands. As a result the water temperature around the island groups that were modelled is much colder than the water temperature around the island group that the model was calibrated against. This could have two major affects. Firstly, rats may be less willing to enter the water in the two southern systems than in the northern system. Secondly, if rats do enter the water in the southern system they maybe more likely to die of cold stress than their northern counterparts. The violation of this assumption will make the model overestimate the dispersal and colonisation ability of rats in the modelled systems, leading to a more pessimistic view of rat invasion.

Also, because the effects of currents were ignored in this model, if currents affected the colonisation of the Noises Islands then the model will be biased. If currents aided rats in reaching the Noises Islands then the model will overestimate the dispersal ability of rats. On the other hand if currents made the Noises Islands more difficult to invade the model will underestimate the dispersal ability of rat.

The way mainland populations were modelled

The way large mainland populations were included in the model caused a bias. Because of run time problems very large populations (such as that of Stewart Island) could not be included in the model. To overcome this, mainland populations were
modelled as sets of smaller islands with areas of 30 ha. These ‘mainland islands’ were based on large headlands and peninsulas that were within swimming range (estimated at 2500m) of any of the islands in the system, or stretches of coast that were particularly close to an island in the system. This means that the overall mainland population is much smaller in the model than in reality. Thus, there are far fewer migrants in the migrant pool from the mainland. This bias leads the model to underestimate the rate at which islands in the system are colonised.

2.6 Parameter estimation

The parameters of the stochastic swimming model and demographic model (hereafter referred to as the combined model when used together) are shown in Table 2.1. A variety of methods were used to estimate the parameter values, and the uncertainty around those parameter values.
Table 2.1 Parameters estimates used in the combined model for the modelled experiments on Tia Island and the Boat Group. The estimates are the average value expected after many runs as they are the centre of the uniform distribution from which values were chosen randomly at the start of each simulation. The upper and lower limits of the uniform distribution are also shown.

<table>
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<th>Parameter</th>
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<th>Estimate</th>
<th>limits of uniform distribution</th>
<th>Method of estimation</th>
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<td>R. rattus R. rattus R. norvegicus R. rattus R. norvegicus R. norvegicus R. norvegicus</td>
<td>0.21 0.134 0.355 0.511 0.202 0.396 0.358 0.409</td>
<td>0.322 0.428 0.216</td>
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<td>Maximum likelihood output (see text in section 2.6.2)</td>
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Table 2.1 continued

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sources Used</th>
<th>Species</th>
<th>values from study</th>
<th>Estimate</th>
<th>limits of uniform distribution</th>
<th>Method of estimation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter size</td>
<td>Moors 1985</td>
<td><em>R. norvegicus</em></td>
<td>6</td>
<td></td>
<td></td>
<td>Upper and lower limits of the uniform distribution estimated using 95% confidence limits based on values in column 4, rounded to the nearest whole number.</td>
</tr>
<tr>
<td>Bettesworth 1972</td>
<td><em>R. norvegicus</em></td>
<td>6.5</td>
<td></td>
<td></td>
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<tr>
<td>Innes <em>et al.</em> 2001</td>
<td><em>R. norvegicus</em></td>
<td>7.6</td>
<td></td>
<td></td>
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<tr>
<td>Innes <em>et al.</em> 2001</td>
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<td>7</td>
<td></td>
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</tr>
<tr>
<td>Taylor 1986</td>
<td><em>R. norvegicus</em></td>
<td>7.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moller &amp; Tilley 1984</td>
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<td>6.7</td>
<td></td>
<td>7</td>
<td>8</td>
<td>The Estimate is the average of the values in Column 4, rounded to the nearest whole number.</td>
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<td>7.5</td>
<td>7</td>
<td></td>
<td>6</td>
<td></td>
</tr>
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<tr>
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<td>0.398</td>
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</tr>
<tr>
<td>King &amp; Moller 1997</td>
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<td>0.405</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>King &amp; Moller 1997</td>
<td><em>R. rattus</em></td>
<td>0.09</td>
<td>0.329</td>
<td>0.437</td>
<td>0.222</td>
<td></td>
</tr>
</tbody>
</table>

Mortality for age class 0

| Mno                                | Cullhoun 1963     | *R. norvegicus* | 0.17              | 0.17      | 0.45                           | 0.119               |
|                                    |                  |                |                   |           |                                | Estimate based on study in shown in column 2 Upper and lower limits are explained in notes a and b respectively |

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Table 2.1 continued

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sources Used</th>
<th>Species</th>
<th>values from study</th>
<th>Estimate</th>
<th>limits of uniform distribution</th>
<th>Method of estimation</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>upper</td>
<td>Lower</td>
</tr>
<tr>
<td>Ma</td>
<td>Moller &amp; Tilley 1984</td>
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<td>0.59</td>
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</tr>
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<td>0.518</td>
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<tr>
<td></td>
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</tr>
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<td>King &amp; Moller 1997</td>
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<td>0.45</td>
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<td>The Estimate is the average of the values in column 4.</td>
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<td></td>
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<tr>
<td>Female breeding factor</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Bno</td>
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<td>0.858</td>
<td>0.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ba</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bC</td>
<td>0.1</td>
<td>0.4</td>
<td>0.07</td>
<td></td>
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</tr>
</tbody>
</table>

This value is arbitrary, and was not varied in the modelled experiments.

Upper and lower limits are explained in notes a and b respectively.

See section 2.6.3 for an explanation of the estimate.

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Stochastic computer simulation of island colonisation by *R. norvegicus*.

Table 2.1 continued

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sources Used</th>
<th>Species</th>
<th>values from study</th>
<th>Estimate limits of uniform distribution</th>
<th>Method of estimation</th>
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<td></td>
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<td></td>
<td></td>
<td>upper</td>
<td>Lower</td>
</tr>
<tr>
<td>K</td>
<td>Taylor 1986</td>
<td><em>R. norvegicus</em></td>
<td>8.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Brown <em>et al.</em> 1996</td>
<td><em>R. rattus</em></td>
<td>7.15</td>
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<td></td>
<td>Daniel 1972</td>
<td><em>R. rattus</em></td>
<td>1.83</td>
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<tr>
<td></td>
<td>Moors 1985</td>
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<td>3.4</td>
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<td>Bettesworth 1972</td>
<td><em>R. norvegicus</em></td>
<td>5</td>
<td>5.24</td>
<td>8.71</td>
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<tr>
<td>Initial female population</td>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>Initial male population</td>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>1:50 000 topographic series LINZ</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Island distance</td>
<td>1:50 000 topographic series LINZ</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Island shape</td>
<td>1:50 000 topographic series LINZ</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a: This limit was used so that the relationship could tend towards density independence.
b: Because a logical estimate for the upper and lower limits could not be obtained the arbitrarily figure of the estimate plus or minus 30 percent was used.

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2.6.1 Parameter estimation for the stochastic swimming model

In the stochastic swimming model there are five parameters that need to be estimated (MD, PP, Pp, Ps, Mt), and two parameters taken from maps of the island system (island position and island shape). The two parameters that are taken from maps are entered into the model as GP's. The GP of an island's four corners describe its position in relation to all other islands in the system and the islands' shape, relative to all other islands in the system (here shape also includes an island's orientation).

MD is the number of pixels a migrant can travel before it is considered dead. The upper and lower limits of MD for the modelled experiments on Tia Island and the Boat Group are 250 and 150 respectively. This range was estimated from the eradication and re-invasion of the Noises Islands. The population of R. norvegicus on the Noises Islands was eradicated, and then re-established 5 times between 1978 and 2001 (J. Russell, pers. comm). The assumed source of the invasions was Rakino Island. Motuhoropapa Island was consistently the first island in the Noises group on which the re-invasion was detected (J. Russell, pers. comm.). The upper limit is based on the shortest distance a rat would have to swim to reach Motuhoropapa Island from Rakino Island if no steppingstone islands were used, which is roughly 2500m. Thus, using Eq. 2.15 in appendix 1 the upper limit of MD = 250 pixels. The lower limit is based on the shortest distance a rat would have to swim to reach Motuhoropapa Island from Rakino Island if it used steppingstone islands, which is roughly 1500m. Using Eq. 2.15 in appendix 1 the lower limit of MD = 150.

Both PP and Ps determine the turning frequency. PP is the number of pixels moved every jump, and determines the number of directional decisions that are made before a migrant is considered dead. If PP = MD then the migrant only chooses a swimming...
direction once, and then makes a single jump in that direction. On the other hand if PPJ is small, then each migrant makes many directional decisions (if PPJ = 1 then each migrant makes MD directional decisions). This gives the migrant more opportunities to turn. An upper limit of PPJ = 5 was used because any value larger than this and migrants could miss smaller islands by jumping over them (the smallest islands included in this model were only 5 pixels wide).

Ps is the probability that a migrant will jump in the same direction it jumped in the previous turn. Ps interacts with PPJ to determine turning frequency. The lower PPJ the more directional decisions a migrant makes and thus, the more opportunities a migrant has to turn. But as Ps gets closer to 1 a greater proportion of directional decisions are made not to turn.

Pp is the proportion of breeding age females that are pregnant when density = K, and was calculated by taking the 95% confidence limits of the values in the studies shown in Table 2.1. It seems a reasonable assumption that averaging all the studies mentioned in Table 2.1 would give a good approximation of the proportion of breeding age females that are pregnant when density = K. Because it is assumed that migration from an island only occurs when the population on that island is above K, the pregnancy rate of adult females in the migrant pool must be equal to the pregnancy rate when density = K. Given the definition of K used in this study (see Eq. 2.1). Pp is the same for all islands in a system (the assumption that all islands are of the same quality).

Mt is defined in section 2.3.1.

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2.6.2 Parameter estimation using maximum likelihood

Sufficient empirical data could not be found to estimate the parameters PPJ, Ps and Mt, therefore an alternative approach had to be used. Maximum likelihood is a process that utilizes an observed outcome from an empirical experiment (or some other form of real world data), and out of a set of models finds the model or sub-set of models whose output most closely matches the observed outcome. The methodology used in this study is as follows.

Firstly, a set of models was created that were tested for fit. The structure of the model was kept constant (section 2.2, 2.3 and 2.4 for structure of the combined model). The parameters PPJ, Ps and Mt were varied in levels (Table 2.2 shows levels used for each parameter). The levels shown in Table 2.2 were tested in every combination possible (with one exception outlined below), so that in all 64 combinations were tested. All other parameters were varied between the limits shown in Table 2.1, with the exception of MD, which was held constant at 250, and Pp, which was held constant at 0.322.

The observed outcome used in this test was re-invasion data from the Noises Islands in the Hauraki Gulf. The length of time (in months) between eradication and detection of the re-invasion was used as the observed outcome (this information was kindly provided by J. Russell). The Noises Islands were eradicated and re-invaded 5 times, thus there are five observed outcomes.

The relative positions of Rakino Island, the Haystack and Motuhororopa Island were entered into the model. The combined model was then run 200 times using each combination of parameters. For each run, the time it took for a population of four
females and four males to establish on Motuhoropapa Island was recorded. The likelihood that the parameter set tested resulted in the observed outcome was calculated by:

\[
\text{Likelihood} = F_1 \times F_2 \times F_3 \times F_4 \times F_5 \quad \text{Eq. 2.7}
\]

Where: \( F_j \) = the frequency of the \( j^{th} \) observed time between eradication and detection in the output of the combined model using the parameter set being tested.

Table 2.2 The levels used in the maximum likelihood test for each parameter that was estimated using maximum likelihood.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Levels for maximum likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>PPJ</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>5</td>
</tr>
<tr>
<td>Ps</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>0.95</td>
</tr>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Mt</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>1.47</td>
</tr>
<tr>
<td></td>
<td>1.73</td>
</tr>
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<td></td>
<td>2</td>
</tr>
</tbody>
</table>

In all 64 combinations were tested. If all combinations of parameters in Table 2.2 were tested there would be 72 combinations. The difference results from the interaction between PPJ and Ps. When Ps = 1 there is no need to test it in combination with PPJ because the migrant will only make one initial directional decision and then jump straight in that direction. Thus, only four combinations including Ps = 1 were tested.

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tested instead of 12, which is the number of combinations that included each of the other 5 Ps values.

It was the spread of the observed outcomes (the shortest time between eradication and detection was 8 months, while the longest was 60 months) more than the actual values that determined the likelihood. Many parameter combinations that could reproduce short reinvasion times could not reproduce longer ones, and many parameter sets that could produce longer reinvasion times could not reproduce shorter ones. This meant that many of the parameter combinations tested had likelihood of zero, as if any of the $F_j$ terms in Eq. 2.7 are zero then the resulting likelihood is also zero. The parameter sets that resulted in a non-zero likelihood are shown in Table 2.3 below. In Table 2.3 the log of the likelihood is shown because it is easier to read than the actual likelihood values.

Table 2.3 On the left is shown the log likelihood resulting from the parameter combination on the right. Only parameter combinations that resulted in a non-zero likelihood are shown.

<table>
<thead>
<tr>
<th>Log Likelihood</th>
<th>Parameter values</th>
<th>PPJ</th>
<th>Mt</th>
<th>Ps</th>
</tr>
</thead>
<tbody>
<tr>
<td>-5.2012</td>
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<td>1.1</td>
<td>0.84</td>
<td></td>
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<tr>
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<td>1.47</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td>-5.5379</td>
<td>4</td>
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<td>0.84</td>
<td></td>
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<tr>
<td>-5.8397</td>
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<td>1.1</td>
<td>0.8</td>
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<td>-6.1138</td>
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<tr>
<td>-6.3026</td>
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<tr>
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<td>-6.6031</td>
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<td>-7.3208</td>
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<td>1.1</td>
<td>0.84</td>
<td></td>
</tr>
</tbody>
</table>

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It can be seen in Table 2.3 that no combination holds a Ps value above 0.84. This is because any combination that had a Ps value of 0.9 or greater resulted in the combined model producing only short times until colonisation. Likewise only two of the parameter combinations hold a PPJ value of 3. This is because all but two of the parameter combinations that held 3 resulted in the combined model producing only long times until colonisation. Most of the parameter combinations that produced a non-zero likelihood had a PPJ value of 4 or 5, Mt value of 1.1 or 1.47 and a Ps value of 0.75, 0.8 or 0.84.

The upper and lower limits of PPJ, Mt, and Ps, in Table 2.1 are the highest and lowest values used in the maximum likelihood test that produced a non-zero likelihood. Note that the lower limit for PPJ in Table 2.1 is 4, but in Table 2.3 two combinations that produced a non-zero likelihood held a value of 3 for PPJ. 3 was not used as the lower limit for PPJ because when PPJ = 3 the model took so long to complete a suitable number of simulations that it became unusable.

2.6.3 Parameter estimation for the demographic model

This modelling exercise is mostly concerned with *R. norvegicus*, but *R. rattus* has similar reproductive rates, both have a gestation period of approximately 23 days (Best 1968; Innes *et al.* 2001) and both are assumed to have a visible pregnancy duration of 18 days (Best 1968). Also the ageing method for both species is identical as the tooth wear calibration was based on both *R. norvegicus* and *R. rattus* (Karnoukhova 1971). For the purposes of this study *R. rattus* is used as a surrogate species for *R. norvegicus* when not enough information can be found on *R. norvegicus* alone, as can be seen in Table 2.1.

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Estimation of mortality rates.

Mortality rate for age classes 1, 2, and 3 were estimated from population age structure data in the papers shown in Table 2.1 using the formula from Fitzgerald, Karl and Moller (1981):

\[
\text{Monthly survivorship} = \exp\left(\frac{\ln Y}{t}\right) \quad \text{Eq. 2.8}
\]

Where: \( Y \) = the proportion of individuals surviving from one tooth wear class to the next.

\( t \) = the time in months between the mid point of each tooth wear class.

The ageing method of Karnoukhova (1971) was used in all studies and the lengths of the tooth wear classes were obtained from Karnoukhova (1971).

Monthly survivorship was turned in to mortality per turn for adult age classes (1, 2 and 3, denoted by \( a \)) by:

\[
\text{Mortality per turn}_a = 1 - \left(\text{monthly survivorship}\right)^3
\]

Monthly survivorship was raised to the power of three to give the proportion of individuals surviving for three months (the length of one turn).

The mortality rate for age class 0 was modelled as a non-linear density dependant relationship. The parameter \( M_{n0} \) is an estimate of the mortality rate when density is zero. This estimate was obtained from a study of rats in an enclosure where the rats...
were given ample food and water (Calhoun 1963). It is assumed that under these conditions density will not affect the mortality rate. The number of individuals surviving from day 0 to day 90 was calculated using Eq. 2.8, except that:

\[ Y = \text{The proportion of individuals that survived 100 days.} \]

\[ t = 100 \text{ days.} \]

With these changes Eq. 2.8 gives the proportion of individuals that survive per day. This was converted to a mortality rate per turn for age class 0 by:

Mortality per turn\textsubscript{0} = 1 - (daily survivorship\textsuperscript{90})

The term m\textsubscript{C} in the juvenile mortality curve is an estimate of mortality when \text{N}_{\text{total}} = K. The estimate used here is the average juvenile mortality rate from the papers in Table 2.1. This assumes that on average the populations in these studies were at carrying capacity.

To calculate juvenile mortality first the average number of litters per female was calculated following the method of Best (1968). The number of litters per female per month is given by:

\[ I_p = \text{percent pregnant} \cdot t \quad d \quad \text{Eq. 2.9} \]

Where: \( I_p \) is the number of litters born per female in period \( t \).

