Improving the success of mouse eradication attempts on islands

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The house mouse is a weed: quick to exploit opportunity, and able to withstand local adversity and extinction without harm to the species. This means it has to be able to breed rapidly, tolerate a wide range of conditions, and quickly adjust to changes in its environment. These traits are responsible for the success of the species in so many parts of the world.

Professor R.J. Berry (1981)

Abstract

The house mouse is a highly commensal rodent species that has been accidentally spread across the world by humans. Mice have significant negative impacts on the ecosystems they invade and mouse eradication is an important conservation tool. A number of mouse eradication attempts have failed for unknown reasons and basic knowledge about mouse populations on New Zealand islands was lacking so this research project was commissioned to investigate mouse biology with the aim of improving eradication attempts. A review of all mouse eradication attempts reported up to May 2007 revealed a failure rate of 38%, far higher than the 5-10% reported for invasive rat species. A series of possible reasons for mouse eradication failure were identified and these formed the basis of the rest of the research. The eradication database was updated in February 2011 and several successful eradication attempts since 2007 lead to a revised failure rate of 33%. Mouse population densities and ranging behaviour on islands were unknown so these were investigated over an 8 month period on 6 ha Saddle Island culminating in mice being successfully eradicated from the island. The worldwide distribution of mice shows they are effectively able to invade new areas but how they behave when they arrive had never been studied. In the first experiment of its kind, I experimentally released pairs of male and female mice onto Saddle Island, simulating a new invasion with each release. The released animals showed dramatic changes in behaviour which are possibly adaptations to avoid mate-finding Allee effects. Anticoagulant resistance and behavioural differences between subspecies were also identified as possible reasons for eradication failure during the database review. A phylogeographic approach was used to identify the source population and subspecies of mice obtained from island and mainland sites in New Zealand with different mouse control regimes, with the aim of identifying links between mtDNA D-loop haplotype and control outcome. Results were inconclusive but several promising avenues for further research were identified. Population genetics and trapping records were used to investigate population structure of mice living on Saddle Island prior to the eradication. Population structure was shown to change through the year and genetic analysis suggested that the population was founded by a small number of individuals. The overall conclusion of this research is that with proper planning it is possible to eradicate mice from islands and to maintain mouse-free sanctuaries. A series of management recommendations drawn from this research are listed.

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Chapter 1. Introduction

1.1. Invasion biology

Human-mediated dispersal of plants and animals has lead to countless species being introduced to new areas far beyond their native ranges. A subset of introduced species cause problems in their new ranges (Mack et al., 2000) and these are referred to as invasive species (Colautti and MacIsaac, 2004). The negative impacts of invasive species have been well documented (Vitousek et al., 1997, Mack et al., 2000, Mooney and Cleland, 2001, Courchamp et al., 2003) and they have been estimated to cost the economy of the USA alone over $120 billion per year (Pimentel et al., 2005). Management of invasive species is best thought of as a three-stage approach (Hulme, 2006): prevention, eradication and control. In almost all cases preventing a species establishing is preferable to control or eradication (Leung et al., 2002). Once a species has become established in an area the ultimate goal should be eradication (Towns and Broome, 2003, Howald et al., 2007) although in many cases this is unfeasible so control is the only option (Hulme, 2006).

Invasive species offer excellent opportunities for research (Mack et al., 2000, Sakai et al., 2001), a field known as invasion biology (Simberloff, 2009). Fundamental ecological questions can be tested using populations of species that are undesirable and therefore can be experimentally manipulated in ways that would be impossible with native species. The benefits of ecological research into invasive species are huge, indeed, Hulme (2006) commented that "the application of ecological knowledge to manage (rather than describe) biological invasions probably represents one of the most powerful valedictions for the current investment of public funds in ecological research". Research must be targeted to provide maximum benefit (Puth and Post, 2005), which means scientists must collaborate with managers to identify key research priorities (Byers et al., 2002). Each of the three stages outlined earlier must be studied in order to effectively manage invasive species.

Some of the worst impacts of invasive species are seen on oceanic islands (Courchamp et al., 2003). Such islands tend to have high levels of endemism and in many cases there are no native mammals, meaning the native fauna and flora are at high risk of damage from invading mammals (Diamond, 1989, Blackburn et al., 2004, Phillips, 2010). However, islands are also excellent targets for conservation management because they offer discrete areas of

habitat that in many cases it is possible to eradicate invasive species from (Towns and Broome, 2003, Howald et al., 2007, Phillips, 2010) and, through effective quarantine measures, keep them free of invasive species (Russell et al., 2008a, Oppel et al., 2010). Once islands are free from invasive species populations of native species that survived the impacts of invasive species often recover naturally and extirpated species can be reintroduced as part of the process of ecosystem restoration (Towns and Ballantine, 1993, Courchamp et al., 2003)

In 2006 consultations with conservation managers in New Zealand identified the house mouse (*Mus musculus*) as a particular species of concern (E. Murphy, Department of Conservation, pers. comm.). A number of eradication attempts on islands had failed (Howald et al., 2007) and information about key aspects of mouse population dynamics and behaviour in New Zealand ecosystems was lacking (Dilks and Towns, 2002, Clapperton, 2006, White and King, 2006).

This thesis represents the culmination of a four-year research project into the biology of house mice on New Zealand islands with the aim of improving the success of eradication attempts. The main focus of the thesis is New Zealand but findings have worldwide relevance. The remainder of this introductory chapter will introduce the star of this research, the house mouse, one of the most remarkable mammals in existence.

1.2. The house mouse

1.2.1. Preamble

As its name suggests, the house mouse (*Mus musculus*) has a long joint history with humans (Berry and Jakobson, 1975) and as a result is found throughout the world (Rowe, 1973, Bronson, 1979). Mice have been alternately worshipped and vilified throughout history (Berry, 1981) due to their close association with human dwellings and it is estimated that nearly 2% of dwellings in the UK have house mouse infestations (Langton et al., 2001). Domestic populations of mice cause damage to stored food (Berry, 1981, Murphy et al., 2003) and can spread disease and cause damage to wiring inside buildings (Timm, 1994). As a result, commensal populations are usually controlled (Murphy et al., 2003).

House mice are one of the most widely used laboratory animals (Morse III, 2007) with the first recorded use occurring in 1664 when Robert Hooke used mice in air pressure experiments (Berry, 1981). The use of rats and mice in research in the USA is not covered by the Animal Welfare Act so research institutes are not required to report the numbers used

(Trull and Rich, 1999) although it has been estimated that at least 15 million rats and mice are used for research annually in the USA alone (Carbone, 2004). The long history of mice as a laboratory animal means that there is a vast amount of literature about domesticated mice available; for example, *The Mouse in Biomedical Research (Second Edition)* stretches to four volumes covering every aspect of laboratory mouse research (Fox et al., 2007). The process of domestication is likely to have altered mouse behaviour making it difficult to compare laboratory studies with studies of free-living wild mice (Clapperton, 2006) but laboratory studies are a useful background to the behaviour of the species.

Mice are not only found in houses and laboratories. Free-living feral populations of house mice are found throughout the world far from human habitation (Ruscoe and Murphy, 2005). The house mouse shows remarkable levels of behavioural flexibility, enabling it to establish and thrive just about anywhere it finds itself (Berry, 1981). House mice have often considered little more than a nuisance with no significant impact on ecosystems (Simberloff, 2009). By the end of this chapter it should be clear that this is not the case.

1.2.2. Origins of the species

The first member of the genus *Mus* appeared in the fossil record around 5.5 million years ago in the Indian subcontinent (Boursot et al., 1993). No fossils linking this species (*Mus auctor*) and *Mus musculus* have been discovered, so the date of divergence has been estimated via molecular methods to be around 0.5 million years ago (Boursot et al., 1993). Divergence occurred in the Indian subcontinent and *Mus musculus* spread from there across the world (Bronson, 1979, Din et al., 1996, Gabriel et al., 2010).

1.2.3. Taxonomic status

The taxonomic status of house mice is relatively complex, as would be expected for as widely dispersed a species. The main debate centres on whether or not the main commensal forms of house mice are separate species ("binomial form" e.g. *M. musculus* and *M. domesticus*) or a group of subspecies of *Mus musculus* ("trinomial form", (Prager et al., 1998)). A comprehensive review of phylogenetic relationships in the genus *Mus* favoured the trinomial system to describe house mice (Lundrigan et al., 2002) and most recently published studies use the trinomial form (e.g. Searle et al., 2009a, Searle et al., 2009b, Hardouin et al., 2010). I therefore consider that this is the correct nomenclature for house mice. A large amount of work on mice takes place in Australia and this country remains one of the few places in the world where authors routinely use the binomial form, referring to

the house mouse as *M. domesticus* (e.g. Singleton et al., 2007, Kaboodvandpour and Leung, 2008, Kelly et al., 2010). No review of house mouse phylogenies in Australia exists but for the purposes of this thesis I am going to assume that the house mouse present in Australia is *M. m. domesticus*; the same subspecies found throughout New Zealand (Searle et al., 2009a). In addition to *M. m. domesticus*; *M. m. musculus* and *M. m. castaneus* are also found in areas of New Zealand. There is also evidence of hybridisation between subspecies with *musculus* or *domesticus* nuclear DNA and mitochondrial DNA from one of the other subspecies (Searle et al., 2009a). A similar phenomenon has been observed in the USA and Norway adding further weight to house mice being a collection of subspecies rather than true species (Orth et al., 1998, Jones et al., 2010).

From an ecological perspective it is unlikely that there are major differences in the ecological roles of the different subspecies of house mice, so in this thesis little distinction will be made between the subspecies. The exception to this will be Chapter 5 where I will describe an investigation into house mouse phylogeography.