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Percent pregnant: is the percent of mature females in a sample that are pregnant.

$t$: is the period in which you want to know how many litters are born, in this case 30 days.

$d$: is the duration of visible pregnancy. For both *R. norvegicus* and *R. rattus* 18 days is used (Best 1968).

The number of juveniles is then calculated by:

\[
Nb = \text{number of adults} \times 0.5 \times \text{litter size} \times Ip
\]

Eq. 2.10

Where:  

*Nb*: is the number of 0 to 30 day olds

Number of adults: is the number of individuals in tooth wear classes 4, 5, 6 and 7 (see Karnoukhova 1971 for lengths of age classes). Tooth wear class 4 was use as the point of adulthood as it was the youngest age class where a reliable estimate of relative numbers in each tooth class could be obtained, as there was an apparent bias against trapping individuals that were tooth wear class 3 and below. It is likely that many females in tooth wear class 3 could breed (Greenman & Duhring 1923; Innes *et al.* 2001). For this reason the juvenile mortality is under estimated.

0.5 is used as roughly half the number of adults are female.
Litter size: is the average number pups per litter per female.

Mortality of individuals less than tooth wear class 4 in age is given by:

\[ M_j = \exp\left(\frac{\ln Y}{t}\right) \]  \hspace{1cm} \text{Eq. 2.11}

Where: \( M_j \): is the mortality rate per month of individuals less than tooth wear class 4 in age (considered to be juveniles for the purposes of this study).

\[ Y = \frac{\text{no. tooth wear class 4}}{\text{Nb}} \]  \hspace{1cm} \text{Eq. 2.12}

\( l \): is the length of the tooth wear class 4 in months, value taken as 5 months (Karnoukova 1971)

\( t \): is age of tooth wear class 4 in months + (0.5*\( l \)) (this value is taken as 8.33 months based on age class lengths in Karnoukova 1971).

\( M_j \) is then converted into the juvenile mortality rate per turn (mC) by: \( M_j^3 \) (a turn is three months in length).

**Female breeding factor estimation**

FBF was originally an estimate of the number of litters per female per turn. This relationship is modelled as a density dependant relationship with three factors, Bn0, bC and ba (the effect of each of these parameter is explained earlier in the text). Eq. 2.9 was applied to data from several papers to obtain an estimate of bC. A rate of one

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litter per month per female (three litters per turn) was estimated for Bn0. However when realistic values from the literature were used for these three parameters the results of the demographic model were unrealistic. In a population with a carrying capacity of approximately 50, the population reached 40,000 (approximately 800 times higher than K) after 50 turns and was still rising. The parameters used for FBF are those that resulted in a population that fluctuated around carrying capacity. The values of Bn0 and bC were chosen retrospectively to make the output of the demographic model more realistic. Only changes in these parameters solved the problem of the demographic model producing runaway populations.

Initial male and female populations, litter size, k, and area.

Initial male and female population size is the number of male and females that an island has at the beginning of the simulation. If both male and female initial populations are zero then the island is empty. If the initial population for males and females is greater than zero then the island is considered a source. Litter size is defined in Eq. 2.16 in appendix 3. K is defined under Eq. 2.1. Area is determined by the size of the island in reality, or if the model run is not based on any real island system then area is set at an arbitrary value.

2.7 Sensitivity analysis

2.7.1 Sensitivity analysis of the demographic model

Finding the most important parameters and interactions between parameters in the demographic model

The sensitivity analysis of the demographic model was carried out separately from the combined model and for only one island. Because only one island was used emigration is simply a loss to the system, and so was made zero. It must be kept in Shaun Coutts
mind that, where this sensitivity analysis is involved, “mortality” is loss to the island, and therefore combines both deaths and emigration.

In this sensitivity analysis “interaction term” is used to describe the product of the value of two parameters. Interactions between parameters are written as “parameter1*parameters2”. To demonstrate take the interaction term $K\times \text{area}$, if $K = 5$ and area $= 10$ then $K\times \text{area} = 5\times 10 = 50$.

The sensitivity analysis combined age classes 1 and 2 as rats in both are considered physiologically and behaviourally identical. Mortality rates for both sexes were also equal.

This left the following 13 parameters as variable (listed in Table 2.1):

- $M_{1/2}$ Initial female population
- $M_3$ Initial male population
- $M_0$, which is composed of:
  - $Mn_0$
  - $ma$
  - $mC$
- FPB, which is composed of:
  - $Bn_0$
  - $ba$
  - $bC$
- Litter size
- $k$
- Area

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If all these variables were to be tested in all possible combinations the number of tests that would have to be carried out would be too large. Hence the approach used was to set sensible upper and lower limits for each variable, then for each run the computer randomly selected a value for each variable within the set limits. Each run consists of 100 simulations of 50 turns. At each run the values of the variables used for that run were recorded, as were the selected measures.

The upper and lower limits for Litter size, k, M_{1/2}, M_3 and mC were 95% confidence limits based on the studies shown in Table 2.1 (the limits for litter size are rounded to the nearest whole number).

The upper limit used in the sensitivity analysis for the parameter M_{no} was set so that the relationship could tend towards density independence. The difference between M_{no} and mC determines how density dependant the relationship is. The smaller the difference the more density independent the relationship is, when the difference is zero the relationship is density independent. The upper limit of M_{no} was made equal to the lower limit of mC so the M_{0.51} curve could become a flat line (density independent) in some runs. B_{no} and bC were made to relate in a similar way with the lower limit of B_{no} equal to the upper limit of bC. Although unlike the upper and lower limits of mC the limits of bC are arbitrary (see section 2.6.3).

mC - M_{no} measures how density independent M_{0.51} is, and B_{no} - bC measures how density independent FBF is. The smaller these density independence measures the more density independent the relationship they describe. The interaction terms M_{no}*mC and B_{no}*bC describe the curve as a whole, as the interaction terms will be high when both components are high (the curve is lifted) and the interaction terms...
will be low when both components are low (curve is depressed). Because these interaction terms each describe a single curve they are treated as variables and included in the best subsets analysis despite the fact that individually $B_n$, $b_C$, and $M_n$ were found to be relatively poor predictors of proportion extant (this term is explained below).

Because logical limits for $M_n$ (lower), $B_n$ (upper and lower) and $b_C$ (upper and lower) could not be found the arbitrary figure of the estimate plus (upper limit) or minus (lower limit) 30 percent was used (see Table 2.1). The upper and lower limits of $m_a$ and $b_a$ were set so that the curve could vary between a straight line (1) and a threshold relationship (60) (see Fig. 2.4 for the way $m_a/b_a$ changes the density dependant relationships). $m_a$ and $b_a$ were only varied for the sensitivity analysis of the demographic model. The upper and lower limits for the parameters; Area (15 and 2 respectively); Initial female population (1 and 10 respectively); and Initial male population (1 and 10 respectively) were arbitrary.

This analysis requires a measure to test the effect of any change in the model resulting from the changes in parameters. The measure must be appropriate to the questions that are going be asked of the model to allow easy interpretation of what a change in the measure means. For the sensitivity analysis the proportion of populations still extant after 50 turns (12.5 years) was chosen, from here on called proportion extant. This was chosen as the measure because it tells us something that will be important when the demographic model is combined with the swimming model. This measure tells us how likely a population is to survive long enough to become established and produce emigrants.

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Best subset analysis was done using MINITAB 12 with all the variables included. This analysis showed which factors were important in determining proportion extant. The variables that increased the fit of the model to the data the most (as measured by $R^2$) are shown in Table 2.4.

**Table 2.4** Variables found to be good predictors of proportion extant and the improvement in $R^2$ each variable caused when added to the model. Cumulative $R^2$ shows the amount of variation in proportion extant explained by the model containing all terms above and including the current row.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Improvement in $R^2$ (%)</th>
<th>Cumulative $R^2$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>41.8</td>
<td>41.8</td>
</tr>
<tr>
<td>Initial female</td>
<td>7.1</td>
<td>48.9</td>
</tr>
<tr>
<td>$K$</td>
<td>5.1</td>
<td>54</td>
</tr>
<tr>
<td>$M_{1/2}$</td>
<td>2.1</td>
<td>56.1</td>
</tr>
<tr>
<td>$MC$</td>
<td>1.1</td>
<td>57.2</td>
</tr>
<tr>
<td>Litter Size</td>
<td>1.1</td>
<td>58.3</td>
</tr>
<tr>
<td>$Bn_0$</td>
<td>1</td>
<td>59.3</td>
</tr>
</tbody>
</table>

A stepwise procedure with one step was used to find the most useful terms to include in a best subset analysis containing both single predictors and interaction terms. This stepwise procedure was carried out in the following manner. A multiple regression including all variables, first order interactions between those variables shown in Table 2.4, and the interaction terms $Mn_0*mC$ and $Bn_0*bC$ (see page 58 for an explanation of why these are included) was carried out. MINITAB 12 automatically removed any variables that were highly correlated with any other variable. Any variable or interaction effect that had a non-significant coefficient was removed from the analysis. This left 7 variables and 12 interaction effects (19 in all).
Best subset analysis was performed on this set of variables and interaction terms to find at which point adding more predictors ceased to usefully increase the fit of the regression model (as measured by $R^2$). As more predictors were added to the regression model the increase in fit caused by each addition reduced (see “Improvement in $R^2$” column in tables 2.4 and 2.5) until the improvement became vanishingly small by the time the 19th predictor was added to the regression model. An eight-predictor model explaining 62.9% of the variation in proportion extant was chosen. The predictors in this model and their effect on $R^2$ when added to the model are shown in Table 2.5 below.

Table 2.5 Predictors of proportion extant in the best regression model, and the improvement they caused in $R^2$ when they were added to the model. Cumulative $R^2$ shows the amount of variation in proportion extant explained by the model containing all terms above and including the current row.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Improvement in $R^2$ (%)</th>
<th>Cumulative $R^2$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area*mC</td>
<td>36.1</td>
<td>36.1</td>
</tr>
<tr>
<td>MC</td>
<td>7.8</td>
<td>43.9</td>
</tr>
<tr>
<td>M1/2*Initial female population</td>
<td>4.3</td>
<td>48.2</td>
</tr>
<tr>
<td>M1/2</td>
<td>5.1</td>
<td>53.3</td>
</tr>
<tr>
<td>K*mC</td>
<td>5.4</td>
<td>58.7</td>
</tr>
<tr>
<td>K*Area</td>
<td>1.5</td>
<td>60.2</td>
</tr>
<tr>
<td>Bno*bC</td>
<td>1.4</td>
<td>61.6</td>
</tr>
<tr>
<td>M1/2*Litter size</td>
<td>1.3</td>
<td>62.9</td>
</tr>
</tbody>
</table>

A multiple regression was then done using the predictors in Table 2.5. One data point was having a large affect on the result (i.e. an outlier) and so was removed. The equation:

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Proportion extant = $1.34 - 2.30 \times M_{1/2} - 1.76 \times mC + 0.0.965 \times "M_{1/2} \times "initial female population" + 0.14 \times "M_{1/2} \times Litter size" - 0.00462 \times "K \times area" + 0.12 \times "area \times mC" + 0.109 \times "K \times mC" + 0.576 \times "Bn_0 \times bC"

was obtained.

Elasticity analysis for the demographic model

To determine which of the important predictors most affects proportion extant an elasticity analysis was carried out (Hunter et al. 2000). Following the concept of Hunter et al. (2000), the proportion extant was calculated by substituting the average value across all runs for each parameter (see Table 2.1) into Eq. 2.13. This gave proportion extant. In turn each predictor was then varied by +10 percent, and substituted back into the regression equation with all other predictors held at the estimated values. Eq. 2.13 now gives the proportion extant when that parameter is increased by 10 percent, denoted by proportion extant. The percentage change in proportion extant was used as a measure of how sensitive proportion extant is to the predictor that was varied. Percentage change in proportion extant is given by:

$$\% \text{change in proportion extant} = \frac{(\text{proportion extant}_+ - \text{proportion extant}_-)}{\text{Proportion extant}_-} \times 100$$

Eq. 3.2

2.7.2 Sensitivity analysis of the combined model

Finding the most important parameters and interaction terms in the combined model

A simple source and target island system was set up. The source island was started with a randomly chosen female and male population. The shape of the source island was 30 pixels square. The source island was 20 ha in size. The distance from the source island to the target island was varied randomly, as was the shape and size of
the target island (see below). A sensitivity analysis on the combined model was
carried out on this island system as outlined below.

The sensitivity of the combined model to changes in parameter estimates was
determined in the same way as for the demographic model and is explained in section
2.7.1. The parameters that were varied are shown below in Table 2.6. Many of the
parameters that were varied in this sensitivity analysis are discussed in sections 2.6,
the exceptions being Target distance, Length and Width. Target distance is the
distance of the target from the source island. Length and Width determine the size of
the perimeter of the target island and its shape. If the target island lay directly east of
the source then Length would refer to the length of the target island along its east-west
axis, and Width would refer to the length of the target island along its north-south axis.

M₃ was no longer varied independently of M₄/₂ in the sensitivity analysis of the
combined model. Instead these two mortality rates were assumed to be the same and
were combined under the term Adult mortality. This was done firstly because in the
sensitivity analysis of the demographic model M₃ had no effect on the proportion
extant and its coefficient was not significantly non-zero. Secondly this finding
conforms to standard ecological theory, which predicts that older age classes have
little or no effect on the population. There are fewer individuals in older classes of
small short-lived mammals so vital rates applied to older age classes affect only a
small part of the population, and have limited potential to affect the population as a
whole (Oli et al. 2001).
The terms $ma$ and $ba$ were also not varied in the sensitivity analysis of the combined model because in the sensitivity analysis of the demographic model they had no effect and their coefficients were not significantly non-zero.

Table 2.6 Parameters that were varied in the sensitivity analysis of the combined model.

Demographic model refers to parameters in the demographic model. Swimming model refers to parameters of the stochastic swimming model.

<table>
<thead>
<tr>
<th>Demographic Model</th>
<th>Swimming Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial female population</td>
<td>PPJ</td>
</tr>
<tr>
<td>Initial male population</td>
<td>Ps</td>
</tr>
<tr>
<td>$k$</td>
<td>MD</td>
</tr>
<tr>
<td>Area</td>
<td>Mt</td>
</tr>
<tr>
<td>$Bno$</td>
<td>$Pp$</td>
</tr>
<tr>
<td>$BC$</td>
<td>Target distance</td>
</tr>
<tr>
<td>Adult mort</td>
<td>Width</td>
</tr>
<tr>
<td>$Mno$</td>
<td>Length</td>
</tr>
<tr>
<td>$MC$</td>
<td></td>
</tr>
<tr>
<td>Litter size</td>
<td></td>
</tr>
</tbody>
</table>

The parameters in Table 2.6 were varied randomly between the upper and lower limits shown in Table 2.1. There were several exceptions to this. The upper and lower limits of $Length$ and $Width$ were set so that the target island could vary from a 10 pixel by 10 pixel square to a 100 pixel by 100 pixel square. $Length$ and $Width$ were varied independently so that island shape also varied, for example $Length$ may have been 10 pixels and $Width$ 100 pixels, which would give a long skinny island orientated square to the source. $Target$ distance was randomly varied between upper and lower limits of 1600m and 1000m respectively. $Area$ was also varied between the arbitrary limits of 5ha and 30 ha.
Altogether 3600 simulations were carried out. After each simulation the value of each parameter in Table 2.6 was recorded. The number of turns it took for one male and one female to exist on the target island at the same time was also recorded, from here on this will be called ‘time to invasion’. As in section 2.7.1 best subsets analysis was carried out on MINITAB 12 using ‘time to invasion’ as the response and all the terms in Table 2.6 as the predictors. Table 2.7 shows the model that was selected. This model explained only 18.1% in the variation observed in ‘time to invasion’.

Table 2.7 Variables found to be good predictors of the ‘time to invasion’ and the improvement in \( R^2 \) each variable caused when added to the model. The set of predictors this model was selected from is shown in Table 2.6. Cumulative \( R^2 \) shows the amount of variation in the time it took to invade the target island explained by the model containing all terms above and including the current row.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Improvement in ( R^2 ) (%)</th>
<th>Cumulative ( R^2 ) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ps</td>
<td>5.1</td>
<td>5.1</td>
</tr>
<tr>
<td>Target distance</td>
<td>4.3</td>
<td>9.4</td>
</tr>
<tr>
<td>Bn0</td>
<td>3.0</td>
<td>12.4</td>
</tr>
<tr>
<td>mC</td>
<td>1.9</td>
<td>14.3</td>
</tr>
<tr>
<td>MD</td>
<td>1.3</td>
<td>15.6</td>
</tr>
<tr>
<td>PPJ</td>
<td>1.2</td>
<td>16.8</td>
</tr>
<tr>
<td>k</td>
<td>1.3</td>
<td>18.1</td>
</tr>
</tbody>
</table>

A new set of predictors was then created that contained all the predictors in Table 2.6, plus all first order interaction terms between the predictors shown in Table 2.7, 39 predictors and interaction terms in all. MINITAB 12 only allows 20 terms to be entered as predictors in best subset analysis. The new set of predictors was reduced from 39 terms to 20 using a stepwise process where a regression model containing all 39 terms was run, then removing the predictor with the least significant p-value. Another regression model was then created containing all terms except the removed one, and again the predictor with the largest p-value was removed. This process was

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repeated until the set of potential predictors was reduced from 39 terms to 20. Best subsets analysis was then carried out on the reduced set. The selected model is shown in Table 2.8.

Table 2.8 Variables found to be good predictors of the ‘time to invasion’ and the improvement in $R^2$ each variable caused when added to the model. The set of terms this model was chosen from includes the terms in Table 2.6 and first order interaction terms between the terms in Table 2.7. Cumulative $R^2$ shows the amount of variation in ‘time to invasion’ explained by the model containing all terms above and including the current row.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Improvement in $R^2$ (%)</th>
<th>Cumulative $R^2$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Ps*B_{no}$</td>
<td>7.4</td>
<td>7.4</td>
</tr>
<tr>
<td>$mC*Target distance$</td>
<td>5.7</td>
<td>13.1</td>
</tr>
<tr>
<td>$B_{no}*Target distance$</td>
<td>2.2</td>
<td>15.3</td>
</tr>
<tr>
<td>$Ps*Target distance$</td>
<td>&lt;1.8</td>
<td>&lt;17.1</td>
</tr>
<tr>
<td>Target distance</td>
<td></td>
<td>&lt;19.3</td>
</tr>
<tr>
<td>$PPJ*Ps$</td>
<td></td>
<td>&lt;21.7</td>
</tr>
<tr>
<td>$PPJ*Target distance$</td>
<td>&gt;2.1</td>
<td>23.8</td>
</tr>
<tr>
<td>$MD*Target distance$</td>
<td>1.6</td>
<td>25.4</td>
</tr>
<tr>
<td>$k*Target distance$</td>
<td>1.7</td>
<td>27.1</td>
</tr>
</tbody>
</table>

There are gaps in Table 2.8 because some terms eliminated others. For example, the best model that contained four predictors held the terms “$Ps*B_{no}$”, “$B_{no}*Target distance$”, “$Ps*Target distance$”, and “Target distance”. Notice that “$mC*Target distance$” has subsequently been dropped from the regression model and both “$Ps*Target distance$” and “Target distance” have been included. This affected regression models that contained four, five, six, and seven predictors. The exact cumulative $R^2$ values for these models are therefore unknown, but the calculation does give their maximum. The increase in $R^2$ caused by adding “$Ps*Target distance$”, “Target distance”, “$PPJ*Ps$” and, “$PPJ*Target distance$” is therefore, also unknown.

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The nine predictor model in Table 3.6 explains only 27.1% of the variation in 'time to invasion'. Even the model that contained all the predictors in Table 2.6 and all first order interaction effects between the predictors in Table 2.7 explained only 33.8% of the variation in 'time to invasion'.

A linear regression containing all the predictors shown in Table 2.8, with 'time to invasion' as the response variable was then carried out using MINITAB 12. Of 3600 simulations 32 cases were having a large effect on the outcome and were removed as outlier. The linear regression was redone and the linear regression model shown in Table 2.9 was obtained.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-105.921</td>
</tr>
<tr>
<td>Target distance</td>
<td>1.971</td>
</tr>
<tr>
<td>Ps*Target distance</td>
<td>-1.127</td>
</tr>
<tr>
<td>Bno*Target distance</td>
<td>-0.54</td>
</tr>
<tr>
<td>Ps*Bno</td>
<td>66.757</td>
</tr>
<tr>
<td>PPJ*Target distance</td>
<td>-0.072</td>
</tr>
<tr>
<td>PPj*Ps</td>
<td>10.230</td>
</tr>
<tr>
<td>mC*Target distance</td>
<td>0.185</td>
</tr>
<tr>
<td>MD*target distance</td>
<td>-0.00004</td>
</tr>
<tr>
<td>k*target distance</td>
<td>-0.008</td>
</tr>
</tbody>
</table>

The regression model in Table 2.9 gives the equation:

\[
\text{Time to Invasion} = -105.921 + \text{Target distance} \times 1.971 + \text{"Ps*Target distance"} \times -1.127 + \text{"Bno*Target distance"} \times -0.54 + \text{"Ps*Bno"} \times 66.757 + \text{"PPJ*Target distance"} \times -0.072 + \text{"PPj*Ps"} \times 10.230 + \text{"mC*Target distance"} \times 0.185 + \text{"MD*target distance"} \times -0.00004 + \text{"k*target distance"} \times -0.008
\]  

Eq. 2.14
Elasticity on the combined model

Again the approach of Hunter et al. (2000) was followed. The average value across all runs for each predictor was substituted into Eq. 2.14 to predict ‘Time to Invasion’. Then each predictor was increased by 10 percent and substituted back into the regression equation with all other predictors held constant at the estimated values. Eq. 2.14 now gives the value of ‘time to invasion’ when that parameter is increased by 10 percent, denoted by ‘Time to Invasion’. The percentage change in ‘time to invasion’ was used as a measure of how sensitive ‘time to invasion’ is to the predictor that was varied. Percentage change in ‘time to invasion’ is given by:

\[
\% \text{ change in Time to Invasion} = \frac{(\text{Time to Invasion}_\text{varied} - \text{Time to Invasion}_\text{baseline}) \times 100}{\text{Time to Invasion}_\text{baseline}}
\]

2.8 Modelled experiments carried out with the combined model

2.8.1 Can Tia Island be eradicated of R. norvegicus, and what effect do age biased mortality rates have on population levels of R. norvegicus

To explore these questions the model was set up so that the positions and orientations of all the relevant islands and source populations (Weka, Tia and the two Stewart Island headlands) in the model were analogous to the real world. Because the model assumes islands are rectangles that sit square to a reference grid, the island system in the model will be similar to, but different from the real system seen in Fig. 1.2. The initial population of Tia Island was set to zero to replicate a successful eradication. To represent a permanent or semi permanent poisoning or trapping campaign the adult mortality and pre-adult mortality on Tia Island (but not the surrounding sources) was varied in the combinations shown in Table 2.10.
Stochastic computer simulation of island colonisation by *R. norvegicus*. 68

Table 2.10 The Combinations of adult and pre-adult mortality rates for Tia island tested. Read 0.9/0.8 as adult mortality = 0.9 and pre-adult mortality = 0.8.

<table>
<thead>
<tr>
<th>Adult Mortality Rates</th>
<th>Pre-adult Mortality Rates</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.9</td>
<td>0.9/0.9 0.9 0.9/0.8 0.9/0.6</td>
</tr>
<tr>
<td>0.8</td>
<td>0.8/0.9 0.8 0.8/0.8 0.8/0.6</td>
</tr>
<tr>
<td>0.6</td>
<td>0.6/0.9 0.6 0.6/0.8 0.6/0.6</td>
</tr>
</tbody>
</table>

Parameter uncertainty was incorporated into the model as shown in section 2.1 (stochasticity). The upper and lower bounds for each parameter and an explanation of how they were worked out are given in Table 2.1. For simplicity mortality rates on Tia Island are assumed to be constant.

500 simulations were carried for each combination of juvenile and adult mortality shown in Table 2.10. Two measures were recorded from these runs, the number of turns it took for the island to become invaded, and the average population of rats on Tia Islands for 12 turns after it was invaded. The model produced distributions of 500 possible outcomes for each measure.

A randomisation was used to test whether the different combinations of adult and pre-adult mortality had an effect on the two measures. The summary statistic used in this case was the observation at the 95th percentile. This summary statistic was chosen because it tells us that you would expect the model to produce a population or time to invasion smaller than this value 95 percent of the time.

The randomisation was carried out by combining the distributions of possible outcomes produced by the model for each combination of adult and pre-adult mortality. This combined distribution was then randomly shuffled so that each...
observation had an equal chance of being put in any group. The observation at the 95% percentile was then recorded for the randomly generated group. This process was repeated 3000 times. This produced a distribution of summary statistics that represented the null model that there was no difference between any of the mortality combinations, in respect to the summary statistic. This is because if the null were true and there were no difference between any of the treatments, then observations drawn at random from any of the distributions should form a randomly generated distribution with the same properties as all the observed distributions. So if any of the observed distributions are compared to the randomly generated distribution they should be the same. When many random distributions are produced it is possible to determine how likely the observed distribution is if the null hypothesis were true. Thus, the proportion of observations in the randomly generated distribution of summary statistics as or more extreme than the observed summary statistic is the probability of seeing that observed summary statistic (or one more extreme) if the null hypothesis were true.

Any significant results were then compared to one another to see if there was a difference between them. For example, the combinations 0.9/0.8 and 0.8/0.9 may both be significantly different from the null model, which states that all mortality combinations are the same, but this does not tell us whether these two combinations are different from each other. To do this a randomisation was done to compare each significant result with every other significant result. This set of randomisations was carried out by combining the two distributions being compared, then randomly shuffling the combined distribution so that each observation had an equal chance of being placed in one of two groups. The summary statistic for this randomisation was absolute value of $95^{th}$ percentile$_1$ - $95^{th}$ percentile$_2$, where $95^{th}$ percentile$_1$ is the

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observation which 95 percent of observations in group 1 are less than and 95\textsuperscript{th} percentile\textsubscript{2} is the observation which 95 percent of observations in group 2 are less than. After each shuffle the summary statistic was recorded. This process was repeated 3000 times for each comparison. This produced a distribution of summary statistics that represents the null model that there is no difference between the two groups. This is because if the null model were correct, and there were truly no difference between the observed groups, then it would be possible to shuffle the observed groups randomly and produce two new groups that are as different as the observed groups. Thus, the proportion of observations in the randomly generated distribution that show a difference as or more extreme than the difference between the observed groups is taken as the probability of seeing the observed difference if the null model were correct.

2.8.2 Does protecting islands in an island group affect the other islands in that group?

The position of all islands in the Boat Group and mainland sources were entered into the combined model (see Fig. 1.3 for their relative positions). Various islands in the Boat Group were 'protected' from invasion in each run by raising the mortality rate on the protected island or islands to 1 for both adults and pre adults, this means that any migrants that reach the protected island will die. The islands or island combinations that were protected for each run were:

- Control (no islands were protected)
- Kundy
- Betsy
- Rat
- Rat | Betsy
- Kundy | Rat
- Kundy | Betsy

Each island or combination of islands that is protected is considered a treatment that the system is exposed to.
Uncertainty was incorporated into the combined model for this question in the same way as is explained in section 2.1 (subsection: stochasticity). The upper and lower limits used in this question and are shown in Table 2.1.

Two things were measured from each simulation, the time it took for each island in the Boat Group to be invaded for the first time, here after referred to as ‘time to invasion’. The average time to extinction for the four small islets, Ka, Kb, Ra, Ca (see Fig. 1.3 for their positions within the system), here after referred to as ‘time to extinction’, was also recorded. The term invasion is defined as one female and one male existing on an island or islet at the same time. A population was defined as extinct when it had zero members after mortality was calculated.

To explore the effect each treatment had on ‘time to invasion’ for each island in the system a randomisation was used. A randomisation was carried out on each island or islet in the system for each treatment (61 in all). The model produced a distribution of 300 possible ‘times to invasion’ for each treatment, each ‘time to invasion’ was used as an observation. The variation within each distribution of possible ‘times to invasion’ was caused by two sources of uncertainty that were built into the model, uncertainty caused by stochastic events and the uncertainty around parameter estimates (see section 2.1, subsection: stochasticity). The distributions were summarised with two measurable statistics, the median and the proportion of simulations in which the island of interest took longer than 100 turns to be colonised. Each simulation was only 100 turns long, which is why this limit was chosen. The summary statistics from the observed data are referred to as the observed summary statistics. The median indicated how far along the x-axis the centre of the distribution
lies. The proportion of simulations in which it took longer than 100 turns to invade an
island indicates how likely it is that an island will never be invaded within 100 turns.

Given the risk adverse nature of island eradication, for practical purposes it is more
useful to know the likelihood that a particular island will be never be invaded within a
given time period. Thus, of the two summary statistics it is the proportion of
observations greater than 100 turns that is potentially more useful to managers.

All the distributions for the different treatments for the island of interest were
combined and randomly shuffled so that each observation had an equal chance of
being placed in any of the treatments. In each randomly generated distribution the
median and the proportion of observations greater than 100 turns was recorded. This
shuffling and recording process was repeated 3000 times for each randomisation test.
The randomly generated distribution of summary statistics represents the null
hypothesis that none of the treatments affected the distribution of ‘time to invasion’
for the island of interest in respect to the summary statistics (see section 2.8.1 for an
explanation). The proportion of observations in the randomly generated distribution of
summary statistics as or more extreme than the observed summary statistic is taken as
then probability of seeing that observed summary statistic if the null hypothesis were
true.

The average time to extinction was measured on the four small islets to test the rescue
effect (Lande et al. 1998; Gotelli & Kelley 1993). To do this a randomisation test was
carried out. The data from each set of simulations where the main source island was
protected were compared to the data from each set of simulations where the main
source island was not protected. The datasets compared for each of the small islets
being tested for the rescue effect are shown in Table 2.11.
Table 2.11 Datasets compared when testing the rescue effect for each small islet. The data sets in each column for each islet were combined into one data set.

<table>
<thead>
<tr>
<th>Islet tested</th>
<th>Main source</th>
<th>Data sets where the main source is unprotected</th>
<th>Data sets where the main source is protected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ka</td>
<td>Kundy</td>
<td>Control</td>
<td>Kundy protected</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rat protected</td>
<td>Kundy</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Betsy protected</td>
<td>Kundy</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rat</td>
<td>Betsy protected</td>
</tr>
<tr>
<td>Kb</td>
<td>Kundy</td>
<td>Control</td>
<td>Kundy protected</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rat protected</td>
<td>Kundy</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Betsy protected</td>
<td>Kundy</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rat</td>
<td>Betsy protected</td>
</tr>
<tr>
<td>Ra</td>
<td>Rat</td>
<td>Control</td>
<td>Rat protected</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Kundy protected</td>
<td>Rat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Betsy protected</td>
<td>Rat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Kundy</td>
<td>betsy protected</td>
</tr>
<tr>
<td>Ca</td>
<td>Kundy</td>
<td>Control</td>
<td>Kundy protected</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rat protected</td>
<td>Kundy</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Betsy protected</td>
<td>Kundy</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rat</td>
<td>Betsy protected</td>
</tr>
</tbody>
</table>

The island nearest to islet in question was taken to be the main source, except in the case of Ca where Kundy Island was taken as the main source. This was done as Ca’s two closest neighbours (Big Island and Chimney’s Island) were never protected and it was only when Kundy Island was protected that the number of times Ca was invaded reduced. This suggests that Kundy Island was an important source for Ca.

A randomisation was used to test if there was a difference between the distributions of possible extinction times. The summary statistic used in this randomisation was the absolute value of median\textsubscript{1}-median\textsubscript{2}. Where median\textsubscript{1} is median of the distribution of possible times to extinction when the main source is protected, and median\textsubscript{2} is the median of the distribution of possible times to extinction when the main source is protected.
unprotected. The randomisation was carried out by combining both protected and unprotected datasets, then randomly assigning each observation in the new combined dataset to one of two groups. The absolute value of ‘median of group 1 – median of group 2’ was recorded after each random shuffle. This randomisation process was carried out 3000 times for each islet. The distributions of summary statistics produced by this randomisation process represent the null hypothesis that protecting the main source has no effect on the average time to extinction. The proportion of times a summary statistic as or more extreme than the observed summary statistic appears in the randomised dataset is taken as the probability of seeing the observed summary statistic given that the null hypothesis is correct.

Note that when the main source to an islet was cut off it got invaded far less often or, the islet did not get invaded at all. Thus, the datasets where the main source was protected are far smaller than the datasets where the main source was unprotected, because simulations where the islet was never invaded were discarded. This was taken into account in the randomisation by making the two randomly generated groups the same size as the two observed groups.
3 Results

3.1 Can Tia Island be kept rat free?

The modelled experiment on Tia Island was carried to test whether Tia Island could be kept rat free, either by repeated eradication, or permanent poisoning operations. This modelled experiment also asks how age biased mortality affects population suppression. More importantly this modelled experiment asks whether the current knowledge state can answer these questions with enough precision to be useful to managers.

3.1.1 The effect of raised mortality on the population of Tia Island

It was expected that raising mortality would suppress the population, but it was unclear how much each mortality level would suppress the population. It can be seen in Fig 3.1 that raising mortality rates markedly affects the population on Tia Island. The distributions become obviously more skewed towards the left as both adult (from top to bottom) and pre-adult (left to right) mortality rates increase. This indicates that as mortality rates increased, a greater proportion of the distribution of possible outcomes becomes concentrated in the smaller population classes.

The initial randomisation showed that all the distributions in Fig. 3.1 were significantly different at the five percent level, with respect to the value of the observation at the 95th percentile, from what was expected if the null model were correct and all the distributions in Fig. 3.1 were the same. However the direction of differences varied. The combination 0.6/0.6 (read adult mortality = 0.6/pre-adult mortality = 0.6) and the control produced significantly larger observed values at the 95th percentile than expected if the null model

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Stochastic computer simulation of island colonisation by *R. norvegicus*. was correct. All other combinations produced a significantly smaller observed value at the 95<sup>th</sup> percentile than expected if the null model was correct.
Stochastic computer simulation of island colonisation by *R. norvegicus*.

Figure 3.1 continued. Refer to page 78 for caption.

a)

![Graph showing adult mortality rates versus pre-adult mortality rates.]

b)

![Graph showing control mortality rates.]

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Figure 3.1 In all distributions the x-axis is population expressed in number of individuals, size classes are five individuals wide. The y-axis is the frequency, ranging from 0 to 0.9. a) The distributions of possible populations on Tin Island under all combinations of adult and pre-adult mortality rates. The columns are different pre-adult mortality rates applied to Tin Island, while the rows are different adult mortality rates applied to Tin Island. For example show in the lower right corner is the distribution of possible populations on Tin Island when adult mortality is 0.6 and pre-adult mortality is 0.9. b) The distribution of possible populations on Tin Island under the control mortality rates of 0.329 for adult mortality, 0.17 for $M_{pa}$ and 0.622 for $mC$. 