1.2.4. Commensal behaviour and distribution

Mice and humans have been closely associated with each other since the beginning of the Neolithic period (around 13,000 BC) when people first started to settle in one area and construct buildings for shelter and food storage (Cucchi and Vigne, 2006). *Mus musculus* fossils have been found in association with some of the earliest agricultural settlements in Israel (Auffray et al., 1990). All three subspecies of house mouse are highly commensal (literally "eats from the table of man", Braithwaite, 1980), but subspecies radiation (around 0.5 million years ago, Section 1.2.2) predates the beginning of sedantism (settled farming cultures), therefore each subspecies must have developed commensal behaviour independently (Boursot et al., 1993, Din et al., 1996). It has been hypothesised that house mice successfully exploited the new ecological niche presented by human settlements in order to avoid competition with other *Mus* species (Auffray et al., 1990).

Once commensal behaviour was established, the house mouse was set to conquer the world. The spread of the species through Europe has been relatively well documented and was initially driven by the expansion of farming (Cucchi et al., 2005, Cucchi and Vigne, 2006). Rate of spread increased through the Bronze Age as a result of increased trade and by the 1st Century AD house mice were found across Europe and the Middle East (Auffray et al., 1990, Cucchi et al., 2005, Cucchi and Vigne, 2006, Cucchi, 2008, Searle et al., 2009b). One of the

most intriguing archaeological records came from a Bronze Age shipwreck recovered from off the coast of Turkey. In addition to a rich cargo of copper ingots and exotic raw materials the ship was also carrying a stowaway house mouse, the earliest recorded incidence of rodents stowing away on ships (Cucchi, 2008).

House mice have continued to spread around the world through passive transport by humans (Pocock et al., 2005) and they are now found on every continent in almost every habitat (Berry and Jakobson, 1975, Berry and Scriven, 2005). In some areas they are only present as commensals; for example, in the Prioksko-Terrasnyi Biosphere Reserve in Russia house mice are only found in buildings and have not colonised the natural ecosystems within the reserve (Bobrov et al., 2008). In other areas populations are able to successfully establish away from human influence (Ruscoe and Murphy, 2005, Singleton and Krebs, 2007).

1.2.5. Social organisation

The social organisation of house mouse populations is very flexible and can be altered rapidly as conditions change (Butler, 1980). Early studies of mouse population structure in barns found that mice are divided into small breeding units that are called demes (Anderson, 1970). These enclosure studies concluded that demes were closed to immigration, meaning that gene flow between demes is limited (Anderson, 1964, Selander, 1970, Pennycuik et al., 1978). A different picture came from longer-term studies of social structure and gene flow in free-living populations (Singleton and Krebs, 2007). In these populations it was found that social groupings do not restrict gene flow (Berry and Jakobson, 1974, Myers, 1974, Berry et al., 1991, Triggs, 1991). A recent study in Argentina found genetic differentiation between populations on farms and populations in sheds within farms but there was evidence of gene flow between farms (Leon et al., 2010). Overall it seems likely that social structuring in a population merely slows population mixing and that demes are mainly temporary (Berry and Bronson, 1992).

1.2.6. Reproduction

House mice have a very high reproductive potential which is a large part of their success as an invasive species. Females can breed for the first time at 6 weeks of age and can produce litters of 6-8 young every 4 weeks after that (Berry, 1981). Mice in feral populations may not breed so efficiently, but given the right conditions populations can increase dramatically in a short space of time (Ruscoe and Murphy, 2005, Section 1.2.9). Mice in feral populations do

not normally breed over winter but if sufficient food is available winter breeding may occur (Murphy, 1992).

1.2.7. Diet

House mice are omnivorous and are able to fulfil their dietary requirements from a wide variety of sources (Ruscoe and Murphy, 2005). Dietary flexibility is likely to contribute significantly to the success of mice as an invasive species as it enables mice to make use of whatever food is present in the new area they find themselves. Mice are characteristically intermittent feeders meaning they visit a food source on many occasions only taking a small amount of food each time thus allowing them to determine which foods are safe (Lund, 1988, Clapperton, 2006). Much of the damage caused by house mice is a result of their feeding behaviour so specifics of mouse diet will be discussed under Impacts (Section 1.2.8).

Mouse diet usually consists of varying proportion of animal and plant material (Tann et al., 1991, Canova and Fasola, 1993, Miller and Webb, 2001). Plant material may be seeds or green parts depending on the season. Animal material tends to be invertebrates (Ruscoe and Murphy, 2005), but birds and lizards are also taken (Newman, 1994, Wanless et al., 2007). Diet is dependent on season and mice will take advantage of resources as they become available (Berry and Bronson, 1992). Mice are able to obtain most of their water needs from their food so in most situations they do not require access to a water source (Fertig and Edmonds, 1969).

1.2.8. Impacts

As befits a species with as wide a geographic range, the impacts of house mice are very varied. Their omnivorous feeding habits mean that their negative impacts can influence whole ecosystems. The negative effects of mice can be divided into primary impacts (direct effects caused by feeding) and secondary ones (where the presence of mice leads to indirect negative effects on another species) and these will be discussed separately. The worldwide impacts of house mice are almost worthy of a thesis on their own, therefore, this section is designed to provide an overview with some key examples rather than to provide an exhaustive list. In here somewhere mice destry nearly all seed they eat and do not act as seed dispersxers (Williams et al., 2000)

1.2.8.1. Primary impacts

Many invertebrate species worldwide are negatively affected by mice (Ruscoe and Murphy, 2005, Singleton and Krebs, 2007, Angel et al., 2009, St Clair, 2011), although this field is under-researched so the full impact may be higher than thought (St Clair, 2011). Mice on Skokholm Island in the UK were found to have a fairly typical diet consisting of a mixture of arthropods (mainly Lepidoptera) and plant material (Berry, 1968). Interestingly, faecal analysis showed that mice in one area of Skokholm had a diet consisting largely of a littoral amphipod species (Berry and Jakobson, 1974). In my own work, mice were recorded foraging on the beach only twice in over 300 radio-tracking fixes obtained from 21 mice living on a small island (unpublished data), so it seems unusual that Skokholm mice were so dependent on beach fauna for food. Mice on sub-Antarctic Marion Island have caused a decrease in the average size of two invertebrate prey species by selectively feeding on larger individuals (Chown and Smith, 1993). There have been a number of dietary studies of mice on sub-Antarctic islands showing that mice eat large numbers of native invertebrates (Copson, 1986, Rowe-Rowe et al., 1989, Chown and Smith, 1993, Jones et al., 2002, Smith et al., 2002). Angel et al. (2009) reviewed the impacts of mice on sub-Antarctic islands and concluded that they do the most damage when they are the only introduced rodent present. Mouse diet in New Zealand is biased towards invertebrates (Badan, 1986, Miller and Miller, 1995, Miller and Webb, 2001), with one island study finding that the diet consisted largely of an endemic orthopteran (Miller and Miller, 1995).

Mice are capable of eating many hundreds of seeds a day (Ruscoe and Murphy, 2005) and most seeds are not ingested whole (Williams et al., 2000) meaning that mice can have a significant impact on plant reproductive success. In New Zealand, mice have been recorded feeding on the seeds of many native species including beech (*Nothofagus* spp.), rimu (*Dacrydium cupressinum*), kauri (*Agathis australis*), sand tussock (*Austrofestuca littoralis*) and pingao (*Desmoschoenus spiralis*) (Wilson et al., 2007b, Badan, 1986, Beveridge, 1964, Miller and Webb, 2001). Predation of rimu and beech seeds by mice may alter forest composition in New Zealand by displacing seedling regeneration of these species away from the parent trees (Wilson et al., 2007b). Sand tussock and pingao are important sand dune-binding plants in New Zealand and mouse predation on the seeds of these species depresses recruitment. Mouse impacts on plants have also been well studied on sub-Antarctic islands (Angel et al., 2009). These islands are characterised by a depauperate flora (Smith and Steenkamp, 1990), members of which are highly susceptible to damage by introduced mice

(Angel et al., 2009). Damage by mice to flora has been reported from Antipodes, Marion, Macquarie and Guillou Islands (Smith and Steenkamp, 1990, Le Roux et al., 2002, Smith et al., 2002, Jones et al., 2003). In most cases mice remove seed heads and prevent recruitment (Chown and Smith, 1993) but adult plants, such as the cushion plant (*Azorella selago*) on Marion Island, can also be damaged by mouse burrows (Phiri et al., 2009).

House mice are poor competitors when they coexist in an area with native small mammal species (Singleton and Krebs, 2007). This was highlighted in a study of the diet of small mammals inhabiting a region of Italy. In this area house mice diet consisted largely of the green parts of plants followed by seeds. Invertebrates were only a minor constituent of the diet, probably due to competition with shrews (Canova and Fasola, 1993). A similar situation was observed in Cuba. Here house mice are part of an assemblage of other small mammals and the majority of their diet consists of plant material (Borroto-Paez, 2009). This contrasts to most non-commensal populations where invertebrates make up a large part of the diet (Ruscoe and Murphy, 2005).

House mice have been implicated in one mammal extinction, *Malpaisomys insularis* in the Canary Islands, Atlantic Ocean (Harris, 2009). Experimentally reducing house mouse numbers in an area of Thevenard Island, Western Australia lead to an increase in numbers of the endemic rodent *Leggadina lakedownensis* (Moro, 2001). One of the more disturbing stories of mouse damage comes from sub-Antarctic Gough Island. High numbers of injured or dead seabird chicks were observed (Cuthbert and Hilton, 2004) and later video footage revealed that house mice were feeding on the chicks while they were still alive (Wanless et al., 2007). As shown by R.J. Berry's work on Skokholm (Berry, 1968), mouse impacts are not limited to terrestrial ecosystems. In New Zealand, mice are known to feed on inanga (*Galaxias maculaus*) eggs. Inanga are a native fish species which migrate to estuaries to lay their eggs on bank-side vegetation during high spring tides. The eggs are left exposed and vulnerable to mouse predation until the next spring tide when they hatch (Baker, 2006, Hickford et al., 2010).