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The two distributions in Fig. 3.1 that had a significantly larger value at the 95th percentile in the initial randomisation were compared with each other. The difference between the observed value at the 95th percentile of the distribution produced by the mortality combination 0.6/0.6 and the observed value at the 95th percentile of the distribution produced by control mortality rates was significantly greater at the five percent level than would be expected if the difference between the two distributions was random, with a p-value of p < 0.000333. The rest of the distributions in Fig. 3.1 were compared to one another to test if any pair of distributions that produced significantly smaller observed values at the 95th percentile in the initial randomisation were more different from each other than expected at random. The results of these pair wise comparisons are shown in Table 3.1.
Table 3.1 Comparisons of the mortality combinations that produced significantly smaller observed values at the 95th percentile in the initial randomisation. The probability of seeing a difference between values of the observation at the 95th percentile for each pair of mortality combinations as large as the observed difference at random is shown in the central part of the table (for example when the mortality combination 0.6/0.8 was compared with the mortality combination 0.6/0.9 [top left hand p-value] there was a $<0.00033$ chance of seeing a difference as large as $47.17 - 24.5 = 22.67$ at random).

<table>
<thead>
<tr>
<th>Adult mortality</th>
<th>Pre-adult mortality</th>
<th>Observation at the 95th percentile</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.6 0.6</td>
<td>0.8 0.8</td>
<td>0.8 0.8</td>
</tr>
<tr>
<td>0.8 0.9</td>
<td>0.6 0.8</td>
<td>0.9 0.9</td>
</tr>
<tr>
<td>0.8 0.8</td>
<td>0.9 0.6</td>
<td>10.83</td>
</tr>
<tr>
<td>0.8 0.9</td>
<td>0.6 0.9</td>
<td>53.5</td>
</tr>
<tr>
<td>0.9 0.6</td>
<td>0.8 0.8</td>
<td>17.17</td>
</tr>
<tr>
<td>0.9 0.9</td>
<td>0.9 0.9</td>
<td>7</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>47.17</th>
<th>24.5</th>
<th>65.17</th>
<th>22.5</th>
<th>10.83</th>
<th>53.5</th>
<th>17.17</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
</tr>
<tr>
<td></td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
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<tr>
<td></td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
</tr>
<tr>
<td></td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
</tr>
<tr>
<td></td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
<td>&lt;0.00033</td>
</tr>
</tbody>
</table>

It can be seen in Table 3.1 that all mortality combinations produce significantly different values for the observation at the 95th percentile, except for the comparison of 0.8/0.8 and 0.6/0.9, which produces a p-value of 0.545. This suggests that all the distributions in Fig. 3.1 are significantly different from each other at the five percent level with respect to the value of the observation at the 95th percentile (with the above mentioned exception).
3.1.2 The effect of age biased mortality rates on the population of Tia Island

It is shown above that increasing mortality tends to decrease the population. This modelled experiment was also set up to determine if age biased mortality affected how much the population was suppressed. To do this the mortality rates in this question were divided into adult and pre-adult rates so that the effect of any age bias in the success rate of a poisoning or trapping campaign could be explored. One way to assess the effect that age class biased mortality rates had is to look at the comparative rate of change in the value of the observation at the 95th percentile that was triggered by a change in either adult or pre-adult mortality. The change in the value of the observation at the 95th percentile for each distribution in each row and column in Fig. 3.1 is plotted in Fig. 3.2. The three plots in Fig. 3.2 compare the trends in the value of the observation at the 95th percentile when adult mortality is held constant and pre-adult mortality rate is varied, versus the trend when pre-adult mortality rates are held constant and the adult mortality rate is varied. It should be noted that in chart a), for example, the first data point represents the value of the observation at the 95th percentile when both adult and pre-adult mortality is 0.6. Obviously this value is the same whether it is adult or pre-adult mortality that is varied. P-values in Table 3.1 show that the four other data points in each chart are significantly different at the five percent level.
Figure 3.2 Charts a) b) and c) shows the trends of the values of the observation at the 95th percentile when adult mortality (solid line) or pre-adult mortality (dashed line) is held constant at 0.6, 0.8 and 0.9 respectively, and the other mortality rate (adult or pre-adult depending on the rate being held constant) is varied.
It can be seen that in all three charts in Fig. 3.2 the value of the observation at the 95th percentile changes more rapidly when pre-adult mortality is varied than when adult mortality is varied. This is demonstrated in all three cases by the solid line having a steeper slope than the dashed line. This indicates that pre-adult mortality has a greater effect on the population than adult mortality.

The comparisons in Table 3.1 also indicate that age biased mortality had a large impact on population suppression. For example the value of the observation at the 95th percentile for the mortality combination 0.9/0.6 is 53.5, while the value of the observation at the 95th percentile for the mortality combination 0.6/0.9 is 24.5. Despite the sum of the two mortality combinations being the same the distribution of possible populations produced by the combination with higher pre-adult mortality is significantly more skewed to the left than the combination with higher adult mortality.

3.1.3 The effect of increased mortality rates on the precision of outcome of the modelled experiment on Tia Island

One of the main features of Fig. 3.1 is that as mortality rates increase for both adults and pre-adults the spread of the predictions decreases. For example in the distribution produced by the lowest mortality rates for both adult and pre-adults (in the bottom left hand corner) the predictions are spread over the widest range of any of the distributions (except the control). While the distribution produced by the highest mortality rates for both adult and pre-adults (in the top right hand corner) has the smallest range of any of the distributions produced. Also it can be seen in Fig. 3.2 that as the mortality rate

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increased the value at the observation at the 95\textsuperscript{th} percentile decreased significantly at the five percent level (Table 3.1 shows that the three points used to plot each line were significantly different). This means that as mortality rose 95 percent of the predictions fell into a smaller and smaller range, thus as mortality rose the predictions of this modelled experiment became more precise.

3.1.4 the reinvasion rate of Tia Island in the modelled experiment

One option for managers of Tia Island is to periodically completely eradicate Tia Island. Weather or not this is a feasible option will depend on the time it takes for Tia Island to be re-invaded once it is eradicated. Table 3.2 displays how long it took, in turns, for Tia Island to be invaded. It can be seen that three values are significantly smaller than you would expect to see if the null model were correct (Recall the null model states that ‘time to invasion’ is random with respect to the mortality combination used). The mortality combinations 0.6/0.6, 0.6/0.9 and the control all had significantly shorter ‘times to invasion’ at the five percent level than expected if the null model were correct. The other value of interest in Table 3.2 is the longer than expected observed ‘time to invasion’ produced by the mortality combination 0.9/0.9. This value was nearly significant at the five percent level, producing a p-value of 0.072. Although theses differences are statistically different, they are trivial biologically. The difference between the longest and the shortest observed time is only four turns, or roughly one year.
Table 3.2 The observation at the 95th percentile in this case refers to the time, in turns, that 95 percent of times fell below in each distribution produced by the mortality combinations shown in the first two columns. The two right hand columns show the proportion of times a value at least as large or as small as the observed value in column three is seen in the distribution of summary statistics produced by the randomisation test. Significant or near significant results at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Adult mortality</th>
<th>Pre-adult mortality</th>
<th>Observation at the 95th percentile</th>
<th>Proportion ≥ observed</th>
<th>Proportion ≤ observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.6</td>
<td>0.6</td>
<td>3</td>
<td>1</td>
<td>0.0003</td>
</tr>
<tr>
<td>0.6</td>
<td>0.8</td>
<td>6</td>
<td>0.972</td>
<td>0.936</td>
</tr>
<tr>
<td>0.6</td>
<td>0.9</td>
<td>5</td>
<td>0.999</td>
<td>0.024</td>
</tr>
<tr>
<td>0.8</td>
<td>0.6</td>
<td>6</td>
<td>0.973</td>
<td>0.931</td>
</tr>
<tr>
<td>0.8</td>
<td>0.8</td>
<td>6</td>
<td>0.969</td>
<td>0.937</td>
</tr>
<tr>
<td>0.8</td>
<td>0.9</td>
<td>6</td>
<td>0.961</td>
<td>0.929</td>
</tr>
<tr>
<td>0.9</td>
<td>0.6</td>
<td>6</td>
<td>0.966</td>
<td>0.932</td>
</tr>
<tr>
<td>0.9</td>
<td>0.8</td>
<td>6</td>
<td>0.966</td>
<td>0.943</td>
</tr>
<tr>
<td>0.9</td>
<td>0.9</td>
<td>7</td>
<td>0.072</td>
<td>1</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td>3</td>
<td>1</td>
<td>0.001</td>
</tr>
</tbody>
</table>

3.2 Results reporting outcomes of the modelled experiment on the Boat Group

The modelled experiment on the Boat Group was carried out to explore the more complex effects of island eradications. This modelled experiment was used to test what would happen to the rest of the islands in an island group if one of its members was eradicated and kept rat free. Does this affect the time until colonisation of the other
islands in the group? And does it make populations that rely on the protected island for colonisation more prone to extinction due to the ‘rescue effect’.

3.2.1 The effect protecting various island in the Boat Group had on the invasion time of the other members in the Boat Group

It can be seen in Fig. 3.3 that those islands closest to Rakiura Island, Kundy, Rat and unnamed, were almost completely unaffected by the protection of other islands in the group. Those islands in the Boat Group that relied on the inner islands Kundy, Rat, and Besty, as stepping-stone sources for invasion were most affected by the protection of these three islands. Betsy Island is an interesting case. It can clearly be seen in Fig. 3.3 that when Kundy Island, or when both Kundy and Rat island are protected, its distribution of possible ‘times to invasion’ is affected despite migrants being able to reach Betsy Island directly from the Rakiura Island. The other main feature of this set of distributions is the noticeable effect that protecting Kundy Island and Rat Island had on their respective islets, Ka, Kb and Ra. When the islets main source was cut off the far right hand bar (which is the >100 class and represents the number of simulations in which the islet was never invaded) becomes the prominent feature of the distribution.
Stochastic computer simulation of island colonisation by *R. norvegicus.*

Fig 3.3 continued. Refer to page 89 for caption.

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Stochastic computer simulation of island colonisation by *R. norvegicus*.

**Fig 3.3 continued. Refer to page 89 for Caption.**

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<table>
<thead>
<tr>
<th>Island(s) that was protected</th>
<th>Control</th>
<th>Kundy</th>
<th>Rat</th>
<th>Betsy</th>
<th>Kundy</th>
<th>Rat</th>
<th>Kundy</th>
<th>Betsy</th>
<th>Rat</th>
<th>Betsy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Betsy</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Big</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Island being invaded</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chimneys</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.3 Frequency distributions of the number of turns it took each island in the Boat Group to be invaded for the first time. The x-axis in each distribution is the number of turns taken for each island to be invaded for the first time, size classes are five turns wide. The y-axis of each distribution is the frequency, ranging from 0 to 1. Note that the far right hand category on the x-axis, ">100", is infinite in size. The y-axis of the matrix is the island being invaded, the x-axis of the matrix is the island, or islands that were protected. Read Island A|Island B as both Island A and Island B being protected. Under "control" all islands mortality rates were equal. The rates used in control simulations are 0.329 for adult mortality, 0.17 for Mn, and 0.622 for mC.
The series of tables 3.3 through to 3.12 show whether each distribution in Fig. 3.3 is significantly different from any other distribution in the same row, with respect to the summary statistics median 'time to invasion' and proportion of simulations in which it took longer than 100 turns to invade the island of interest. Again, in the series of Tables 3.3 to 3.12 read Island A|Island B as both Island A and Island B being protected.

The most important feature of the Tables 3.3 through to 3.12 is that Kundy Island is clearly the most influential island in the colonisation of the Boat group. It was only when Kundy Island is protected that the outer four islands, Besty (Table 3.8), Big (Table 3.11), Chimney's (Table 3.9), and Ca (Table 3.10), had significantly longer median 'times to invasion' and a significantly higher proportion of simulations in which it took greater than 100 turns to be invaded. This is also evident in Fig. 3.3. When the rows referring to the four outer islands are looked at it can seen that the distributions in the columns referring to islands Kundy, Kundy|Rat, and Kundy|Betsy, being protected are noticeably different from the rest.
Table 3.3 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for Kundy Island when Rat Island, Betsy Island, Rat|Betsy islands or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rat</td>
<td>6</td>
<td>0.961</td>
<td>0.04</td>
<td>0.134</td>
</tr>
<tr>
<td>Besty</td>
<td>6</td>
<td>0.965</td>
<td>0.007</td>
<td>0.954</td>
</tr>
<tr>
<td>Rat</td>
<td>Betsy</td>
<td>6</td>
<td>0.964</td>
<td>0.013</td>
</tr>
<tr>
<td>Control</td>
<td>6</td>
<td>0.969</td>
<td>0.016</td>
<td>0.466</td>
</tr>
</tbody>
</table>

Table 3.4 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for the islet Ka when Kundy Island, Rat Island, Betsy Island, Kundy|Rat islands, Kundy|Betsy islands, Rat|Betsy islands or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>&gt;100</td>
<td>0.0343</td>
<td>0.793</td>
<td>&lt;0.000333</td>
</tr>
<tr>
<td>Rat</td>
<td>23</td>
<td>1</td>
<td>0.174</td>
<td>1</td>
</tr>
<tr>
<td>Besty</td>
<td>25.5</td>
<td>1</td>
<td>0.156</td>
<td>1</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>&gt;100</td>
<td>0.032</td>
<td>0.823</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>&gt;100</td>
<td>0.032</td>
<td>0.898</td>
</tr>
<tr>
<td>Rat</td>
<td>Betsy</td>
<td>26</td>
<td>1</td>
<td>0.188</td>
</tr>
<tr>
<td>Control</td>
<td>23</td>
<td>1</td>
<td>0.153</td>
<td>1</td>
</tr>
</tbody>
</table>
Stochastic computer simulation of island colonisation by \textit{R. norvegicus}.

Table 3.5 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for the islet Kb when Kundy Island, Rat Island, Betsy Island, Kundy|Rat islands, Kundy|Betsy islands, Rat|Betsy islands or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>&gt;100</td>
<td>1</td>
<td>0.87</td>
<td>&lt;0.000333</td>
</tr>
<tr>
<td>Rat</td>
<td>71</td>
<td>1</td>
<td>0.438</td>
<td>1</td>
</tr>
<tr>
<td>Betsy</td>
<td>&gt;100</td>
<td>1</td>
<td>0.562</td>
<td>1</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>&gt;100</td>
<td>1</td>
<td>0.923</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>&gt;100</td>
<td>1</td>
<td>0.977</td>
</tr>
<tr>
<td>Rat</td>
<td>Betsy</td>
<td>&gt;100</td>
<td>1</td>
<td>0.564</td>
</tr>
<tr>
<td>Control</td>
<td>80</td>
<td>1</td>
<td>0.446</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 3.6 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for Rat Island when Kundy Island, Betsy Island, Kundy|Betsy islands, or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>3</td>
<td>0.885</td>
<td>0.003</td>
<td>0.892</td>
</tr>
<tr>
<td>Betsy</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0.117</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>2</td>
<td>1</td>
<td>0.007</td>
</tr>
<tr>
<td>Control</td>
<td>3</td>
<td>0.882</td>
<td>0.013</td>
<td>0.068</td>
</tr>
</tbody>
</table>

Shaun Coutts
Table 3.7 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for the islet Ra when Kundy Island, Rat Island, Betsy Island, Kundy|Rat islands, Kundy|Betsy islands, Rat|Betsy islands or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>24</td>
<td>1</td>
<td>0.2</td>
<td>1</td>
</tr>
<tr>
<td>Rat</td>
<td>&gt;100</td>
<td>0.192</td>
<td>0.816</td>
<td>&lt;0.000333</td>
</tr>
<tr>
<td>Betsy</td>
<td>23</td>
<td>1</td>
<td>0.202</td>
<td>1</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>&gt;100</td>
<td>0.199</td>
<td>0.896</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>25</td>
<td>1</td>
<td>0.182</td>
</tr>
<tr>
<td>Rat</td>
<td>Betsy</td>
<td>&gt;100</td>
<td>0.179</td>
<td>0.854</td>
</tr>
<tr>
<td>Control</td>
<td>22</td>
<td>1</td>
<td>0.179</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 3.8 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for Betsy Island when Kundy Island, Rat Island, Kundy|Rat islands, or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>53</td>
<td>&lt;0.000333</td>
<td>0.34</td>
<td>&lt;0.000333</td>
</tr>
<tr>
<td>Rat</td>
<td>18</td>
<td>1</td>
<td>0.072</td>
<td>1</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>&gt;100</td>
<td>&lt;0.000333</td>
<td>0.528</td>
</tr>
<tr>
<td>Control</td>
<td>19</td>
<td>1</td>
<td>0.055</td>
<td>1</td>
</tr>
</tbody>
</table>

Shaun Coutts
Table 3.9 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for Chimney’s Island when Kundy Island, Rat Island, Betsy Island, Kundy|Rat islands, Kundy|Betsy islands, Rat|Betsy islands or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>61.5</td>
<td>&lt;0.000333</td>
<td>0.373</td>
<td>&lt;0.000333</td>
</tr>
<tr>
<td>Rat</td>
<td>19</td>
<td>1</td>
<td>0.076</td>
<td>1</td>
</tr>
<tr>
<td>Betsy</td>
<td>19</td>
<td>1</td>
<td>0.041</td>
<td>1</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>&gt;100</td>
<td>&lt;0.000333</td>
<td>0.515</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>71</td>
<td>&lt;0.000333</td>
<td>0.422</td>
</tr>
<tr>
<td>Rat</td>
<td>Betsy</td>
<td>19</td>
<td>1</td>
<td>0.067</td>
</tr>
<tr>
<td>Control</td>
<td>19</td>
<td>1</td>
<td>0.042</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 3.10 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for the islet Ca when Kundy Island, Rat Island, Betsy Island, Kundy|Rat islands, Kundy|Betsy islands, Rat|Betsy islands or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>63</td>
<td>&lt;0.000333</td>
<td>0.377</td>
<td>&lt;0.000333</td>
</tr>
<tr>
<td>Rat</td>
<td>22</td>
<td>1</td>
<td>0.076</td>
<td>1</td>
</tr>
<tr>
<td>Betsy</td>
<td>21</td>
<td>1</td>
<td>0.048</td>
<td>1</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>&gt;100</td>
<td>&lt;0.000333</td>
<td>0.528</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>74</td>
<td>&lt;0.000333</td>
<td>0.419</td>
</tr>
<tr>
<td>Rat</td>
<td>Betsy</td>
<td>22</td>
<td>1</td>
<td>0.083</td>
</tr>
<tr>
<td>Control</td>
<td>22</td>
<td>1</td>
<td>0.055</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 3.11 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for Big Island when Kundy Island, Rat Island, Betsy Island, Kundy|Rat islands, Kundy|Betsy islands, Rat|Betsy islands or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>51</td>
<td>&lt;0.000333</td>
<td>0.333</td>
<td>&lt;0.000333</td>
</tr>
<tr>
<td>Rat</td>
<td>15</td>
<td>1</td>
<td>0.069</td>
<td>1</td>
</tr>
<tr>
<td>Besty</td>
<td>14</td>
<td>1</td>
<td>0.027</td>
<td>1</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>99</td>
<td>&lt;0.000333</td>
<td>0.498</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>65</td>
<td>&lt;0.000333</td>
<td>0.389</td>
</tr>
<tr>
<td>Rat</td>
<td>Betsy</td>
<td>14</td>
<td>1</td>
<td>0.047</td>
</tr>
<tr>
<td>Control</td>
<td>14</td>
<td>1</td>
<td>0.039</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 3.12 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded is shown for Unnamed Island when Kundy Island, Rat Island, Betsy Island, Kundy|Rat islands, Kundy|Betsy islands, Rat|Betsy islands or no islands (control) were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>3</td>
<td>1</td>
<td>0.01</td>
<td>0.743</td>
</tr>
<tr>
<td>Rat</td>
<td>3</td>
<td>1</td>
<td>0.009</td>
<td>0.732</td>
</tr>
<tr>
<td>Besty</td>
<td>3</td>
<td>1</td>
<td>0.017</td>
<td>0.154</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>3</td>
<td>1</td>
<td>0.007</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>3</td>
<td>1</td>
<td>0.026</td>
</tr>
<tr>
<td>Rat</td>
<td>Betsy</td>
<td>3</td>
<td>1</td>
<td>0.006</td>
</tr>
<tr>
<td>Control</td>
<td>3</td>
<td>1</td>
<td>0.01</td>
<td>0.729</td>
</tr>
</tbody>
</table>

Shaun Coutts
A further randomisation was carried out to determine if there was any difference between protecting Kundy Island alone, protecting both Kundy Island and Rat Island or both Kundy Island and Betsy Island. In this randomisation only the observations produced by the model when Kundy Island, Kundy|Rat islands and Kundy|Betsy islands were protected were shuffled to produce the distributions that represented the null model. This means that in this randomisation the null model states that ‘time to invasion’ is random with respect to the three above treatments. The results of this randomisation are shown in Tables 3.13, 3.14, 3.15 and 3.16.

Table 3.13 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded for Betsy Island when Kundy Island and Kundy|Rat islands were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>53</td>
<td>1</td>
<td>0.34</td>
<td>1</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>&gt;100</td>
<td>&lt;0.000333</td>
<td>0.528</td>
</tr>
</tbody>
</table>
Stochastic computer simulation of island colonisation by *R. norvegicus*.

Table 3.14 Both the median 'time to invasion' and the proportion of times it took longer than 100 turns to be invaded for Chimney's Island when Kundy Island, Kundy[Rat islands, and Kundy[Betsy islands were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median 'time to invasion' or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>61.5</td>
<td>0.997</td>
<td>0.373</td>
<td>0.999</td>
</tr>
<tr>
<td>Kundy[Rat</td>
<td>&gt;100</td>
<td>0.004</td>
<td>0.515</td>
<td>0.0003</td>
</tr>
<tr>
<td>Kundy[Betsy</td>
<td>71</td>
<td>0.784</td>
<td>0.422</td>
<td>0.747</td>
</tr>
</tbody>
</table>

Table 3.15 Both the median 'time to invasion' and the proportion of times it took longer than 100 turns to be invaded for the islet Ca when Kundy Island, Kundy[Rat islands, and Kundy[Betsy islands were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median 'time to invasion' or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>63</td>
<td>0.999</td>
<td>0.377</td>
<td>0.999</td>
</tr>
<tr>
<td>Kundy[Rat</td>
<td>&gt;100</td>
<td>0.006</td>
<td>0.528</td>
<td>&lt;0.000333</td>
</tr>
<tr>
<td>Kundy[Betsy</td>
<td>74</td>
<td>0.723</td>
<td>0.419</td>
<td>0.826</td>
</tr>
</tbody>
</table>

Shaun Coutts
Table 3.16 Both the median ‘time to invasion’ and the proportion of times it took longer than 100 turns to be invaded for Big Island when Kundy Island, Kundy|Rat islands, and Kundy|Betsy islands were protected. The p-value is the proportion of times you would expect to see a value equal to or greater than the observed median ‘time to invasion’ or proportion > 100 turns if the values of these summary statistics were random with respect to the island or islands protected. Results that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Island(s) protected</th>
<th>Median time to Invasion</th>
<th>p-value</th>
<th>Proportion &gt; 100 turns</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kundy</td>
<td>51</td>
<td>0.999</td>
<td>0.333</td>
<td>0.998</td>
</tr>
<tr>
<td>Kundy</td>
<td>Rat</td>
<td>99</td>
<td>&lt;0.000333</td>
<td>0.498</td>
</tr>
<tr>
<td>Kundy</td>
<td>Betsy</td>
<td>65</td>
<td>0.608</td>
<td>0.389</td>
</tr>
</tbody>
</table>

In all four tables 3.13 to 3.16 it is only when Kundy|Rat islands are protected that the observed values for both measures, for all four outer islands, was significantly larger than expected if the value of these summary statistics were random with respect to the island or islands protected. It can also be seen in tables 3.13 through to 3.16 that when only Kundy Island, or both Kundy and Betsy Islands were protected, values greater than or equal to the observed values for both measures for all four outer islands were seen more than five percent of the time in the distribution of possible summary statistics produced by the null model. Thus, protecting only Kundy Island or protecting both Kundy and Betsy Islands did not significantly increase the median ‘time to invasion’, or decrease the chances of an island being invaded within 100 turns, compared to protecting both Kundy and Rat Islands. Although all three treatments had significantly more effect than the other protection regimes (see tables 3.3 through to 3.12)
3.2.2 The precision of the outcomes for the modelled experiment on the Boat Group

Another feature of Fig 3.3 is the difference in spread of the predictions. It can be seen that the predictions for the four outer islands, Betsy, Big, Chimney's and Ca, are far less precise when Kundy Island (either by itself or along with Rat or Betsy Island) was protected. When Kundy Island was protected the distributions of predicted times to first invasion for the four outer islands had a very low peak and were spread more evenly across the x axis. This means that the combined model predicted almost every time to first invasion less than 100 turns with roughly equal likelihood. It can also be seen that in the more spread distributions a great proportion of the predictions are in the far right class, > 100 turns. This class is infinite in size and thus, the > 100 turns class is likely to have been spread across the x axis, extending the tail and the reducing the precision, if the modelled experiment had been run for more than 100 turns.

The distributions of the islets Ka, Kb, and Ra were also much more spread out and imprecise when their main sources were cut off. This is indicated by the very flat, low distributions for each of the islets in the columns relating to their respective sources being cut off. These distributions indicate that the three islets are unlikely to be invaded within 100 turns if their main source is protected.

3.2.3 The rescue effect in the modelled experiment on the Boat Group

As indicated in Fig 3.3 and shown in Tables 3.4, 3.5, 3.7, and 3.10 the islets Ka, Kb, Ra and Ca all had a significantly greater proportion of simulations in which it took longer
than 100 turns to become invaded when their respective main islands were protected. This suggests that these small islets are reliant on the larger islands for colonisation. The islets in this system may also be reliant on larger islands to supplement their populations and extend the time it takes populations on the islets to become extinct. To determine if this was really happening a randomisation was done comparing the average times it took populations on each islet to become extinct in simulations where its main source was protected versus simulations where its main source was unprotected. The results of this randomisation are shown Table 3.17.

Table 3.17 Each islets median of the distribution of ‘times to extinction’ produced when the islets main source was protected and unprotected. The p-value is the proportion of times you would expect to see a difference as large, or larger, than the observed difference between the two medians at random. n indicates the number of observations in the distribution which the median in the row above is based on. P-values that are significant at the five percent level are in italics.

<table>
<thead>
<tr>
<th>Islet</th>
<th>Median when source unprotected</th>
<th>Median when source protected</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ka</td>
<td>8.67</td>
<td>6</td>
<td>0.002</td>
</tr>
<tr>
<td>n</td>
<td>1020</td>
<td>146</td>
<td></td>
</tr>
<tr>
<td>Kb</td>
<td>9</td>
<td>7</td>
<td>0.153</td>
</tr>
<tr>
<td>n</td>
<td>611</td>
<td>69</td>
<td></td>
</tr>
<tr>
<td>Ra</td>
<td>5</td>
<td>4</td>
<td>0.033</td>
</tr>
<tr>
<td>n</td>
<td>980</td>
<td>133</td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>36.5</td>
<td>&gt;100</td>
<td>0.0003</td>
</tr>
<tr>
<td>n</td>
<td>1136</td>
<td>504</td>
<td></td>
</tr>
</tbody>
</table>

Table 3.17 shows that the distributions of possible ‘times to extinction’ for Ka and Ra had significantly shorter median ‘times to extinction’ when their main source was cut off. While these differences are statistically significant it is unlikely that the differences are
biologically significant given that the difference in median 'time to extinction' is only
2.67 turns for Ka and one turn for Ra. The largest difference in medians of the
distribution of possible 'times to extinction' is for Ca, with a difference of >63.5. This
difference is in the opposite direction than expected under the rescue effect hypothesis.
The population on Ca tended to go extinct more quickly when its main source, Kundy
Island, was unprotected and was more persistent when Kundy Island was cut off.

An important general note is that in all 216 significance tests were carried out, and thus
some of the significant results here are likely to be false. If the null hypothesis were true
in all the significance tests then we would still expect to see 216*0.05 = 10.8 false
significant results due to the number of significance tests carried out. As it is 86
significant results were obtained, meaning that 75.2 of the significant results are true.
However it is impossible to know which of the 86 significant result obtained are true and
which are false.

3.3 Results of the elasticity analysis

3.3.1 Results of elasticity analysis of the demographic model

The results of the elasticity analysis are shown in Table 3.18.
Table 3.18 The percentage change in proportion extant when the predictor in the left hand column was increased by 10%. Positive number indicates a positive relationship, that is it took longer to invade the target when the value of the predictor increased. Negative values indicates a negative relationship, it took a shorter time to invade the target if the value of the predictor increased.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>% change in proportion extant</th>
</tr>
</thead>
<tbody>
<tr>
<td>mC</td>
<td>-14.34</td>
</tr>
<tr>
<td>$M_{1/2}$</td>
<td>-9.91</td>
</tr>
<tr>
<td>area*mC</td>
<td>6.57</td>
</tr>
<tr>
<td>$K*mC$</td>
<td>4.65</td>
</tr>
<tr>
<td>$M_{1/2}*\text{Litter size}$</td>
<td>4.24</td>
</tr>
<tr>
<td>$M_{1/2}*\text{initial female population}$</td>
<td>2.29</td>
</tr>
<tr>
<td>$K*\text{area}$</td>
<td>-2.15</td>
</tr>
<tr>
<td>$B_{00}*bC$</td>
<td>1.11</td>
</tr>
</tbody>
</table>

The direction of the changes in Table 3.18 provide the most information on how the demographic model responded to changes in it parameters. The two mortality related predictors, $mC$ and $M_{1/2}$, show the expected negative relationship. This relationship means that as mortality increases the population is more likely to go extinct. The interpretation of the interaction terms in Table 3.18 is less clear. $mC$ is involved in two interaction terms "area*mC" and "$K*mC". Both these terms are positive which indicates that as these terms get bigger the population has a better chance of survival. This makes sense for the predictor area and $K$, but not for $mC$. $M_{1/2}$ shows a very similar pattern being in the interaction terms "$M_{1/2}*\text{Litter size}$" and "$M_{1/2}*\text{initial female population}$". Both these interaction have a positive relationship with proportion extant. This is logical for Litter Size and initial female population, as you would expect a population to have a
better chance of survival if it produces offspring a faster rate or if the founding population is larger. But the positive relationship is more difficult to explain in terms of $M_{1/2}$, which alone has a negative relationship with proportion extant (see row two of table 3.18). The negative relationship between proportion extant and the interaction term “$K\times area$” suggests that as an island can support a smaller population the chances of that population surviving increase. This is counter intuitive and was not the expected result. The positive relationship between the interaction term “$Bno\times bC$” and proportion extant indicates that as a greater proportion of females breed, the chances that the population will survive increases.

### 3.3.2 Results of elasticity analysis of the combined model

Table 3.19 Percentage change in ‘time to invasion’ when the predictor in the left hand column was increased by 10 percent. A Positive number indicates a positive relationship (it took longer to invade the target when the value of the predictor increased). Negative values indicate a negative relationship (it took a shorter time to invade the target if the value of the predictor increased).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>% Change in Time to Invasion.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Target distance</td>
<td>291.68</td>
</tr>
<tr>
<td>$Ps\times Target distance$</td>
<td>-133.09</td>
</tr>
<tr>
<td>$Bno\times Target distance$</td>
<td>-76.34</td>
</tr>
<tr>
<td>$Ps\times Bno$</td>
<td>57.96</td>
</tr>
<tr>
<td>$PPj\times Target distance$</td>
<td>-53.48</td>
</tr>
<tr>
<td>$PPj\times Ps$</td>
<td>46.67</td>
</tr>
<tr>
<td>$mC\times Target distance$</td>
<td>17.02</td>
</tr>
<tr>
<td>$MD\times target distance$</td>
<td>-13.7</td>
</tr>
<tr>
<td>$K\times target distance$</td>
<td>-5.80</td>
</tr>
</tbody>
</table>
Stochastic computer simulation of island colonisation by *R. norvegicus*.

Target distance is obviously very important in determining 'time to invasion', appearing in six of the eight interaction terms and also as the only non-interaction term. Target distance is the predictor the model is most sensitive to, with a 10 percent change in Target distance causing a 291.68 percent change in 'time to invasion'. Other predictors that appear more than once are Ps, Bn₀ and PPJ. The directions of the changes in Table 3.19 are also relevant. As Target distance gets larger so does 'time to invasion', this makes sense as it means that an island further away from a source takes longer to be invaded.

The interpretation of some of the interaction effects in Table 3.19 is unclear. 'Time to invasion' decreases as “Ps*Target distance” gets larger. This indicates that straighter swimming migrants are more likely to find a long distance target island. The term “PPJ*Target distance” shows the same trend and it is likely that the same reason applies as PPJ also influences the tendency for migrants to swim straight. The relationship between 'time to invasion' and “PPJ*Ps” is positive. Thus, the straighter migrants tended to swim the less likely they are to reach the target island. When PPJ or Ps were included in interaction terms with Target distance they tended to reduce the 'time to invasion' as they increased, but when PPJ and Ps are include in the same interaction term they tended to make time to invasion longer as they jointly increased. The predictor Bn₀ shows this same discrepancy. When Bn₀ was included in the interaction term “Bn₀*Target distance” ‘time to invasion’ decreased as Bn₀ increased. However when Bn₀ was included in the interaction term “Bn₀*Ps” ‘time to invasion’ increased as Bn₀ increased.
As the interaction term “K*Target distance” increased ‘time to invasion’ decreased. This was probably caused by K controlling the size of the population, which in turn affected the number of migrants. The more migrants there were the more likely the target island was to be found. The interaction term “mC*Target distance” showed a positive trend, and probably affected ‘time to invasion’ in the same way as “K*Target distance” except in the opposite direction. As mC increased the population tended to decrease, so there were less migrants and the target island was less likely to be found. The term “MD*Target distance” had a negative effect on ‘time to invasion’ so the further migrants could swim the more quickly the target island was colonised.
4.0 Discussion

4.1 Can rats on Tia Island be controlled?

4.1.1 The effect of age biased mortality rates on population suppression in the modelled experiment on Tia Island

It was demonstrated that raising mortality rates on Tia Island significantly shifted the distribution of simulated populations to the left (meaning the populations produced by the model tended to be smaller). The one exception to this was that there was no significant difference between the distributions of possible populations produced by the mortality rates 0.8/0.8 and 0.6/0.9. As expected these results suggest that the higher the mortality rate that can be inflicted on the rat population of Tia Island the lower the rat population will be. The results also highlighted that pre-adult mortality rates affect population size to a far greater extent than adult mortality rates. This would have important consequences if managers were to try and suppress rat populations on Tia Island through a continuing trapping or poisoning campaign.