1.2.8.2. Secondary impacts

House mouse populations in New Zealand undergo periodic irruptions (see Section 1.2.9) in response to beech (*Nothofagus* spp.) mast seeding events (King, 1983, Murphy, 1992, Fitzgerald et al., 2004). Mast seeding refers to a plant reproductive system where large amounts of seed are synchronously produced some years with little seed production in

other years (Kelly and Sork, 2002). Population irruptions are driven by an increase in the food source allowing the mice to reproduce more effectively (Ruscoe and Murphy, 2005). Beech flowers are produced in large numbers prior to a mast year and this leads to an increase in some of the litter-dwelling arthropods that mice feed on (Alley et al., 2001, Fitzgerald et al., 1996). The combination of these two abundant food sources (arthropods and beech seeds) leads to winter breeding and dramatic population increases (King, 1983, Murphy, 1992). Population densities can increase from less than one mouse/ha in non mast years (Ruscoe et al., 2001) to peaks of up to 50 mice/ha in mast years (Ruscoe et al., 2003). Increased mouse numbers results in increased stoat numbers, which in turn leads to increased predation pressure on endangered endemic birds such as the mohua (*Mohua ochrocephala*) (King, 1983, Murphy and Dowding, 1995, O'Donnell and Phillipson, 1996). This is a simplified summary of a complex interaction, but it is a good illustration of house mice having an indirect effect on an endangered species. Another example of mice indirectly impacting a bird species comes from the sub-Antarctic. On Marion Island the lesser sheathbill (*Chionis minor*) is declining despite the eradication of feral cats, a major predator of the species, from the island (Huyser et al., 2000). The reason for this appears to be that house mice are eating large numbers of the terrestrial invertebrates (Smith et al., 2002) that lesser sheathbills depend on for food during winter and decreased foraging success has lead to decreased breeding success and a population decline (Huyser et al., 2000). A final example from the sub-Antarctic concerns nutrient cycling. Smith and Steenkamp (1990) suggest that mouse predation pressure on soil-dwelling invertebrates may lead to a decrease in nutrient cycling on the island. Similar concerns have been raised in New Zealand on islands colonised by rats (Towns et al., 2009) and in mainland areas where introduced wasps, rats and mice are present (Wardle et al., 2010).

1.2.9. Population irruptions

In Section 1.2.8.2 I described how a seasonally abundant food source in New Zealand forests can cause mouse populations to rapidly increase in number which leads to indirect negative effects on an endemic bird species. In Australia such mouse irruptions are known as mouse plagues and densities can reach over 800 mice/ha over very large areas (Singleton et al., 2005). Periodic mouse plagues occur in cereal-producing regions of South-Eastern Australia and when they occur they have a significant negative economic impact on the regions they affect (Singleton et al., 2005). Mouse plagues in Australia have been the focus of a substantial body of research, large amounts of which are cited throughout the data chapters that make

up the remainder of this thesis. Irruptive population dynamics have also been reported in other ecosystems. Wilson and Lee (2010) observed mouse populations increasing in number in response to mast seeding of an alpine grass species in New Zealand in a very similar manner to the beech forest irruption described in Section 1.2.8.2. In Peru, house mice show seasonal fluctuations in density between 10 and nearly 400 mice/ha (Arana et al., 2006). Mice have become an important food source for native burrowing owls (*Athene cunicularia*) in this system and the owls have synchronised their reproduction to combine with peaks in mouse density (Arana et al., 2006). Mouse populations typically show cyclical changes in population density (Ruscoe and Murphy, 2005) but the range of densities exhibited here warrant a place in the irruptions category. This example is interesting because it shows how a native species has adapted to take advantage of an invasive species as a food source. In this instance mice could almost be considered beneficial to the ecosystem; although I suspect that if mouse diet were investigated any perceived benefit would evaporate rapidly.

1.2.10. Control

One of the earliest documented methods of mouse control was reported by Berry (1981). Hwyel Dda ("Hwyel the Good") was a Welsh chief who published a standard price list for the sale of cats and a cat that had caught a mouse was granted the highest price of fourpence (Berry, 1981). Cats were introduced to a number of islands in an attempt to control mice (e.g. Marion Island, Bester et al., 2002), but invariably cats ended up doing more damage than mice and they too have been the target of numerous eradication attempts (Nogales et al., 2004). Trapping has been used to eradicate mice from small islands (Howald et al., 2007) and mouse traps are commonly used in domestic mouse control (Timm, 1994) but the most effective and widely used form of control is poisoning (Buckle and Smith, 1994, Courchamp et al., 2003).

1.2.10.1. Poisoning

A range of different poisons have been used for mice control over the years but the most commonly used in recent times is the second generation anticoagulant brodifacoum (Eason et al., 2002, Howald et al., 2007). Laboratory trials have confirmed the susceptibility of mice to brodifacoum (Rowe et al., 1978, O'Connor and Booth, 2001, Cleghorn and Griffiths, 2002, Morriss, 2007) and it has been used as the main toxin in a large number of successful eradication campaigns against mice (Howald et al., 2007). Further reviews of poisoning

methods and the issue of anticoagulant resistance (Greaves, 1994) can be found in Chapter 2 and Chapter 5 respectively.

1.2.10.2. Immunocontraception

Virally-vectored immunocontraception (VVIC) is being researched as a method of widespread mouse control (Redwood et al., 2007, Arthur et al., 2009). A modified virus which causes infertility is created and released into a population. As it spreads, more individuals become infertile, initially reducing growth of the population and eventually resulting in its decline as individuals die and are not replaced through recruitment (Singleton et al., 2002, Hardy et al., 2007, Jacob et al., 2008). A suitable mouse-specific virus has been identified and trialled (Arthur et al., 2009) but at the time of writing the technique is still in the experimental stage and not ready for widespread release.

1.2.10.3. Benefits of control

Detailed studies into how ecosystems respond to mouse eradications are rare. Mice were eradicated from Mana Island, New Zealand in the early 1990s following concerns about the impact they were having on endemic lizards and insects (Hook and Todd, 1992). Following the successful eradication, captures of three species of concern (*Cyclodina macgregori*, *Hoplodactylus maculatus* and *Deinacreda rugosa*) all increased significantly indicating that the mouse eradication was justified (Newman, 1994). Selvagem Grande Island in the Eastern Atlantic was cleared of mice and rabbits (*Oryctolagus cuniculus*) by ground-based poisoning beginning in 2002 (Olivera et al., 2010). Vegetation plots, seabird and land bird breeding success and numbers, and invertebrate abundance and diversity were all monitored before and after the eradication (Zino et al., 2008, Olivera et al., 2010). Because two invasive species were removed simultaneously, ecosystem recovery is difficult to assign to one species or the other but the evidence presented by Olivera et al. (2010) suggests that the eradication was beneficial for all taxa monitored. Well planned and comprehensively reported monitoring such as this is crucially important in invasion biology (Courchamp et al., 2003) and managers attempting mouse eradications should aim to quantify ecosystem responses to eradication as such information provides valuable justification for other planned operations.

1.2.11. Summary

By this point it should be clear that mice are a serious ecological problem. Mice are quite happy to live in close proximity to humans, and their small size means they are often

overlooked, thus aiding their accidental spread around the world. One of the key words to associate with mice is flexibility. It applies to their diet, their reproductive biology, their social structure and just about every aspect of their behaviour. The negative impacts mice have on ecosystems they invade are significant and varied making their eradication desirable wherever feasible.

1.3. Thesis aims

As discussed in Section 1.1, effective invasive species management requires a three-stage approach focussing on prevention of invasion occurring, eradication of established populations and, if eradication isn't an option, control of the population (Hulme, 2006). On islands the first two approaches are the most relevant since eradication is far more feasible on islands than it is on the mainland (Courchamp et al., 2003, Towns and Broome, 2003, Howald et al., 2007, Phillips, 2010). New Zealand leads the world in eradicating invasive species from islands (Howald et al., 2007) and is at the forefront of research into invasive species management. As a result, gaps in knowledge are well defined and the New Zealand Department of Conservation actively finances and supports research that will target these gaps. This Ph.D. research was commissioned by the Department of Conservation (DOC Investigation 3951) to investigate house mouse eradication failures. All research was approved by the University of Auckland Animal Ethics Committee (Approval R579). Each of the five data chapters in this thesis was planned to provide more information about house mice in relation to eradicating them from islands and preventing them from invading new islands. The background to each chapter is discussed in brief below; chapters were written as stand-alone papers so each chapter contains a full introduction and discussion of results.

1.3.1. Eradicating mice from islands: successes, failures and the way forward

Howald et al. (2007) reported that 19% of mouse eradication attempts worldwide had failed. In order to provide a sound basis for the rest of my research I independently reviewed all reported mouse eradication attempts with the aim of determining why mice are so much harder to eradicate than rats and to identify possible operational factors that may influence eradication success. As a result of this review I was able to identify areas where further research was needed and some of these areas became the focus of later data chapters. The database used for analysis for this chapter was compiled in and published in 2007 (MacKay et al., 2007). It was updated in 2011 for inclusion in this thesis but analyses other than recalculating the failure rate were not updated.

1.3.2. A successful mouse eradication explained by site-specific population data

The aim of this chapter was to obtain detailed baseline population data from mice living on a small island prior to eradicating the population. There was little information available about mouse population densities (White and King, 2006) or behaviour on islands in New Zealand and mouse behaviour could have contributed to some eradication failures (Cleghorn and Griffiths, 2002). The detailed population data was then used to audit the successful eradication and make recommendations for future projects. This work was presented in February 2010 at the Island Invasives: Eradication and Management conference held at the University of Auckland and the paper (MacKay et al., in press) will be published in the proceedings in mid-2011.

1.3.3. See how they run: potential mate-finding Allee effect avoidance in house mice

The experiment described in this chapter was the first investigation into the invasion behaviour of mice, something that was raised as a research need by Dilks and Towns (2002). Most invasive species research targets established populations but knowing how species invade is critical (Byers et al., 2002). The worldwide distribution of house mice is testament to their remarkable colonisation ability and I used experimental releases of pairs of mice to examine exactly how mice colonise new areas. The results of this work provide valuable insights into mouse invasion biology and recommendations are made to assist in maintaining mouse-free sanctuaries.

1.3.4. Phylogeography of New Zealand house mice in relation to control

Searle et al. (2009a) investigated the origins of New Zealand house mouse populations using phylogeographic methods. House mice in New Zealand are a mixture of three different subspecies and mtDNA haplotypes present in New Zealand can be linked to a diverse range of source populations. The aim of this chapter was to use a phylogeographic approach to investigate whether or not there was a link between mouse subspecies or mtDNA haplotype and eradication success.

1.3.5. Population structure and colonisation history of house mouse on a small island

The final data chapter utilised genetic samples and trapping records collected in the fieldwork described in Chapter 3 to describe the population structure of mice on a small island through spatial and population genetic methods. The aim was to discover whether the two methods came to the same conclusion about population structure on the island and

also to attempt to describe the colonisation history of the mouse population through an examination of genetic diversity apparent in the population.

Chapter 2. Eradicating mice from islands: successes, failures and the way forward

2.1. Abstract

The house mouse has been spread throughout the world by the actions of humans. It causes severe impacts to native ecosystems, especially in areas where there are no native mammals. It is possible to eradicate mice from islands but they are harder to eradicate than rats. A review of reported eradication attempts found that 17 attempts on 45 islands worldwide failed; a failure rate of 38%. The effect of operational factors on eradication success was examined, but no significant model was formed. Brodifacoum is the most widely used poison and has a 49% success rate. Mouse eradications should be attempted wherever possible and recommendations to help increase the success of a house mouse eradication attempt are given. Including eradication attempts that occurred since 2007 changes the failure rate to 33% and if only eradication attempts since 2007 are considered the rate is 9%.

2.2. Introduction

The house mouse (*Mus musculus*) originated in the north of India around 900,000 years ago (Boursot et al., 1996). The species then spread in several directions, radiating to form three distinct sub-species (*M. m. domesticus, M. m. musculus* and *M. m. castaneus*) with distinct ranges (Boursot et al., 1993, Boursot et al., 1996). All subspecies show a high level of commensal behaviour (Boursot et al., 1996, Berry and Scriven, 2005) but they are also able to survive away from human settlements (Berry and Scriven, 2005, Ruscoe and Murphy, 2005). The commensal behaviour of house mice means they have been spread throughout the world by humans, and house mice are present on all continents and many islands from the sub-Antarctic to the tropics (Bronson, 1979, Rowe, 1973). The effect of introduced, invasive house mice has often been overshadowed by invasive rats (*Rattus* spp.) however (e.g. Atkinson, 1985, Simberloff, 2009), especially where they co-exist and mice are dominated by rats (Caut et al., 2007). Non-commensal populations of house mice can have severe negative impacts on native ecosystems, especially in areas where the native biota evolved in the absence of mammals (Courchamp et al., 2003, Angel et al., 2009), and house mice have been recorded as damaging populations of invertebrates (St Clair, 2011), lizards (Newman, 1994), birds (Jones, 2007, Wanless et al., 2007) and seed production in forests (Wilson et al., 2007b).

Eradication of invasive rodents is an important management tool to redress their negative impacts (Courchamp et al., 2003) and a recent review recorded that introduced house mice have been successfully eradicated from 30 islands worldwide, using a number of different methods (Howald et al., 2007). Despite this progress, seven attempts failed which is a 19% failure rate, compared to a 5% failure rate for Norway rats (*Rattus norvegicus*) (Howald et al., 2007). Is there a reason that introduced mouse populations are harder to eradicate from islands than introduced rat populations? In order to answer this question, I compiled, reviewed and analysed a database of all known mouse eradication attempts. The database was compiled from the published literature, "grey" literature, and through conversations with researchers and managers involved in house mouse eradication attempts (see Appendix 1). The database used for analysis for this chapter was compiled in 2007 when it was presented at the Managing Vertebrate Invasive Species Symposium in Colorado, USA and subsequently published (MacKay et al., 2007). Section 2.6 contains details of eradication attempts that have taken place since this chapter was initially published.

2.3. Island mouse eradications

The first reported mouse eradication took place on Flatey Island in Iceland in 1971 (Moors et al., 1992). Since then, eradication attempts have occurred worldwide from Rasa Island in the Gulf of California (Tershy et al., 2002) to Enderby Island in the sub-Antarctic (Torr, 2002). Different poisons and poison broadcast methods have been used in conjunction with trapping in some cases. Fifty-six eradication attempts have taken place on a total of 51 islands ranging in size from 0.7 ha Crusoe Island in New Zealand (Lee, 1999) to 800 ha St. Paul Island in the French Sub-Antarctic (Micol and Jouventin, 2002). Successes and failures have occurred across the full range of island sizes (see Appendix 1). Two eradication attempts were stopped before completion for operational reasons and six are yet to be confirmed. Taking into account the eradication attempts of unknown outcome, successful eradication of house mice was achieved on 28 of 45 islands that the result is known for. However, sometimes it took more than one attempt. On Mokoia Island, New Zealand the first two operations failed but the third attempt was successful. All four operations on Limestone Island, New Zealand have failed. This gives a failure rate of 38% which is higher than reported by Howald et al. (2007) and much higher than failures reported for rat species. A total of over 3,600 ha of island habitat worldwide have been cleared of mice.

We categorised each house mouse eradication attempt by four operationally defined factors which might affect the likelihood of successful eradication (Table 2.1). Eradication may also be affected by mouse behaviour or genetic factors but these were impossible to model and became the focus of later research. In order to identify which (if any) of these factors most influence eradication success or failure a logistic general linear model was fitted with success/failure as the response factor and details of the eradication attempt entered as explanatory variables. The software package JMP (SAS Institute, North Caroline, USA) was used for this analysis. No significant model was formed with any combination of explanatory variables meaning there is no evidence that success or failure of mouse eradications to date has been consistently caused by any of these operational factors. Nonetheless we report success and failure rates relative to each factor.

Table 2.1 Factors investigated in analysis of eradication attempts

Factor	Description
Island area	Size of the island in hectares
Bait application method	Aerial , bait station or hand spreading
Toxin (generation)	Diphacinone (1), pindone (1), warfarin (1), brodifacoum (2), bromadiolone (2) or flocoumafen (2)
Other introduced mammals	Competitors, predators or no direct effect

2.3.1. Poisons

Nearly all recorded mouse eradication attempts used some form of anticoagulant poison. These compounds are used in eradication attempts worldwide (Eason et al., 2002, Hoare and Hare, 2006) and act by inhibiting the production of clotting factors within the animal normally leading to death by internal haemorrhage within 10 days (O'Connor and Booth, 2001). Seven poisons have been used in mouse eradication attempts; three first-generation anticoagulants (diphacinone, pindone and warfarin) were used as the main poison in six attempts, three second-generation anticoagulants (brodifacoum, bromadiolone and flocoumafen) were used as the main poison in 49 attempts and an acute poison (1080) in one. Five attempts used multiple poisons and two attempts followed up poisoning with trapping. Brodifacoum was used as the main or secondary poison in 80% of mouse eradication attempts (including multiple attempts on the same island), 49% of which were successful (45 attempts, 22 successful). Other poisons have a higher success rate but the sample size is much lower. A single eradication attempt using 1080 (Varanus Island, Australia, 1993) is likely to have failed because it has been shown that mice can detect the presence of 1080 in baits (O'Connor et al., 2005). Poisons were distributed on islands in a number of matrices including wax blocks and cereal pellets. The poison bait matrix used is dependent on the

poison broadcast method and in a number of cases this information was not reported so this was not included in the model.

2.3.2. Bait delivery

Three main methods of bait delivery have been used in mouse eradication attempts. The method chosen depends on island topography, non-target issues, economics and the habitat on the island (Howald et al., 2007). Information is scarce on the earliest recorded mouse eradication attempt (Flatey Island, Iceland, 1971) but it has been assumed that bait stations were used.

1. Bait stations were used as the main method of bait delivery in 30 out of 56 eradication attempts (including multiple attempts on the same island). They were also used to supplement aerial delivery in two attempts. The grids used for bait station delivery varied in size from 10 m to 50 m; 20 m to 25 m being the most common spacing used. Bait station grids are normally maintained for 1-2 years (Thomas and Taylor, 2002) but some attempts went on for much longer. Bait stations were first placed on 37 ha Limestone Island, New Zealand in 1999 and have been regularly serviced for over 6 years (J. Craw, Auckland Regional Council, New Zealand, personal communication) but mice are still present, despite three aerial attempts and one ground-based attempt, and prolonged periods of non-detection (C. Mitchell, Limestone Island Ranger, New Zealand, personal communication). Bait stations are relatively labour intensive and track maintenance can damage island habitat; particularly with smaller grid spacing; but if the support required to service bait stations is available this is a relatively effective method with 48% of eradication attempts succeeding. The largest island successfully cleared of mice using this method was 253 ha Flat Island in Mauritius using a 25 m by 25 m grid (Bell, 2002).
2. Hand broadcasting of baits was used in two eradication attempts; both run by French teams; where one attempt was successful and the other failed. Fajou Island in Guadeloupe is the largest island (120 ha) where mouse and rat eradication was attempted using this method and poisoning in this instance was supplemented by trapping (M. Pascal, National Institute for Agricultural Research, France, personal communication). A recent visit to the island found mice present at low numbers but the reason for eradication failure is unclear (M. Pascal, personal communication). Hand broadcast is a valuable method to consider when aerial broadcast is not possible and when the continued support needed to maintain a network of bait

stations is unavailable. Hand broadcasting of baits has been used to supplement a number of bait station and aerial operations to ensure bait reaches all areas of islands (Stephenson et al., 1999, Merton et al., 2002).