Several authors have found an age bias when trapping *R. norvegicus* or *R. rattus*, with an apparent bias against trapping individuals younger than age class three or four (Moller & Tilly 1984; Moors 1985; Taylor 1986; King & Moller 1997; Innes *et al.* 2001). This translates to an age of three to six months (Karnoukhova 1971), by which age *R. norvegicus* have been weaned for two to five months (Moors 1990) and are generally sexually active (Moors 1985). The results of this model suggest that the most important part of the population to target when attempting to suppress a rat population is hardest to trap, pre-breeders. It should be noted that the studies of the above authors dealt with

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trapping, and it is possible that young rats enter poison station, or feed on lose baits more readily than they enter to traps. However difficulty in trapping juveniles may reflects their smaller home range. If so poison stations and baits are also likely to be encountered less often by juveniles, and thus, display the same reduced success among juveniles.

One possible mechanism for increased pre-adult rat mortality being more likely to suppress population growth than adult mortality is the numerical predominance of pre-adults. Given an average litter size of seven there could be any where between 0.7 and 4.62 offspring per adult female, depending on the density at the time (the relationship is density dependant, see section 2.1 for evidence of density dependant breeding). Consequently it is only during very high densities that there are more adults than pre-adults in the population. Because in this modelled experiment the population is being suppressed through raised mortality rates, it is unlikely to reach densities where adults out number pre-adults. Thus, when higher mortality rates were imposed on pre-adults in the modelled experiment, a larger portion of the population was affected by the higher mortality rate. Therefore, the average mortality rate per individual, irrespective of age class would have increased more when pre-adult mortality rates rose than when adult mortality rates rose.

Another possible mechanism driving this finding could be that pre-adult mortality takes the “first bite” out of the population, removing individuals before they can breed. To take an extreme example, if pre-adult mortality is 100 percent, no individuals will ever become adults and breed, therefore the population will go extinct in one generation. On
the other hand if high mortality does not start affecting individuals until they are older then some litters will still be produced, so the population will live past one generation. In this way pre-adult mortality not only reduces the population by removing individuals, but also by increasing the number of births that never go on produce more litters. This in turn leads to less adults which leads to less offspring, most of which will never breed, which then leads to less adults, and so on.

Regardless of the mechanism, age bias in trapping and poisoning campaigns should be more fully researched to see if and when target mortality is most effective in reducing population size. For example, is the effect of mortality constant across all densities? Does aerial poisoning also have an age bias, and does this bias occur in all seasons? If age biased mortality rates are found to be widespread in pest eradication campaigns, then the obvious next step is research into ways to remove the age bias from eradication campaigns.

4.1.2 managing rat populations on near shore islands where complete eradication is impossible

If managers are to use the approach of permanent poisoning of trapping campaigns to protect near shore islands like Tia Island (located only 660m from Stewart Island), then they will have to decide what an ‘acceptable rat’ population constitutes. Ecological damage thresholds (Moller 1989) have rarely been calculated for introduced mammals in New Zealand, and never for any species of rat. Fig. 3.1. shows that the distributions of possible populations always contain some non-zero observations, even when mortality is 90 percent for both adults and pre-adults. When the whole population was subjected to 90 percent...
percent mortality, 95 percent of the time the model predicted that the population would be seven or below. Seven individuals over a 23ha island may seem insignificant, but the damage that each individual can do and the sensitivity of the native biota to predation must be taken into account. It is possible that just one or two individual *R. norvegicus* could decimate ground nesting seabird populations. The habit of *R. norvegicus* is to kill and hoard far more food than it can eat so an individual may kill from three to twenty birds each day (Austin 1948). *R. norvegicus* can also depredate eggs. Austin (1948) reports that a single rat ruined over 200 clutches of tern eggs in two days. Obviously even a very small population of *R. norvegicus* could do enormous damage to some seabird breeding colonies.

4.1.3 *Uncertainty in the modelled experiment on Tia Island and the response of uncertainty to population suppression*

Because of the costs involved and limited resources, pest management strategies are by necessity cautious. If a management intervention has an uncertain chance of success, it will most likely be abandoned in favour of a more sure option. The range of distributions of modelled populations in Fig. 3.1 indicates that the ‘knowledge state’ is insufficient to make predictions with enough precision to be considered useful to managers. In the worst case, the model predicted that under the mortality rates 0.6/0.6 (see section 3.1 for definition) the average population of Tia Island was between zero and 90, 95 percent of the time. Thus a manager could not know with any certainty whether population suppression by raising mortality rates to 60 percent would lead to a *R. norvegicus* population of 10, 20, 50 or 90 individuals. However, as Fig. 3.1 demonstrates, when

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mortality rates increased, uncertainty in the model outcome decreased, and increasing pre-adult mortality reduces uncertainty more than increasing adult mortality.

There are two mechanisms that are working to reduce uncertainty with increasing mortality. Firstly, mortality rates on Tia Island were subject to only demographic uncertainty, not parameter uncertainty. As higher mortality rates became a more dominant parameter, the outcome of the model became less uncertain. For example, when the mortality rates are 0.6/0.6, there is still 40 percent of the population that is subject to parameter uncertainty and demographic uncertainty. But when mortality rates are raised to 0.9/0.9, only ten percent of the population is subject to both parameter and demographic uncertainty. Secondly, the outcome of the model becomes far more dependant on just one process as mortality rates rise. As a greater proportion of individuals die there are fewer individuals to participate in other stochastic processes such as birth, immigration and emigration. As mortality rates increase more of the uncertainty in the outcome of the model depends solely on uncertainty in mortality rates. A model with only one source of uncertainty is more predictable than a model with multiple sources of uncertainty, partly because there are fewer sources of uncertainty, but also because there are no interactions between uncertain processes.

These mechanisms are not just artefacts of the model, they represent an understanding of the real world. The first mechanism indicates that if mortality rates achieved by poisoning or trapping campaigns are indeed less variable and uncertain than natural mortality rates, then the higher the control efficiency less uncertain the outcome of the operation, in

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terms of population suppression. The second mechanism suggests that even if mortality rates achieved by poisoning or trapping campaigns are uncertain, inflicting higher mortality rates on a population will reduce the amount of uncertainty surrounding the overall outcome of the campaign. This may be why a wide range of pest eradication have been successful despite only superficial knowledge of their biology being available (Simberloff 2003).

4.1.4 The feasibility of periodic eradication to keep Tia Island rat free

An alternative option to population suppression is periodic eradication. To be cost effective this approach relies on Tia Island being reinvaded infrequently. The model predicts that 95 percent of the time Tia Island will be reinvaded within three turns (~9 months) if mortality on Tia Island is not altered. Even if mortality rates on Tia Island can be raised to 0.9 for both adults and pre-adults, the model predicts that 95 percent of the time Tia Island will be reinvaded within seven turns (~21 months). The increase in reinvasion time from three turns to seven turns is a statistically significant increase, but biologically and economically a time span of 12 months makes no difference to the feasibility of periodically eradicating Tia Island of R. norvegicus.

A successful eradication of R. norvegicus, R. exulans, and feral house cat (Felis cattus) was carried on Tuhua Island in 2000 (Towns & Broome 2003). This eradication cost $114/ha. Applying this cost to Tia Island means that eradicating R. norvegicus would cost $2622 per time. Thus, to keep Tia island rat free for 10 years could cost about $34,960 if mortality on Tia Island was unaltered, and $14,980 if mortality was raised to 0.9 for both
adults and pre-adults between eradication events, a task which itself would incur an economic cost. The above costs are crude estimates. An eradication of Tia Island would be different to the eradication on Tuhua Island. Firstly, Tuhua Island is far larger than Tia Island (1283 ha versus 23 ha). This means that the eradication of Tuhua achieved economies of scale that would not be possible on small islands like Tia (Towns & Broome 2003). Secondly, the eradication of Tuhua was done using a helicopter; it may be more cost-effective to use poison silos for an island the size of Tia (Towns & Broome 2003).

The cost of keeping Tia Island rat-free by periodic eradication is also subject to uncertainty and weakness in the ‘knowledge state’. The predictions of the model itself are uncertain, and the measure used here is the predicted reinvasion time that 95 percent of predicted reinvasion times fell below. In many simulations, reinvasion time was far less than seven turns, even when mortality on Tia Island was increased to 0.9 for both adults and pre-adults. Thus, these costs are substantially underestimated, highlighting that the ‘knowledge state’ pertaining to rat invasions of islands is not strong enough to make adequately precise predictions about the possible costs of keeping a near-shore island like Tia Island rat-free using periodic eradication.
4.2 The effect of protecting various islands in the Boat Group on colonisation times for other members of the Boat Group

4.2.1 The role of Kundy Island in the invasion of the Boat Group

The main prediction of the modelled experiment on the Boat Group is that Kundy Island has the most effect on the colonisation of the rest of the group. It was only when Kundy Island was protected that the median ‘time to invasion’ and the proportion of times an island took longer than 100 turns to be invaded (from here on referred to as proportion > 100 turns) increased significantly for the three larger outer islands, Betsy Island, Chimney’s Island, and Big Island. It was also found that protecting both Kundy Island and Rat Island significantly increased the median ‘time to invasion’, and the proportion > 100 turns on the outer islands of the group, compared to protecting only Kundy Island or both Kundy Island and Betsy Island. This type of information is useful for managers and birders because it suggests that the investment in rat control in the Boat Group should focus mainly on Kundy Island.

Kundy Island is important because it is only 910m from Stewart Island, and can be reached from Stewart Island in all simulations (keep in mind that the distance that migrants could swim changed for every simulation). This is also true of Rat Island, which is only 180m from Stewart Island. But migrants from Kundy Island could reach Betsy Island (a distance of 1135m) in every simulation and Big Island (a distance of 2090m) in just under half the simulations. Migrants from Rat Island however, could only reach Betsy Island (1820m away) in about 75% of simulations and Big Island (2400m away) via the islet Ra. Also, migrants from Kundy Island were more likely to reach Betsy Island...
and Big Island before migrants from Rat Island because Kundy Island is closer to these islands than is Rat Island. This is why when Kundy Island was protected the median ‘time to invasion’ increased.

4.2.2 The role of Betsy Island as a stepping-stone to Big Island

Under every treatment, Big Island had shorter median ‘times to invasion’ than Betsy Island and a smaller proportion of simulations in which it was never invaded. This indicates that Betsy Island was less likely to be invaded than Big Island, and that Betsy Island had no practical effect on the invasion of Big Island. This is an unexpected result because all the potential source islands (Kundy Island, Rat Island and Unnamed Island) are common to both Betsy Island and Big Island, with Betsy Island being closer to all the potential sources (Betsy Island is; 955m closer to Kundy Island, 545m closer to Rat Island and 200m closer to Unnamed Island). Thus, it was expected that migrants would find Betsy Island more quickly. It was also expected that Betsy Island would be reachable in a greater proportion of simulations than Big Island, because the maximum swimming distance of migrants was randomly varied for each simulation, and in many simulations Big Island would have been out of swimming range while Betsy Island would have been within the maximum range. Further, it was expected that Betsy Island could act as stepping-stone to Big Island given its position roughly halfway between Kundy Island and Big Island, and about three quarters of the way between Rat island and Big Island. None of these predictions were born out by the model. The most likely reason for this is that Betsy Island is far smaller than Big Island, and so was harder for swimming migrants to find.

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Some models of island colonisation assume that the rate of island invasion is affected mainly by isolation (Hanski 1993), but the results of the model presented here suggest that this assumption should be questioned. In the case of Betsy Island and Big Island it appears that island size was, if anything, more important than isolation. This conclusion may be wrong if rats can swim directionally and orientate themselves towards specific islands.

4.2.3 The effect of Rat Island on the colonisation of the Boat Group

An interesting point is that Rat Island had no significant effect on the colonisation of the rest of the group when it alone was protected. Yet when Rat Island was protected along with Kundy Island, the colonisation of the group was affected far more than if Kundy Island alone was protected. This raises the question, if the protection of Rat Island alone has no measurable effect on the colonisation of the rest of the group, how can protecting that same island suddenly have a discernable effect just because it is being protected along with Kundy Island?

One possible answer is that ‘time to invasion’ measures the time until an island is invaded for the first time. This means that if migrants from Kundy Island were consistently invading the outer islands of the group before migrants from Rat Island, migrants from Rat Island would not have determined the ‘time to invasion’, because they were not first to the outer islands. Once the migrants from Kundy Island were stopped however, immigrants from Rat Island would start to determine the ‘time to invasion’ of the outer islands because the Kundy Island migrants would no longer be beating them to
it. If this mechanism were found to be a true representation of reality, it would signal caution on two counts to those who undertake island eradications or research island invasion. Firstly, discovering the source of early migrants that reach an island may not tell you the complete story, as migrants from other sources may take longer to reach the island. Thus, if only the source of the initial migrants is known then an important secondary source of invasion may be missed. Secondly, the above mechanism describes a situation where resident rats 'exclude' immigrants. Immigrants from Kundy Island became residents on the outer islands first, and then exclude any subsequent immigrants from having a measurable effect on the colonisation those islands. There is evidence that this occurs in systems cohabited by *R. norvegicus* and *R. rattus*. *R. rattus* and *R. norvegicus* tend not to have overlapping distributions where they occur together in forested habitats (Harper 2002) and offshore islands that have populations of *R. rattus* or *R. exulans* tend not to have populations of *R. norvegicus* (Russell 2002). The cause of *R. norvegicus* and *R. rattus* tending to have non-overlapping distributions in forests and on offshore islands has been attributed to *R. rattus* displacing *R. norvegicus* (Moors 1990; Harper 2002). This means that pest managers need to be cautious when determining if an island can be invaded, especially if multiple species of rat a involved.

It is easy to envisage a situation where *R. rattus* is resident on an offshore island, and is preventing *R. norvegicus* from establishing on that island. Pest managers taking a snap shot look at this system (relatively speaking of course, as invasion patterns may be played out over decades) may conclude that *R. norvegicus* cannot reach the island on the basis that it is not already there. However this conclusion would be faulty if the reason *R.
norvegicus could not invade the island was due to the presence of R. rattus. A miscalculation such as this would have serious consequences if R. rattus were eradicated from the hypothetical island, opening the way for R. norvegicus to invade it. There is anecdotal evidence that this has occurred on a small scale at least once. Koi is a tiny islet (0.28 ha) 250m off the southern side of Waiheke Island. R. rattus were eradicated from Koi, and R. norvegicus subsequently invaded (Lee 1999). It must be stressed again that this is an anecdotal account, and one instance does not prove the existence of a recurring process.

Proof that island residents prevent subsequent immigrants from establishing would be very difficult to obtain by observation. It is all but impossible to detect failed invasions, however the effect could be tested experimentally. An island that is surrounded by many islets and supports a population R. norvegicus would be used. Populations of R. rattus would then be established, and supplemented if necessary, on all the islets. Periodic live trapping would be used to determine whether R. norvegicus established on any of the islets while R. rattus was present. After a given time frame (in the order of years) rats would be eradicated from all the islets. The islets would then be trapped, or markers such as baited gnaw sticks and clay eggs could be left on the islets, to detect if R. norvegicus established on any of the islets. If the rate of colonisation by R. norvegicus were greater when R. rattus is absent from the islets it would suggest that R. rattus could stop immigrant R. norvegicus from establishing on islets. A variation of this experiment could also be used where the experimenter does not rely on natural invasion, but instead periodically introduces R. norvegicus to the islets. This however involves the

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experimenter making assumptions about the typical size and demographic make up of migrant influxes. These experiments would in all probability be too long term and expensive to be feasible, and there is a risk that the experimentally established rat populations could not be eradicated. For these reasons the best approach to this question is developing detailed, spatially explicit, multi-species models, with special emphasis on inter-species interactions.

The finding that protecting Rat Island has no effect on the colonisation of the outer islands unless Kundy Island is also protected could also be an artefact of the statistical analysis used. The randomisation test tells use whether or not an observed result was larger than we would expect to see if there were no differences between treatments (in this case protecting various islands). However what does “no difference” look like? You cannot use the control as a comparison because all the treatments might be different from the control but not from each other. To overcome this problem and create the null models all the distributions were combined and randomly shuffled into new groups. Thus, a treatment will only be found significantly different from the null model if that treatment produces results greater than all the rest of the treatments. This is exactly what occurred. The set of treatments that included protecting Kundy Island (i.e. protecting Kundy alone, protecting both Kundy and Rat, and protecting both Kundy and Betsy) produced larger median ‘times to invasion’ and larger proportions > 100 compared to the rest of the treatments (including protecting Rat Island). The results produced by treatments that included protecting Kundy Island were part of the combined output. Therefore, protecting
Stochastic computer simulation of island colonisation by *R. norvegicus*.

Rat Island may have produced significantly larger median 'times to invasion' and proportions > 100 compared with the control treatment or protecting Betsy Island, but still had a non-significant result when compared with the combined output of all treatments. When comparing the treatments of protecting Both Rat Island and Kundy Island and protecting Kundy Island alone this problem did not occur. This was because only the treatments that included protecting Kundy Island were combined to create the null models in this analysis, thus, the effect of Kundy Island was controlled for.