3. Aerial broadcast of bait using helicopters is becoming more common and the preferred method of bait delivery for introduced rodent eradications (Towns and Broome, 2003). This technique has been used in 25 mouse eradication attempts around the world. In some cases aerial operations have been supplemented by hand broadcast or bait stations, but the majority of attempts rely solely on bait distributed by helicopter. Forty eight percent of eradication attempts using aerial broadcast have been successful. The amount of bait distributed onto the island and the number of bait applications varies. This information is not always available but the mean quantity of bait used in 16 operations was 15.3 kg/ha (range 10-39 kg/ha). The number of applications varies between one and three. The highest bait density was used on Frégate Island in the Seychelles where the presence of crabs meant a large amount of bait had to be used (Merton et al., 2002). The flight paths of the helicopters are crucial to ensuring eradication success. Overlapping flight paths and second aerial applications at right angles to the first are good methods of ensuring complete coverage of the island. Modern global positioning system (GPS) satellite technology allows helicopter pilots to plot locations and flight paths very accurately (Lavoie et al., 2007). Five recent eradication attempts in New Zealand had bait distributed by helicopter but we are awaiting confirmation of success. We did not model the amount of bait used, or number of bait applications, but these operational factors, which are island-specific, may affect the outcome of eradication attempts.

2.3.3. Other mammal species

Populations of mice are significantly affected by the presence of other invasive mammal species (Innes et al., 1995, Choquenot, 2000). There have been a number of reported instances where mice have increased in number once rats have been eradicated or brought to low numbers (Caut et al., 2007). The presence of other mammal species may alter the behaviour of mice and make them less likely to come into contact with bait, leading to eradication failure (Innes et al., 1995). Where possible the presence of other introduced mammal species has been recorded on each island where an eradication was attempted. Twenty-seven eradications were attempted in the presence of other mammal species and 13 of these failed (48%). The mammals present were then divided into three categories – competitors (rat

species); predators (cats (*Felis catus*), stoats (*Mustela erminea*) and weasels (*Mustela nivalis*)) and no direct effect (rabbits (*Oryctolagus cuniculus*) and brushtail possums (*Trichosurus vulpecula*)). Interactions between rats and mice are complex and poorly understood and there is likely to be an element of both competition and predation (Caut et al., 2007). Rabbits and possums have no direct impact on mouse populations but can eat bait and therefore stop mice accessing it. On Motuihe, New Zealand, high rabbit numbers may have reduced the amount of bait available to rats and mice but the eradication was still successful (Veitch, 2002). Dividing the mammal species into different categories had no effect on the model.

2.4. Why do mouse eradications fail?

In order for an eradication to succeed every house mouse on an island must have access to the poison. At the most basic level poor operational implementation during the baiting campaign may lead to areas of the island being missed by bait. A retrospective assessment of operational implementation effectiveness could not be included as a variable here due to its subjective nature. However, one of the main reasons for mouse eradication attempts failing could be gaps in poison coverage. An eradication attempt on St. Paul Island in the sub-Antarctic failed because a malfunction in the bait spreader led to gaps in coverage (Micol and Jouventin, 2002). Similar problems with operational implementation may have occurred in other eradications and not been reported. In these cases, reasons for failure are clear and relatively simple to rectify in subsequent attempts. For some eradications, however, reasons for failure may be more complex and harder to demonstrate and resolve. Recently it has become apparent that even aerial operations using helicopters guided by GPS may leave gaps in poison coverage (Josh Kemp, Department of Conservation, New Zealand, unpublished data). Possibly some aspect of mouse behaviour means that some individuals are not being poisoned. These animals may not come into contact with the bait; they may find bait but not eat it. Some commensal mouse populations show aversion to cereal baits, (Humphries et al., 2000) or they may have a level of toxin resistance allowing them to survive eating the bait (Greaves, 1994). For example, mice on Lord Howe Island, Australia are resistant to warfarin, following ongoing control since 1986 (Billing, 2000). Research in laboratory situations has shown critical differences in spatial and social behaviours between wild and laboratory house mice (Augustsson et al., 2005, Augustsson and Meyerson, 2004) and between different chromosomal strains of wild house mice (Ganem and Searle, 1996). Behavioural differences at the subspecies level may also contribute to some of the failures.

Further discussion of anticoagulant resistance and subspecies behaviour can be found in Chapter 5.

Introduced house mice are physiologically very different from invasive rats, and able to sustain island densities orders of magnitude higher. What seems a straightforward eradication for invasive rats may still remain a challenge for introduced mice (Howald et al. 2007). Despite this, eradicating mice should always be attempted provided sufficient information is gathered prior to eradication to ensure correct operational implementation (i.e., bait delivery method and toxicant amounts).

We were unable to create a model predicting success or failure of a mouse eradication attempt based on operational factors. Some operational factors appear to aid success, even if this is not statistically significant. Some observations from the database are as follows:

- Following an aerial bait operation with hand spreading of poison in at risk areas or use of bait station may increase eradication success.
- Hand spreading bait in conjunction with bait stations may lead to an increased chance of success.
- Multiple toxicants may result in success. Five successful eradication attempts combined brodifacoum with another toxicant. This effect may be related to different toxin susceptibility or the response of individual mice to different bait matrices but this was impossible to distinguish from the data available.
- Bait stations spaced at around 20 m apart had the best chance of success.

2.5. Future research

Data on island house mouse populations are scarce, and only a few islands have been studied intensively (e.g., Marion Island (Avenant and Smith, 2004, Ferreira et al., 2006, van Vuuren and Chown, 2007) and Allports Island (Murphy, 1989)). Basic information about home range sizes, ranging behaviour and densities on islands remain largely unknown, especially during critical winter months where on temperate islands mouse impacts may be greatest (Wanless et al., 2007, Angel et al., 2009). The effect of different habitat types on eradication attempt success is also unknown. Mice living in complex habitats with ample food may have small home ranges (Triggs, 1991) and therefore not come into contact with bait (Rowe et al., 1974). The response of mouse populations to poisoning has not been investigated on islands and nothing is known about how mouse populations re-colonise

areas following a failed eradication attempt. Also, mouse invasion behaviour is unknown. How do mice behave when they invade a new area? Can they be detected and removed?

Genetic samples should always be taken prior to any eradication attempt to allow failed eradications to be distinguished from re-invasions (Abdelkrim et al., 2007). Although eradication failure is never a desirable outcome, much knowledge can still be gained from reflecting on causes of an eradication failure. Recent laboratory work showed that most mice died eight days after first being fed bait, while a few survived for up to 21 days (Morriss, 2007). Trapping on Adele Island in New Zealand eight days after the first aerial poison application failed to detect any mice over 330 trap-nights and 40 tracking-nights across the entire island (unpublished data). Poison resistance on islands where long-term poison campaigns are taking place may also be an issue (Billing, 2000) and could explain why mice are still present despite repeated attempts to eradicate them.

2.6. Eradication database update February 2011

Since I compiled and reviewed a database of mouse eradication attempts on islands in 2007 there have been a number of other eradication attempts around the world. The 2007 database listed six islands as "incomplete" meaning that at the time of writing the eradication hadn't been confirmed as successful or not. Five of these islands had mice successfully eradicated from them but one has since been reinvaded. The remaining island (Ile du Chateau in the sub-Antarctic Kerguelen Group) is still listed as "incomplete", no further information on the island has become available. Adele, Tonga and Fisherman Islands, Abel Tasman, New Zealand are mouse free following two aerial brodifacoum applications in July and August 2007 (Golding, 2010). Rona and Pomona Islands are in Lake Manapouri, Fiordland, New Zealand. These islands also had two aerial brodifacoum applications in July and August 2007 (Shaw and Torr, in press) and the eradication initially appeared to be successful. However, in the winter of 2009 mice were trapped on both islands (Whitehead, 2010). No further mice have been trapped on Rona but unfortunately there is now a mouse population present on Pomona. It is likely that the initial eradication on Pomona was successful and that the current population represent a re-invasion (K. Broome, Department of Conservation, pers. comm.) therefore the operation has been recorded as successful in Appendix 1.

In July and August 2008 two aerial applications of brodifacoum were used to successfully eradicate mice from Coal Island, Fiordland, New Zealand (A. Cox, Department of

Conservation, pers. comm.). At 1100 ha this island now represents the largest island successfully cleared of mice. Montague Island (80 ha), New South Wales, Australia had mice and rabbits eradicated through an aerial brodifacoum operation in 2007 (I. Wilkinson, Department of Environment, Climate Change and Water, New South Wales, pers. comm.). A failed eradication attempt using bait stations and hand spread brodifacoum occurred on Quail Island in Lyttleton Harbour, New Zealand in 2002 (Bowie, 2002). In 2009 a second eradication was attempted using aerial application of brodifacoum. Mice were detected on the island in early 2010 and at the present time it is unclear whether these represent reinvasion or a failed eradication. A range of genetic samples covering pre- and post-eradication island mice, mainland mice and mice from stepping stone islands have been collected and will be used to attempt to distinguish between reinvasion or eradication failure (M. Bowie, Lincoln University, pers. comm.). Mice were eradicated from Saddle Island through trapping and poisoning in 2008, a full description of this eradication can be found in Chapter 3.

Rangitoto (2321 ha) and Motutapu (1560 ha) Islands lie just off Auckland, New Zealand and brushtail possums (*Trichosurus vulpecula*) and brushtailed rock wallabies (*Petrogale penicillata*) were eradicated from the islands in the 1990s (Spurr and Anderson, 2004). In 2009 an ambitious eradication plan was launched aimed at removing all other introduced mammal species (including mice) from the islands (Griffiths, 2008). Three aerial applications of brodifacoum took place between June and August 2009 and these were supplemented with a grid of traps and frequent monitoring to assist in removing all mammals. At the time of writing the eradication has not been confirmed as successful but monitoring suggests that mice and rats may have been eradicated. If this is the case then these islands will represent the largest islands cleared of mice to date.

Two eradication attempts reported from the Seychelles have proven to be problematic. Both Denis and Curieuse Islands were listed in the 2007 database as failed eradications. Further information has been obtained showing that mice were successfully eradicated from Denis in 2003 using hand spread brodifacoum pellets (Parkes, 2008). It wasn't clear from Merton et al. (2002) whether or not mice had been successfully eradicated from Curieuse. Another report from 2002 mentions the presence of rats on the island after the eradication attempt but makes no mention of mice suggesting the eradication was successful (Hill et al., 2002). Haulashore Island, Nelson, New Zealand has been removed from the database as the

eradication was aimed at eradicating rats and not mice therefore it should not be included as a failed mouse eradication attempt.

Overall the updated database records 18 failed eradication attempts on 13 islands and 37 islands where mice have been successfully eradicated changing the eradication failure rate from 38% based on the 2007 database to 33%. If Rangitoto and Motutapu are included in this calculation the failure rate decreases to 32%. Three of the islands where failed eradication attempts occurred have since had successful eradications meaning that 75% of islands that have been the target of mouse eradication attempts are now successfully clear of mice. Eradication methods may also be getting more effective, there has only been one failure out of the 11 attempts (including Rangitoto and Motutapu) that were started in 2007 or later. This increase in the eradication success rate is likely to be largely explainable by the expertise available through the Island Eradication Advisory Group, a group of scientists and managers who audit eradication plans and adapt them to ensure success (Cromarty et al., 2002, Broome, 2009).

Chapter 3. A successful mouse eradication explained by site-specific population data

3.1. Abstract

Invasive rodents have been responsible for the extinction of many species on islands. House mice have proven harder than introduced rat species to eradicate from islands, and research is needed to identify the reasons for this. I studied and successfully eradicated a mouse population on a small (6 ha) island in northern New Zealand to characterise possible behavioural factors influencing eradication failure. Mouse movements were monitored with radio-tracking and trapping to provide guidance on grid-spacing for bait stations, which are a common tool used in rodent eradication and reinvasion monitoring attempts. Mouse densities on the island were estimated during three capture-mark-recapture (CMR) sessions in January, March and May 2008. The island was then trapped almost to extinction in August 2008 and poison was used to target the remaining mice. Removal trapping data combined with WaxTag interference rates provided a final density estimate of mice in winter (August), the period when most eradication attempts occur. Densities on the island ranged from 8.8-19.2 mice/ha, with home ranges varying from 0.15-0.48 ha. Eradication success was monitored intensively using tracking tunnels and WaxTags and was confirmed in December 2008, using a trained rodent monitoring dog. Information gathered during this study is used to make recommendations to improve the success of future mouse eradication attempts.

3.2. Introduction

The house mouse (*Mus musculus*) is a commensal rodent species which has been introduced around the world by humans (Cucchi, 2008, Searle et al., 2009a), making it one of the most widely distributed mammal species in the world (Boursot et al., 1996, Cucchi and Vigne, 2006). House mice spread disease (Langton et al., 2001), consume arable crops (Stenseth et al., 2003), and damage native ecosystems. Some of the worst impacts of mice on native ecosystems are seen on islands where native fauna and flora evolved without mammals (Diamond, 1989, Angel et al., 2009).

Mice have been the target of a number of eradication attempts worldwide but many have failed. Globally, the failure rate for mouse eradication attempts on islands is 38% (Chapter 2, MacKay et al., 2007) compared to only 5% for Norway rats (*Rattus norvegicus*) (Howald et al.,

2007), raising the question: why are mice harder to eradicate than rats? This study was designed to investigate some of the possible behavioural reasons for eradication failure.

New Zealand is an oceanic archipelago of 297 islands (≥ 5 ha) and characterised by a native flora and fauna that evolved in the absence of terrestrial mammals (Clout and Russell, 2006). Mice first arrived in New Zealand in 1824 following a shipwreck and quickly colonised the entire country (Ruscoe and Murphy, 2005). Mice in New Zealand are a mix of three different subspecies, consistent with multiple colonisation events from diverse sources (Searle et al., 2009a). They have a detrimental impact on native flora and fauna in New Zealand (e.g. Newman, 1994, Miller and Miller, 1995, Miller and Webb, 2001, Wilson et al., 2007b) and therefore have been the target of a number of eradication attempts (Howald et al., 2007, MacKay et al., 2007). The impacts of mice on islands may be as severe as those of rats but mice have been relatively understudied (Simberloff, 2009). Sixteen islands in New Zealand have had mice successfully eradicated from them, but 12 eradication attempts have failed (MacKay et al., 2007).

Information about mouse populations on New Zealand islands is scarce in the literature. Few studies have recorded absolute densities of mice (White and King, 2006), either on "mainland" New Zealand or on offshore islands, and little is known about mouse home range sizes or typical nightly movements. With this in mind I chose to study in detail a population of house mice on a small New Zealand island. Through live-trapping and radio-tracking I gathered information about densities and movements throughout the year and also collected demographic information about the population for comparison with other studies. The study culminated in a successful mouse eradication using trapping and poisoning during the Austral winter, when mouse eradication attempts typically take place. This is the first time a free-living population of mice has been studied and eradicated in this way.

3.3. Methods

3.3.1. Study site

This study took place on Saddle (Te Haupa) Island in the Hauraki Gulf, New Zealand (36˚31'S, 174˚47'E; Figure 3.1). The island is long and narrow (650 m by 50-150 m wide; area ~ 6 ha), with steep cliffs around the littoral area and a maximum altitude of 35m above sea level. Norway rats were eradicated from the island by poisoning in 1989 (Howald et al.,

2007) and mice were detected shortly afterwards (Tennyson and Taylor, 1999). This has occurred on a number of islands worldwide and is attributed to rats suppressing the mouse population (Caut et al., 2007, Witmer et al., 2007). Further information about the island's history, fauna and flora can be found in Tennyson and Taylor (1999).

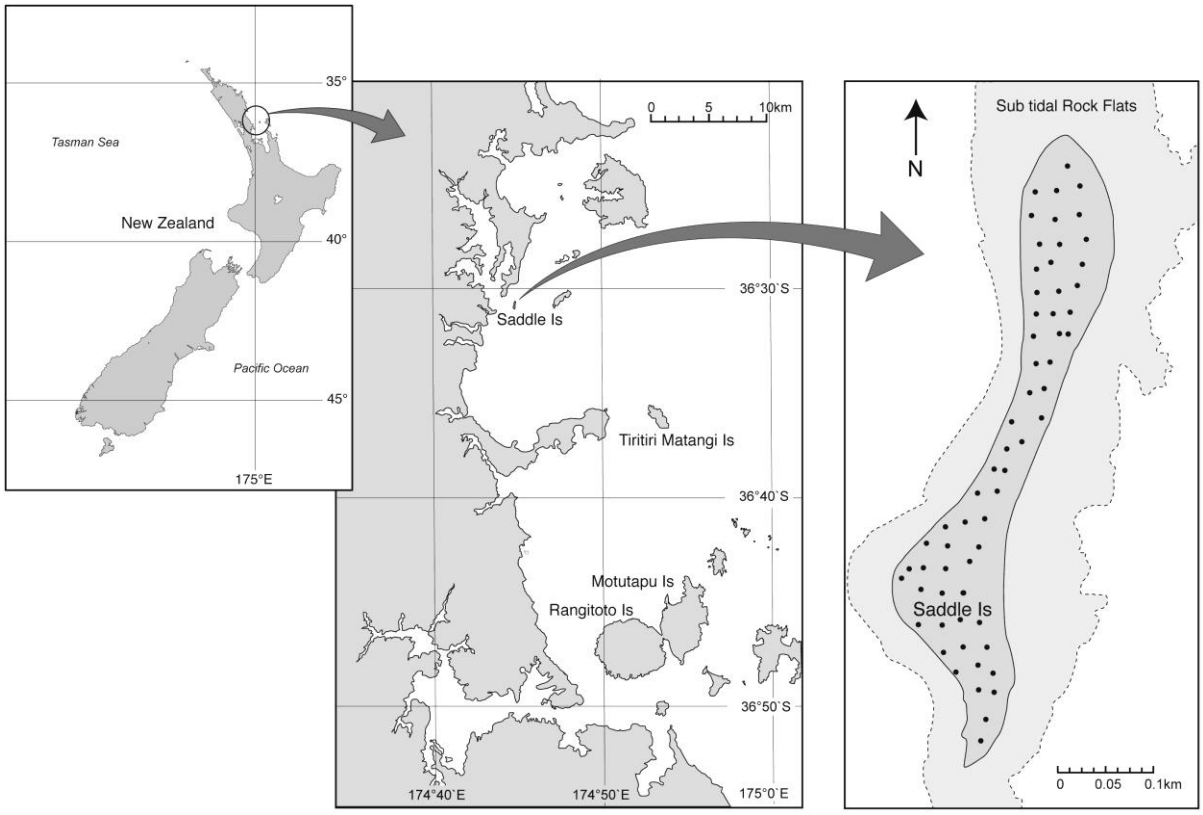


Figure 3.1: Location of Saddle Island and grid layout on the island

Table 3.1 Summary of trapping visits to Saddle Island, New Zealand. *CMR=capture-mark-recapture

Session	Month	Number of trapping nights	Purpose
1	January 2008	5	CMR*
2	March 2008	4	CMR
3	May 2008	4	CMR
4	July 2008	1 + 4 nights telemetry	Radio-tracking
5	August 2008	4	Removal trapping

A grid of 62 stations (Figure 3.1) spaced at 25m intervals was established on the island in October 2007. This grid was used to place traps for live capture trapping, poison bait stations and other devices for monitoring mouse activity, and as an aid for navigation during night work. Trapping took place on the island five times between January and

August 2008 (Table 3.1). A Longworth mouse trap (Chitty and Kempson, 1949) was placed at each station at the beginning of each trapping session. Each trap contained Dacron fibre for bedding with peanut butter on a carrot disk and oats as bait.