4.2.4 *Comparison of the invasion times of Ka and Kb*

One feature of the model results that cannot be easily explained is the comparison between the two islets Ka and Kb. Ka and Kb are both roughly the same size and lie similar distances from their main source, Kundy Island, with Ka being slightly closer (~150 m away) than Kb (~340 m away) (see Fig 1.3 for their relative positions). When Kundy Island (the two islets main source) was not protected the median 'time to invasion' ranged from > 100 turns to 71 turns for Kb, and from 23 turns to 26 turns for Ka. Similarly the proportion > 100 turns ranged between 0.5637 and 0.4375 for Kb and between 0.1879 and 0.1531 for Ka. This shows that it tended to take much longer to invade Kb than Ka, and Kb was never invaded in a far greater proportion of simulations than Ka. There are two plausible explanations for the discrepancy in colonisation patterns between Ka and Kb.

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Firstly Ka and Kb are different shapes. Ka is a long skinny island that has a relatively high perimeter to area ratio, Kb is as wide as it is long, thus, it has the smallest perimeter to area ratio of any island shape that could be represented in this model. In the swimming model migrants find islands by crossing their perimeters, which makes islands with larger perimeters more likely to be found. However, the sensitivity analysis shows that the two factors that determine an island's perimeter, width and length, did not have a significant effect on 'time to invasion'. It is possible though that the relationship between perimeter and 'time to invasion' is not linear, and at perimeters smaller than those tested in the sensitivity analysis the effect of perimeter is much larger.

The second possible explanation is that the relationship between 'time to invasion' and distance from a source is very sensitive to distance. The sensitivity analysis shows that 'time to invasion' is most sensitive to changes in target distance, increasing by 29 percent for every one percent increase in target distance. This means that even a small change in distance (190 m or 19 pixels in this case) could cause a very large change in 'time to invasion'. Thus, it is likely that it is the sensitive nature of the relationship between distance and 'time to invasion', rather than the respective island shapes that caused the discrepancy in 'time to invasion' between two very similar islets.

4.2.5 Uncertainty and the modelled experiment on the Boat Group

There was a great deal of uncertainty in the predictions of the model, with most distributions showing a very shallow or non-existent bump and a very long drawn out tail. In extreme cases, such as Chimney’s Island when Kundy Island was protected, every

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‘time to invasion’ is predicted as being roughly equally likely to occur as every other ‘time to invasion’. This shows that the model has very low predictive power in these cases. It is likely that in cases like this if the model had not been stopped after 100 turns the predicted ‘times to invasion’ would have been spread out over a very wide range, possibly up to 1000 turns or so. This degree of uncertainty indicates that the ‘knowledge state’ is insufficient to deal with multiple island systems of this size. The Boat Group is not a large island system, containing only five large islands and five small islets. It is likely that predictions will become even more uncertain in larger more complex island groups where more invasion pathways are possible.

The predictions for some of the islands were less uncertain. Rat Island, Kundy Island and Unnamed islet, were almost always colonised within the first 15 turns. These islands all have the common feature that Stewart Island is their primary source. This could reduce uncertainty because there are fewer steps in their colonisation. An island with Stewart Island as its primary source has three steps to its colonisation, migrants leaving Stewart Island, migrants reaching the target island, and migrants establishing on the target island. At each step there are two types of uncertainty built into the model, parameter uncertainty and demographic uncertainty, which cause the spread in predicted results. If an island relies on an intermediary to be colonised it has six steps in its colonisation: (i) migrants leaving Stewart Island; (ii) migrants reach intermediate island; (iii) migrants establish on intermediate island; (iv) migrants leaving intermediate island; (v) migrants reaching target island; (vi) and migrants establishing on the target island. Again at each stage there is uncertainty built into the model. In this way the outer islands in the Boat Group were

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affected not only by uncertainty in their own direct colonisation from island sources, but were also affected by uncertainty in the colonisation of those island sources. This should highlight to managers that it is inherently more difficult to predict the invasion of an island that is not invaded directly, but rather through a stepping stone island.

4.2.6 The rescue effect in islets of the Boat Group

The islets of the Boat Group were used to test the rescue effect hypothesis. It was predicted that if the rescue effect were occurring then the islets should have significantly longer median times to extinction when their main source was unprotected (Gotelli & Kelley 1993; Lande et al. 1998). Two out of four islets tested (Ka and Ra) showed extinction patterns consistent with what would be expected if the rescue effect were occurring. Kb showed no significant effect while Ca showed a very significant effect but in the opposite direction expected if the rescue effect alone was operating.

Other studies of small mammal metapopulations have also supported conclusion that the rescue effect is not universal to all islands (Boyett et al. 2000). In a situation where the persistence of the metapopulation as a whole is the main objective (such as in models put forward by Hanski 1994) this would not be a concern, so long as on average the rescue effect was occurring. However, in the study presented here, it is the patch that is the main concern and not the population. This means that managers should not look at the rescue effect as a hard and fast rule. Nor should they discount the possibility that it is occurring.
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Stochastic computer simulation of island colonisation by *R. norvegicus*.

Given that Kb had longer median ‘times to invasion’, and larger proportions > 100 turns compared to the other three islets, it is likely that Kb showed no significant sign of the rescue effect because its immigration rate was not sufficient to adequately supplement its population even when it main source, Kundy Island, was unprotected. This indicates that the immigration rate to Kb must have been very low, because in very small populations even a small immigration rate can have a large affect on preventing extinction (Lande *et al.* 1998).

c showed the strongest treatment effect, with a difference in median ‘time to extinction’ of >63.5 turns between the two treatments. However, the difference was the inverse of that expected when the rescue effect is operating. The population on Ca was more persistent when its main source, Kundy Island, was cut off. One possible reason for this unusual result is that Kundy Island was not the primary source of immigrants to Ca. Instead Ca was invaded more frequently from Kundy Island via Big Island and Chimney’s Island, which are much closer to Ca than Kundy Island is. Because simulations in which Ca was never invaded were discarded from the randomisation test, only those simulations in which Big Island or Chimney’s Island were colonised were uses to test for the rescue effect. Thus, in all the simulations used to test for the rescue effect (whether Kundy Island was protected or not), Big Island and Chimney’s Island acted as the main sources and provided immigrants to supplement Ca’s population.

However this interpretation could only explain why no evidence of the rescue effect was found. It does not explain why there was such a large effect in the opposite direction than

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expected. The latter was likely to have been caused by a selection process that operated to weed out the parameter combinations that made extinction on Ca more likely. In this process it is the uncertainty surrounding the parameters that caused the observed effect. The model randomly chooses new values for each parameter at the beginning each simulation. Some of the parameter sets chosen will make extinctions of small populations less likely, for example those parameter sets with high values for K and low mortality rates. These same parameter sets increase colonisation because higher populations lead to more migrants, and thus a greater number of immigrants for every island (Hanski 1993; Keeling 2002). This means that when the model selected parameter sets that were less likely to cause small populations to go extinct Big Island and Chimney’s Island were more likely to be colonised, and in turn provide a source of immigrants to Ca. Thus, Ca was more likely to be colonised when the parameters of the model were favourable for small population persistence. This effect became more exaggerated when Kundy Island was protected because it was harder for Big Island and Chimney’s Island to be invaded, so more favourable parameters were needed in order for these two islands to be colonised. This in turn meant that when Kundy Island was protected only simulations with very favourable parameters for small population persistence resulted in Ca being colonised. Thus, when Kundy Island was blocked, the population on Ca was more persistent.

The favourable parameter selection effect set out above may have also affected the other islets, but it might only show up in Ca because of the absence of the rescue effect there. On the other islets the rescue effect may have affected the median ‘time to extinction’
more, and in the opposite direction to the parameter selection effect. If so, this would obscure the parameter selection effect and allow the rescue effect to be detected.

It is possible that these complex interactions could have been reasoned out without modelling, but the construction of the model helped their discovery by forcing an explanation of a surprising result. Even though the model has been too uncertain to help decision making by managers and birders it has helped conceptualisation of subtleties of system processes.

4.3 The sensitivity analysis

4.3.1. Sensitivity analysis of the demographic model

In the demographic model the proportion extant is most sensitive to changes in the parameter \( mC \) (pre-adult mortality when density was equal to \( K \) and \( M_{1/2} \)). This is inconsistent with studies on other rodents and short-lived mammals, which find that populations are most sensitive to changes in the fertility of females (Oli et al. 2001; Oli & Dobson 2003). In the sensitivity analysis presented here, the proportion extant was very insensitive to parameters that affected female fertility. The results of the sensitivity analysis are more consistent with results found for a long-lived seabird, whose population was most sensitive to changes in adult survival (analogous to \( M_{1/2} \) in this study) and the re-appearance rate of pre-adults (analogues to pre-adult mortality in this study) (Hunter et al. 2000). This type of discrepancy is not unusual in studies of the effect of demographic rates on population change. A meta-analysis found that distantly related species, which in some cases differed in size by several orders of magnitude, could exhibit very similar

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patterns of sensitivity, while sensitivity patterns within a species or population could be substantially different (Oli & Dobson 2003).

In this case the most likely explanation for the discrepancy between the sensitivities in the rodent studies above (Oli et al. 2001; Oli & Dobson 2003) and the present study is the way that fertility was dealt with in the model presented here. When values from the literature were used to estimate female fertility it resulted in the model producing populations that were ~800 times larger than k after only 50 turns and still growing. To fix this problem the parameters representing female fertility (Bn0 and bC) had to be constrained until the model produced populations that fluctuated around K. This meant that the effect of female fertility on the model was constrained so that the outcome of the model was not greatly affected by it. Changing Bn0 and bC could fix the problem of the model predicating runaway populations. This suggests that rat populations are in fact very sensitive to changes in female fertility.

Bn0 does play an important part in determining ‘time to invasion’ in the combined model, of which the demographic model is a sub model. This suggests that the treatment of female fertility may only be a partial explanation for the lack of sensitivity to female fertility by the demographic model. Another partial answer may be that most sensitivity analyses are concerned with the effect of various parameters on population growth rate (Hunter et al. 2000; Oli et al. 2001; Oli & Dobson 2003). The sensitivity analysis here is concerned with the effect of various parameters on the likelihood of extinction (expressed as the proportion extant). It is possible that likelihood of extinction is more sensitive to

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changes in mortality than fertility, while the population growth rate is more sensitive to changes in fertility than mortality. Again this subtlety could have been reasoned out without modelling, but the exploration of the model's sensitivity helped clarify the effect that female fertility has on the system.

Some of the interaction terms that greatly affected demographic model predictions have no obvious biological interpretation. For example, does the interaction term “M_{1/2} \times \text{Litter size}” mean that the population becomes extinct less often if both M_{1/2} and Litter size are larger? This makes sense for Litter size but not for M_{1/2}, which by itself causes the proportion extant to decrease when it increases.

The interaction term “K \times \text{area}” also behaved in a counterintuitive way. The biological interpretation of this interaction term is: the total population that an island of a given area can hold at carrying capacity. Standard theory assumes that the extinction rate should decrease with population size (Keeling 2002). Therefore, it was expected that as the value of “K \times \text{area}” increased the proportion extant would also increase. However, “K \times \text{area}” and proportion extant displayed a negative relationship, meaning that the higher a population an island could hold at K the more likely it was to go extinct. No explanation is offered for this result.

4.3.2 Sensitivity analysis of the combined model

The combined model has two types of parameters, demographic parameters and migration parameters. Demographic parameters affect the ‘time to invasion’ by affecting

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the number of migrants in the migrant pool. Demographic parameters that lead to higher populations should lead to faster colonisation rates (Hanski 1993; Keeling 2002). Demographic parameters also determine how likely it is that any migrants that do arrive on the target island survive and breed. Migration parameters affect the ability of migrants in the migrant pool to find and reach target islands. Three out of the nine most sensitive terms contained demographic parameters. \( B_{n_0} \) appeared in two interaction terms and \( mC \) also appeared in an interaction term. Of these two demographic parameters 'time to invasion' was more sensitive to \( B_{n_0} \) than \( mC \). In contrast the demographic models predictions of the proportion extant was insensitive to changes in \( B_{n_0} \). This implies that in the combined model, \( B_{n_0} \) reduced 'time to invasion' by making the source population larger, rather than by reducing extinction rate on the target island. Therefore, it is likely that \( B_{n_0} \) has more effect on population growth rate than the likelihood of extinction. This gives support to the idea that it was not only the arbitrary constraining of female fertility that lead to the proportion extant being insensitive to \( B_{n_0} \).

Six out of the nine terms greatly affecting 'time to invasion' contained parameters that affected migration ability. This indicates that the swimming ability of rats is more important in island invasion than demographic rates, although demographic rates also play a part.

The most prominent feature of the sensitivity analysis for the combined model is the predominance of 'Target distance'. 'Target distance' appeared as the only non-interaction term found to be important in determining 'time to invasion', and it appeared in six out of

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eight interaction terms that were found to be important in determining ‘time to invasion’. ‘Time to invasion’ was more than twice as sensitive to changes in ‘Target distance’ than the second ranked term, “Ps*Target distance”. The importance of ‘Target distance’ is not surprising. The further away a target island is, the harder it is for migrants to swim to it. Thus, many more migrants must attempt the crossing before one succeeds in reaching the island.

The question of how to attach biological meaning to interaction terms is again difficult. The most obvious biological interpretation of interaction terms including ‘Target distance’ is that the second parameter in the interaction term had differing effects on ‘time to invasion’ when the target island was at different distances. It is possible that when the target island was close, some parameters had less effect because ‘time to invasion’ was short no matter what the value of the parameters. Alternately it may be that past a certain target distance many parameters ceased to have an effect because no matter what their value the target island always took a relatively long time to be invaded. These two explanations need not be mutually exclusive. They may both affect a single parameter, meaning that that parameter would only have an effect on ‘time to invasion’ in a small, middle range of ‘Target distance’. Also, each one of the explanations may affect different interaction terms.

The parameters Ps and PPJ have a very close relationship in the combined model, and together determine the turning frequency of swimming rats (i.e. how often an individual changes its direction while swimming). This interaction term might be thought of a

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turning frequency index, with higher values indicating less frequent turning and lower values indicating more frequent turning. Maximum likelihood tests indicate that the more frequently migrants turn the less likely they are to find a target island. Thus, it was expected that as “Ps*PPJ” became larger the ‘time to invasion’ would become shorter (a negative percentage change in the sensitivity analysis).

The direction of change in ‘time to invasion’ in response to changes in the interaction terms “Ps*PPJ” and “Ps*Bno” is in opposite direction than expected. As “Ps*PPJ” got larger the target island took longer to be invaded. There is no obvious explanation for this result. The direction of change in ‘time to invasion’ caused by a change in the interaction term “Ps*Bno” was similarly counter intuitive. It was expected that as the value of “Ps*Bno” increased ‘time to invasion’ would decrease. Because, (i) as the value of Bno increases the population should increase, (ii) which in turn will produce more migrants, and (iii), as Ps increases those migrants should be more likely to find the target island. Therefore, when both these terms increase (causing the interaction term to increase) we would expect there to be more migrants who were more likely to find the target island, thus reducing ‘time to invasion’. Again this was not the case as ‘time to invasion’ increased when “Ps*Bno” increased.

It is apparent that combined model is very sensitive to changes in parameters. This reflects a large weakness in the current ‘knowledge state’. Rodent populations as a whole are a well-studied group in terms of demographic rates (see Moors 1985; Taylor 1986;
Innes et al. 2001 for a few examples), yet studies about rats swimming ability and their ability to navigate to offshore islands are lacking.

Clearly, the regression model is less than successful at predicting ‘time to invasion’, accounting for only 27.1 percent of the variation seen in ‘time to invasion’. In the combined model chance plays a very large part in island colonisation. Even if parameters are set so that migrants are highly likely to find islands, they can still take a wrong turn, leave from the wrong side of the island, or swim in circles. If the mechanism of swimming presented in the combined model is a reasonably accurate approximation of how rats really get to offshore islands, then island colonisation by rats may be inherently hard to predict after island eradications.

The combined model suggests two research priorities. Firstly the underlying assumption of the swimming mechanism presented in the combined model is that rats have no knowledge of where potential destination islands are, and swim in random directions until they reach an island or drown. This assumption that the rats are swimming ‘blind’ should be tested. It may be that rats will only swim to an island they can sense, either through smell, sound, or sight. This knowledge would have implications for constructing statistical models about island invasion by rats because it would determine whether factors that advertise an island's presence to rats, such as prevailing wind, island height, or noisy seabirds, should be included in the models.
Secondly, the uncertainty of the combined model suggests that improving our knowledge relating to the swimming and navigation ability of rats may not be the best way to advance our understanding of island colonisation by rats. Because of the inherent uncertainty in island colonisation, even mechanistic simulations grounded in a strong ‘knowledge state’ are probably going to return highly imprecise predictions. This is because just a few “lucky” individuals will lead to very short ‘times to invasion’, while “unlucky” runs lead to long ‘times to invasion’. If the spread of predictions is too large then even a very large number of simulations may not reduce the uncertainty around the prediction to a level that is useful to managers. A more productive and direct approach could be to look at the re-invasion rate of islands and relate these to pertinent factors, such as distance from a source, island size, prevailing current, type of rodent community on source, and so forth, using statistical models. Work of this nature has already been carried out (Russell 2002; Russell & Clout 2004), but these studies have lacked a time component, which is critical in determining re-invasion rate. In order to obtain a time component experimental studies may have to be carried out.