3.3.2. Capture-Mark-Recapture protocol

Traps were checked daily during each four or five night Capture-Mark-Recapture (CMR) session. Captured mice were weighed, sexed and had a numbered tag (National Band and Tag Co., Newport, Kentucky, USA) attached to each ear. After tagging, the mice were released. The tag numbers of previously tagged animals were recorded and the presence of torn ears was noted. Lost tags were replaced only when missing from both ears

3.3.3. Radio-tracking

Traps were set to catch mice to fit with radio collars on July 16th 2008 (Table 3.1) and captured animals were processed according to the protocol above. Any mouse weighing over 12 g were returned to the trap and brought to the camp for further processing. From these, four males and two females were selected for radio-tracking according to their capture location to achieve a spread of animals across the whole island. Mice were transferred to a plastic bag and anaesthetised using a piece of cotton wool soaked in isoflurane. As isoflurane is a rapid acting anaesthetic which wears off quickly, mice required two or three doses to fit the transmitter. Transmitters were a single stage whip aerial type (Model BD-2NC, Holohil Systems Ltd., Carp, Ontario, Canada) weighing 0.6 g, fitted by looping the aerial wire around the mouse's neck and crimping the wire to fasten it. Mice were returned to the trap to recover. All mice, including those not selected for radio-tracking, were returned to their capture locations and released.

Radio-tracking began at 1800hrs on July 17th 2008. Mice were tracked by two operators using TR4 receiver (Telonics, Mesa, Arizona, USA) with a Yagi 3-stage folding antenna (Sirtrack Electronics, Havelock North, New Zealand). As most mice spent much of their time near the beach the most efficient method of tracking was for one person to locate the mouse by walking along the beach while the second person confirmed the location from the cliff face above the beach. When the mouse was between the trackers its location was recorded by recording a bearing and estimating the distance from a marked point on the beach. When a mouse ventured into the interior of the island both people tracked the mouse and a distance and bearing were recorded from the nearest trap site. Marked locations were then revisited in August and mapped with a GPS to 9 m accuracy. Four or five fixes at approximately 90-

120 minute intervals during the night and one daytime den site fix were obtained for each mouse over four nights of tracking. Some night fixes were missed due to adverse weather conditions. Daytime den fixes were confirmed using the telemetry receiver without an antenna to maximise accuracy. At night, so as to minimise disturbance to the mice, they were not approached as closely as during the day. Despite this, the mice tracked were seen on a number of occasions during tracking confirming the accuracy of night fixes.

3.3.4. Eradication

3.3.4.1. Removal trapping

Removal trapping was undertaken over 4 nights in August 2008 (Table 3.1). Each captured mouse was euthanized by cervical dislocation. Mice were then weighed, sexed and any ear tags present from previous trapping sessions or ripped ears were recorded. A small piece of tail tip was taken from each animal and preserved in 70% ethanol for future genetic analysis. Taking genetic samples prior to an eradication attempt has been recommended to allow failed eradications to be distinguished from re-invasion should mice be detected at a later date (Abdelkrim et al., 2007, MacKay et al., 2007). A WaxTag (Thomas et al., 1999) baited with peanut butter was placed at each trap station on August 7th at the end of removal trapping and checked and removed on August 19th when poison was applied to the island. The locations of chewed tags, showing where mice remained following removal trapping, were recorded.

3.3.4.2. Poisoning

The anticoagulant poison brodifacoum was applied to the island on August 19th 2008. Poison was applied in two formulations, wax blocks (Pestoff Rodent Blocks, Animal Control Products, Wanganui, New Zealand) in bait stations and approximately 15kg of pellets (Pestoff 20R Pellets) spread around cliffs on the east coast, the north and south points and areas with dense shrub cover or mixed shrub and open grassland on the west coast. Three wax blocks of toxin were wired to a tree under a plastic cover at each trap station to make improvised bait stations designed to shelter the poison blocks but to allow easy access to mice. Wax blocks in bait stations were not replaced and were removed from the island on 26th September 2009 (Table 3.2). Total bait density of wax blocks and pellets was approximately 4 kg/ha.

3.3.4.3. Monitoring

Following poison application the island was intensively monitored (Table 3.2) using 31 tracking tunnels and 31 WaxTags (Thomas et al., 1999) set at trap stations on alternate lines across the island. Two unsecured poison blocks were placed in each tracking tunnel on September 18th 2008 to create 31 further bait stations. These blocks were left in place until December 3rd 2008 when the island was checked by a Department of Conservation rodent detection dog (Occi, handler Miriam Ritchie). Rodent detection dogs are commonly used in New Zealand and around the world to confirm the success or failure of eradication attempts (Gsell et al., 2010).

Table 3.2 Monitoring visits to Saddle Islandfollowing poison application

Date	Event
19/08/08	Poison bait distributed on the island in bait stations and hand spread on cliffs
16/09/08	Poison bait stations checked and location of chewed blocks recorded; WaxTags and tracking tunnels baited with chocolate nut spread deployed on alternate lines across island.
18/09/08	Detection devices checked; wax poison block placed in each tracking tunnel giving 31 more bait stations
26/09/08	Poison bait stations removed from island; WaxTags and tracking tunnels left in place; poison in tracking tunnels left in place
03/12/08	Eradication confirmation with Miriam Ritchie and trained rodent dog Occi; poison removed from tracking tunnels; traps set around small area of possible mouse sign (since considered to be a response to skinks (M. Ritchie pers. comm. 19/01/10)
15/12/08	Traps and devices checked

3.3.5. Analysis

3.3.5.1. Population size estimates

Four population size estimates of mice on the island were calculated using two different methods. Estimates for January, March and May were calculated using closed-capture models in program MARK (White and Burnham, 1999). MARK was chosen so individual covariates such as weight and age could be included in the models. Trapping data from August were analysed using a removal trapping catch effort method augmented by independent WaxTag data for greater precision (Russell et al., 2009a). Analysis in MARK followed Wilson et al. (2007a), with three covariates used to model heterogeneity in the data. Two categorical variables (sex and age) and one continuous (weight) were used as covariates in four models incorporating both behavioural response to trapping and variation in capture probability between trap nights. As it is difficult to reliably classify mice as adults or juveniles based on external characteristics, we classified animals weighing less than 12g as juveniles. This weight was chosen based on the mean weight of non-fecund mice recorded

during a study at nearby Tawharanui Open Sanctuary (Goldwater, 2007). Six covariate combinations (none; sex; weight; age; sex and weight; sex and age) were tested for each model (Appendix 2). The model-averaging procedure in MARK was used to calculate population estimates based on all models except those where parameters were identified as singular or standard errors of estimates were very large or zero. Confidence limits (95%) of the averaged estimate were adjusted to take into account the actual number of mice caught in each trapping session (White et al., 1999). Population estimates were converted into density estimates by dividing the estimate by 6 to provide a density estimate in mice/ha. A survival estimate was calculated using MARK. Data on captures was pooled for all sessions except July to estimate monthly survival, maximum lifetime and mean lifetime.

3.3.5.2. Ranging behaviour

Information on animal home ranges and ranging behaviour was collected through trapping records and radio-tracking. Home ranges were calculated for all individuals that were trapped five or more times and trapping records for the radio-tracked individuals were combined with radio-tracking data to calculate home-range sizes for these animals. Average movements were described from radio-tracking data alone. Movement information was compared to habitat data from the island (unpub. data) to investigate whether different habitat affected movements. Home ranges were estimated using harmonic mean estimation in RANGES VII (Anatrack Ltd., Wareham, Dorset, UK). We chose a 95% core to avoid outlying fixes biasing the range size estimate upwards (Moro and Morris, 2000). RANGES was also used to summarise animal movements and to estimate the area of the island sampled by traps assuming each trap had a "circle of influence" with a radius equivalent to the average male or average female between fix movements. The combined area of the "circle of influence" for each trap was compared to the total island area to obtain an estimate of the proportion of the island sampled by traps.

3.4. Results

3.4.1. Demographics

Between January and August 154 individuals were caught and tagged on the island (Table 3.3). Many unmarked individuals entered the population in March resulting in a low recapture rate which then generally increased throughout the year (Table 3.3). Many mice were only captured in a single session; only six mice were caught in four trapping sessions

and none in all five. There was a relatively high rate of tag loss between trapping sessions and in each session between 4 and 20% of mice captured were recaptures that had lost both their ear tags between sessions (Table 3.3). This meant that each session had to be treated separately in CMR analysis. Three mice caught in January were captured and killed in August indicating that they were at least 8 months old at time of death. Six mice died in traps during trapping sessions prior to August and 51 mice were trapped and killed in August leaving 97 animals of unknown fate. Assuming tag loss was random, a rudimentary survival analysis in MARK gave a monthly survival estimate of 0.6; a maximum lifetime of 26 months and a mean life span of 5 months. Tag loss between sessions will have artificially biased the survival estimate downwards.

Table 3.3: Summary of captures and recaptures on Saddle Island by trapping session. Unidentified recaptures are mice that were captured after losing both ear tags, evidenced by ripped ears.

Month (2008)	New Animals	Recaptures	% recapture (unidentified)	Total
January	43	2	4 (4)	45
March	68	24	35 (19)	92
May	32	31	49 (10)	63
July	2	18	90 (20)	20
August	9	42	82 (20)	51
Total	154	117	43	271

Table 3.4: Demographic information for mice captured on Saddle Island by trapping session

	Female			Male			Overall	
Month	Juvenile	Adult	Total	Juvenile	Adult	Total	% Female	Captures
January	2	19	21	12	12	24	47	45
March	11	25	36	18	38	56	39	92
May	7	15	22	10	31	41	35	63
July	0	3	3	2	15	17	15	20
August	0	14	14	0	37	37	27	51
Total	20	76	96	42	133	175	35	271

Pregnant or lactating (indicated by prominent nipples) female animals were recorded only in January and March. Most animals had reached 12g in weight before the July trapping session which suggests that breeding had ceased at least a month earlier. The number of females caught tended to decrease through the year with females representing only 27% of the animals caught during removal trapping in August (Table 3.4).