These experiments would probably involve eradicating rodents from small islands and timing how long it takes for them to re-invade. Ideally these islands would have only one possible source of invasion and one invasion pathway, as the results presented in this study show that the greater the complexity of the invasion pathway the more uncertainty there is invasion rate. However, single islands are rare, making finding an adequate number of islands with only one possible source and invasion pathway very hard. One answer could be to use small islets. As there are many more islets than islands (Lee 1999)
it is likely that a greater number of islets will exist in the formation needed. This approach could have problems when scaling the results up to larger islands, whose invasion rates may respond differently to the factors studied. A way around this may be to develop statistical models based on the experimental data from small islets, and then use observed re-invasion rates after island eradications to check that the results work for larger islands.

An alternative experiment would be to densely lay poison stations on all the islands in the group for the duration of the study. The invasion of any of the islands in the group would be detected by poison being taken from the stations. The poison would also prevent populations establishing on any of the islands, stopping any island in the group from becoming a source. This would mean that there was only one source throughout the course of the experiment, and each island in the group could be used as an observation.

The only alternative to an experimental study is observing re-colonisation after a successful eradication. Given the cost of island eradications this may be almost as expensive as a planned experiment. Studying colonisation rates of islands by rats will be difficult to plan and expensive to carry out. Despite the cost research should still be directed towards finding out what factors influence the re-invasion rate of islands, with the goal of being able to give the probability that an island with a given set of factors will be invaded within a specified time. This research is important because with improved technology, cost and technical barriers are no longer major obstacles in the eradication of even medium sized islands (Towns & Broome 2003). One of the main barriers to
eradicating islands of rats now is the ability to predict what islands will remain rat free, and for how long, once the job is completed (Towns & Broome 2003).

### 4.4 Predictive power of the model

There is no way to truly test the predictive power of this model because adequate data sets do not exist (Gotelli & Kelley 1993). However, there are indications that the predictive power of this model is very poor. One of the main indicators that the predictive power of the model is poor is the complete failure of the demographic model, which predicted a runaway population when realistic parameter values were used for female fertility. This is a sign that the demographic model ignored a major process relating to population regulation. The most obvious omission from the demographic model is that it did not include any environmental stochasticity. Fluctuations in the environmental conditions could limit rodent populations by periodically culling their numbers when conditions such as weather became unfavourable. There is evidence rainfall does increase mortality in rodent populations (Lima et al. 2001; Merritt, Liam & Bozinovic 2001). By ignoring the effect of wetter than normal years, or raised mortality during typically wet times of year, the demographic model may have missed a very important limiting factor for *R. norvegicus* populations.

Another process that the demographic model lacked was the density dependence for adult mortality. It is intuitive that every population must be density dependant at some population level. So despite several authors having failed to find evidence for density dependant mortality in adults (Montgomery et al. 1997; Lewellen & Vessey 1998;
Pervot-Julliard et al. 1999; Liam et al. 2001) it is possible that adult survivorship is affected at densities higher than those seen in their studies. If adult mortality is density dependant at very high densities, then the population would start to reduce at the density where adult survival was affected, rather that continuing on an upward trajectory as predicted by the demographic model. This is an example of a preliminary and very imprecise model hinting at the existence of an important population regulation mechanism in rodents that has been missed by field studies. It suggests that the current data needs to be re-examined and new field studies need to be carried out to determine how rodent populations are regulated.

The combined model also failed to predict the observed distribution of rats across the Boat Group. In most simulations the combined model predicted that rats would spread to every island in the Boat Group within 100 turns (the equivalent of about 25 years). Yet in reality the three main outer islands of the Boat Group (Betsy, Big, and Chimney’s) are rat free (Moller et al. 1999). Although it must be noted that the very wide range of predictions for the outer islands means that in some of the simulations one or more of the outer islands was never invaded.

The predicted colonisation rate of Tia Island also appears to be too high. Tia Island already has rats (Moller et al. 1999), and it is impossible to tell how long it took for them to get there. But nearby Ulva Island is of a similar type to Tia Island, and some failed invasion attempts have been recorded there. Like Tia Island, Ulva Island lies in an inlet and is surrounded by Stewart Island on all four sides; also it is very close to potential
source populations, being only 800m from Stewart Island at its nearest point. Ulva Island has permanent poison stations to prevent mammalian pests from establishing populations. In 95 percent of simulations the model predicted that Tia Island would be invaded within three turns. Also, in the model the immigration rate into Tia Island was sufficient to sustain the population despite high mortality rates. The observed experience of Ulva Island however is very different. Rats were eradicated from Ulva Island between 1992-1994. Since that time there have been three detected invasions by Norway rats, occurring at intervals of two to three years (Towns & Broome 2003; Russell 2002). This is clearly much reduced from the invasion rate predicted by the model for Tia Island. However, it is almost impossible to detect failed invasions, meaning that the invasion rate of Ulva Island is almost certainly underestimated. Even so, the extent of the invasion rate predicted by the model for Tia Island would probably be noticed if it were occurring on Ulva Island.

The failure of the combined model may stem from using re-invasion data from only one island group when fitting parameters using maximum likelihood. Estimating parameters using the Noises Islands (a northern island group) and applying them to islands around Stewart Island (southern island groups) would tend to make the combined model overestimate invasion rates. This is because water temperatures around the Noises Islands are likely to be much warmer that those offshore of Stewart Island. A warmer ocean temperature would have two effects. Firstly, swimming rats would survive for a shorter time in colder water. In the combined model this would be expressed by a smaller value for the parameter MD. Secondly rats may be less likely to enter the water in the first
place when ocean temperatures are cooler. In the combined model this would be expressed as a larger value for the parameter Mt.

4.5 Conclusions

4.5.1 Conclusions from the modelled experiment on Tia Island

Attempts should be made to determine if poisoning operations have an age-related bias in the mortality rates that they inflict. The results of this model suggest that targeting young rats will more effectively suppress populations. The other side of this finding is that if there is a bias against killing young rats, then poisoning operations could be made more efficient by removing this bias.

Another finding of the modelled experiment on Tia Island is that the higher the mortality rate that can be inflicted on the population, the less uncertain the result. One likely cause of this is that as mortality gets higher there are fewer individuals left to participate in other stochastic processes such as reproduction, immigration and emigration. If this is the case then it is promising for rat eradications because if a high mortality rate can be achieved then relatively little needs to be known about processes such as breeding biology and dispersal. Historically, many eradications have been carried with a "brute force" approach and rudimentary knowledge of the species population biology (Simberloff 2003).

The modelled experiments on Tia Island predict that re-invasion of Tia Island is very rapid (less than one year and nine months in 95 percent of simulations under the highest
mortality regime). Although this model gave imprecise answers and appears to have very low predictive power, this result still suggests that any eradication of rats from Tia Island would be very risky. I recommend that eradication is not attempted on Tia Island in the immediate future.

4.5.2 Conclusions from the modelled experiment on the Boat Group

The modelled experiment on the Boat Group revealed that one island can dominate the invasion process in small island groups. In this case Kundy Island acted as the main link between Stewart Island and the outer islands of the group. This indicates that some re-invasions could be made less likely by targeting these influential islands. This modelled experiment also suggests that when determining the main sources of invasion to an island, managers need to take care. A small immigration rate from a secondary source would be very hard to detect, but could be important in the re-colonisation of an island if the primary source is somehow taken away. Another conclusion to be drawn from the modelled experiment on the Boat Group is that it should not be assumed that every intermediate island acts as a stepping-stone. In this case Betsy Island, despite being central and a logical stepping-stone, was consistently colonised after the outer islands. However practical management of re-invasion demand that all intermediate islands are treated as stepping-stones, because generally it will be impossible to know whether an island is acting as a stepping stone or not.

The examination of the colonisation patterns of the islets in the system revealed that while the rescue effect does work in some cases, it is affected by an island groups
geography and therefore is not a universal effect. Also it appears that the relationship between invasion, distance from source and island shape can be subtle and complex, at least for very small islets. Ka and Kb are very similar in size and distance from their main source (Kb being 190m further from Kundy Island than Ka), yet their invasion patterns were very different.

4.5.3 conclusions from the sensitivity analysis

The main conclusion to be drawn from the sensitivity analysis is that island invasion is inherently unpredictable. The mechanistic model presented in this study was particularly poor at predicting ‘time to invasion’. It is unlikely that mechanistic models will ever be able to make precise and accurate prediction of island invasions because of the inherent uncertainty in the processes of rat population dynamics, migration by swimming and small population establishment. A much more productive way forward is likely to be building statistical models based on observational and experimental data with the aim of predicting the probability that an island with a given number of factors will be invaded within a set time.

The most revealing feature obtained from the sensitivity analysis of the combined model was that almost all terms found to be the best predictors of ‘time to invasion’ involved an interaction with ‘Target distance’. The biological interpretation of this is that factors that tend to affect ‘time to invasion’ work differently when the target island is at different distances. If this finding is a real world process then it could act as a limitation for any study of the swimming and navigation mechanism of rats in the open ocean, because it
means that findings from invasions could only be applied to stretches of water of a similar scale to those used in the study.

The main research priority for the future should be to develop a database of island invasions that includes information about the island, any possible sources, and most importantly, an estimate of the time it took the island to be invaded. At the moment the absence of this data is severely retarding our understanding of island invasions by rats. This research should be given priority over studies into the mechanics of island invasion because it is unlikely that a mechanistic understanding of rat population regulation and swimming behaviours will be enough to predict a process as stochastic as island invasion. If studies into the mechanics of island invasion are undertaken they need to focus on a wide range of topics. The combined model was most sensitive to parameters that affected population level ($B_{n0}$), and propensity to swim straight ($p_s$ and $PPJ$), with juvenile mortality ($m_C$) and how far the rat could swim before drowning ($MD$), playing a lesser but still substantial role. The elasticity analysis suggests that all these factors interact to determine invasion frequency.

4.5.4 Conclusions about the predictive power of the combined model

The combined model had very little predictive power, being very imprecise and not in accordance with the prior observations. However, it must be noted that a lack of empirical data sets makes testing the model against reality little more than anecdotal comparisons. The lack of the models predictive power was largely expected, as the ‘knowledge state’ was very poor for island colonisation by rats (Towns & Broome 2003), Shaun Coutts
especially in regards to swimming ability and their motivation for entering the water. However, this research did highlight areas of the knowledge state that require more attention.

Ultimately it must be concluded that the ‘knowledge state’ is not yet strong enough to support a predictive model of this nature. Further more, it is concluded that mechanism based simulation models are unlikely to ever possess enough predictive power to be useful to managers of island re-invasions, even when grounded in a very strong ‘knowledge state’.

This mechanistic simulation did however highlight several consequences of poisoning operations and island invasions that empirical studies and statistical modelling may have missed. The outcomes of the modelled experiment on Tia Island showed that there is a relationship between predator control operation efficacy and the uncertainty surrounding the outcome of that control operation. The outcome of the modelled experiment on the Boat Group highlighted that re-invasion of islands can be complicated by secondary sources and the resident species excluding other potential invaders. As well as this it showed that islands that appear to be logical stepping-stones are not always used. Also the modelled experiments on the Boat Group showed that the ‘time to invasion’ is much more uncertain for islands that have rely on one or more stepping-stones for their invasion, and even in a small island group re-invasion patterns can be subtle and unpredictable. The construction of this model showed that when all the available information on rat reproduction and survivorship was entered into the model it returned

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highly unrealistic results. This indicates that our understanding of rat population regulation in New Zealand is missing a key component.
Stochastic computer simulation of island colonisation by *R. norvegicus*.

References:


Stochastic computer simulation of island colonisation by *R. norvegicus*.


Stochastic computer simulation of island colonisation by *R. norvegicus*.


Stochastic computer simulation of island colonisation by *R. norvegicus*.


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\textbf{Appendices}

1. Stochastic swimming algorithm used to calculate which island, if any, a migrant reaches. 

2. Algorithm used to convert mortality rates into number of individuals dying.

3. Algorithm used to calculate the number of births and allocate their gender.
Appendix 1

For NE\textsubscript{a.s.t.i.} run (loop \(k\))

For MD run (loop \(l\))

Start.direction = side or corner

Start.position = a random GP along side

(unless side is a corner then Start.position = GP of corner)

\(GP_1 = \text{Start.position} + \text{a jump of 5 pixels directly away from the island.}\)

If random number between 0 and 1 < \(P_s\) then

Jump.direction = Jump.direction of the previous jump

Else: Jump.direction = random direction

End if.

If Jump.direction = \(y\) then

\(GP_j = GP_{j-1} + \text{a jump of PPJ in direction } y\)

End if

If \(GP_j\) lies inside DI then

\(N_{a.s.t.DI} = N_{a.s.t.DI} + 1\)

If random number between 0 and 1 < \(P_p\) and the migrant is a female of breeding age then

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Stochastic computer simulation of island colonisation by *R. norvegicus*.  

\[ N_{0₁₁₁₁} = N_{0₁₁₁₁} + \text{litter size} \]

End if

Start loop \( k \) again for the next migrant

End if

If \( GP_j \) does not lie within any island then

Start loop \( l \) for the next direction decision and jump

End if

Where:

\( NE_{aₙ₁₁₁} \): is the number of emigrants in age class \( a \), of sex \( s \), at turn \( t \), from island \( i \).

MD: is the maximum number of jumps each migrant can make before it is considered dead. It is given by

**Maximum swimming distance/ Pixel size (Eq. 2.15)**

Where Pixel size is the size of the grid squares and is the smallest distance that can be represented on the reference grid. All distances in the code are measured in pixels. A pixel size of 10 was chosen, as it is easy to divide other numbers by 10 when translating a map into code.

Start.direction: is a line of code that returns a whole number between 1 and 8. Each side and corner of the island is given a number between 1 and 8 so when
Stochastic computer simulation of island colonisation by \textit{R. norvegicus}.

Start direction chooses a number the migrant leaves from the designated side or corner.

$GP_{j}$: is the grid position and is composed of two values. A row position (north/south) and a column position (east/west). If there is no subscript then the grid position refers to a fixed item such as the side or corner of an island. If the subscript is present then the grid position refers to an item that moves every jump (i.e. a migrant).

Jump direction: is a line of code that returns a random whole number between 1 and 8. A swimming rat can move 8 directions in the model; north, northeast, east, southeast, south, southwest, west, northwest. Each direction is given a number so when Jump direction returns a number the migrant moves across the grid in the designated direction for a distance of $PPJ$.

Where $PPJ$ (pixels per jump) is the number of pixels moved every jump.

$Ps$: is the probability that the migrant will travel in the same direction that it travelled the previous turn.

$N_{a,s,t,Dt}$: is the number of individuals in age class $a$, of sex $s$, at turn $t$, on the destination island.

$Pp$: is the proportion of breeding age females pregnant when density $= K$.

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Appendix 2

Number dying \(_{a,s,t}\) = MS run for number of individuals in age class \(a\) of sex \(s\) at time \(t\).

Where: Number dying \(_{a,s,t}\): is the number of individuals that die in age class \(a\) of sex \(s\) at time \(t\).

MS: is a binomial switch that is \(1\) \(_{M_{a,s,t}}\) proportion of the time. When MS = 1, 1 is added Number dying \(_{a,s,t}\).
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Appendix 3

\[ B_{a,f,t} = N_{a,f,t} \times \text{Litter size} \times SI \times MI \times \text{FBF}_t \]  
Eq. 2.16

Where:  
\( B_{a,f,t} \): is the number of births produced by age class \( a \) for sex \( f \) (only females can give birth).

\( N_{a,f,t} \): is the number of individuals in age class \( a \) for sex \( f \) at time \( t \).

Litter size: is the number of offspring per female per successful breeding attempt.

SI: is a binomial season indicator that is 1 for three turns and 0 for one turn. This means that the breeding season in this model is nine months long and the non-breeding season is three months long.

MI: is a binomial indicator that is 1 when the male population is greater than 1 and 0 when the male population is less than 1. This means that when males are not present no offspring are produced.

FBF (Female Breeding Factor): is a correction factor that had to be included for the model to return realistic results. FBF is a density dependant relationship and is given by:

\[ \text{FBF}_t = A * ((N_{\text{total},t} / \text{area})^6) + B_0 \]  
Eq. 2.17

Where:  
\( N_{\text{total},t} = 0_{f1} + 1_{f1} + 2_{f1} + 3_{f1} + 0_{m1} + 1_{m1} + 2_{m1} + 3_{m1} \)  
Eq. 2.18

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Area: Is the area of the island in hectares.

\( a \): is defined in Eq. 2.1

\( B_{t0} \): is the value of FBF when \( N_{\text{total}} = 0 \).

\( A \) is a scaling factor which ensures \( \text{FBF} = bC \) when \( (N_{\text{total}}/\text{area}) = K \) for any given \( a \), and is given by:

\[
A = \frac{(bC - B_{t0})}{k^{a}} \tag{Eq. 2.19}
\]

Where: \( bC \) is the value of FBF when \( (N_{\text{total}}/\text{area}) = K \).

\( K \) is defined in Eq. 2.1.

FBF is artificially bound at \( bC \). The average relationship between FBF and density is shown in Fig. 2.3.

Births at \( t \) from age classes \( 1_{f}, 2_{f}, \) and \( 3_{f} \) plus births from pregnant immigrant females arriving at turn \( t \) are summed to give the number of offspring at \( t \) (\( NS_{t} \)).

SA is then run \( NS_{t} \) times where: SA is a random binomial switch that is 1 half of the time. When \( SA = 1 \), 1 is added to \( 0_{m,t} \). \( 0_{m,t} \) is then worked out by:

\[
0_{m,t} = NS_{t} - 0_{f,t}
\]