3.4.2. Population size

Because models with age covariates consistently ranked higher than models with weight covariates (based on Akaike's information criterion; Burnham and Anderson 2002), weight models were deleted before model averaging. The estimated population size varied between 53 and 112 individuals and was highest in March (Figure 3.2). Confidence intervals for population estimates in January and March were large because of the relatively high number of animals caught only once in these sessions (42% in January, 52% in March). In May this had decreased to only 24%. The MARK models used to calculate population size in each session can be found in Appendix 2. The removal trapping dataset produced an estimate with very narrow confidence intervals. The population estimate (from removal trapping) was 53 animals and 51 were removed from the island in August. Mouse densities varied between 8.8 and 19.2 mice/ha (Table 3.5).

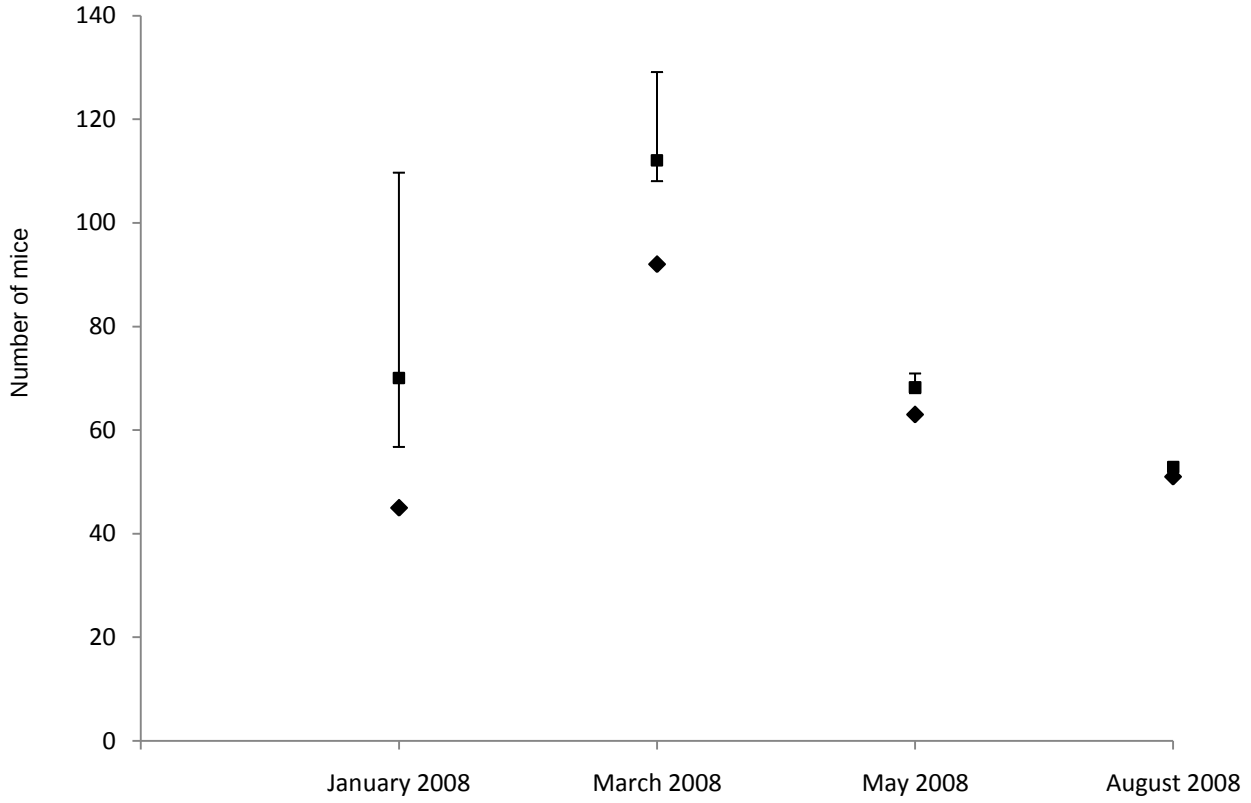


Figure 3.2: Number of mice caught and estimated population size by session. Diamonds represent the number of mice caught and squares the estimated population size with 95% confidence intervals.

3.4.3. Ranging behaviour

A total of 134 radio-tracking fixes were obtained. Average home range size for female mice (n=2) was 0.19 ha and 0.38 ha for males (n=4) (Table 3.6). Radio-tracked mice returned to the

same den site at the end of each tracking night and males M2 and M3 had dens within 1m of each other underneath the same karo (*Pittosporum crassifolium*) bush. Eighteen further home ranges were obtained using trapping information from animals that had been trapped five or more times (range 5-10 locations). Combining trapping and radio-tracking data gives average home range size of 0.28 ha for female mice (n=9) and 0.23 ha for male mice (n=15). The animals with the smallest home ranges and lowest mean distance between fixes were found in areas of the island with denser ground cover; generally with dense shrub cover or a combination of open grass and shrubs.

Table 3.5: Mouse density calculated for each trapping session on Saddle Island. *Density was not calculated in July

Month	Density (range)
January	12.8 mice/ha (8.5-36.2)
March	19.2 mice/ha(16.8-25.8)
May	11.3 mice/ha(10.7-14.3)
July	n/a*
August	8.8 mice/ha (8.7-9.3)

Average movement between fixes for radio-tracked females was 15.8 m and 24.9 m for males. Five out of six tracked mice moved over 25 m at least once during the tracking period so should have come into contact with a bait station. The other animal had a maximum movement between consecutive fixes of 23.5 m (Table 3.6). The maximum distance recorded between fixes was 142 m travelled by a male mouse in just over 2 h. Based on these values, GIS analysis suggested that the trapping grid "circle of influence" covered 78.7% of the island for females and 95.7% for males.

Table 3.6: Summary of movement data obtained in July 2008 for 6 radio-tracked mice (M: males, F: females). Five or six fixes were obtained at 90-120 minutes intervals during the night along with a daily den site fix.

Animal	Number of fixes	First and last capture (2008)	Range area (ha)	Mean (±SE) distance (m) between fixes	Maximum distance between consecutive fixes (m)
F1	26	17/07-04/08	0.23	22.8±3.9	53.0
M2	24	17/07-21/07	0.43	32.8±7.8	142.0
M3	29	08/03-04/08	0.41	26.5±6.1	190.6
M4	29	06/03-04/08	0.48	29.6±5.3	72.3
M5	28	15/05-04/08	0.18	10.8±2.9	50.2
F6	24	08/01-04/08	0.15	8.8±1.7	23.5

3.4.4. Eradication and monitoring

Removal trapping ended on 7th August 2008 and 18 WaxTags were chewed over 13 nights between trapping ending and poison being laid on 19th August. Chewed tags were distributed between lines 1 and 7 at the north of the island and 15 and 23 at the south with

no sign of mouse activity in between. Poison bait consumption from bait stations was minimal with only 13 out of 62 bait stations showing signs of interference when they were checked on 16th September; only two of these showed conclusive signs of interference by mice, the remaining 11 could have been due to invertebrates. The distribution of poison bait eaten from bait stations closely matched that of chewed WaxTags. No further signs of mice were found after this and the eradication was confirmed as successful on December 3rd following a rodent detection dog check (Miriam Ritchie, Department of Conservation, pers. comm.).

3.4.5. Rat incursions

In March 2008 rat sign was detected on the island and DOC 200 traps were deployed. A large male Norway rat was captured on the island on 14th May 2008. No further rat sign was detected until rat-tracked tracking cards were found on 3rd December 2008. However, a rodent detection dog showed no reaction to the cards suggesting that the prints were old. No further evidence of rats has been found on the island.

3.5. Discussion

Mice were successfully eradicated from the island using a combination of removal trapping and poisoning. We are in the uncommon position of having a large amount of data about the mouse population prior to eradication which allows us to address why the eradication was successful.

3.5.1. Demographics

The main predators of mice in New Zealand are stoats (*Mustela erminea*) and cats (*Felis catus*) (Ruscoe and Murphy 2005) both of which are absent from Saddle Island. Mouse population dynamics on the island were therefore influenced largely by food availability and climatic factors. The sex ratio revealed by trapping on the island was biased and 65% of animals captured were male. During removal trapping in August 73% of animals caught were male. Male biased sex ratios have been recorded in other trapping studies in New Zealand (Ruscoe and Murphy, 2005). It has been suggested that sex ratios within mouse populations are generally equal but that trapability differs (Efford et al., 1988). However, our removal estimate of 53 mice on the island at the time of eradication suggests that in August there was a genuine sex bias in the population. This may have been caused by differential mortality due to the physiological demands of breeding. Rodent eradication attempts generally occur

in winter when natural food availability is low and rodent populations are declining (Howald et al., 2007). Mice do not normally breed over winter in New Zealand, except in mast seeding years (Ruscoe and Murphy, 2005), and as there was no evidence of mice breeding on Saddle Island over the winter it is unlikely that young animals were in nests and not exposed to poison bait.

3.5.2. Ranges, movements, and habitat

The average home ranges of animals recorded in this study fall in the middle range of those reported in other New Zealand studies. Average home ranges of mice in forest in a multi-pest situation in the Orongorongo Valley east of Wellington were 0.6 ha (Fitzgerald et al., 1981) whereas mice live-trapped at Tawharanui Open Sanctuary (where they are the only rodent species present) north of Auckland had home range lengths of less than 40 m (Goldwater, 2007). In order for an eradication to be successful every animal on the island must be able to come into contact with poison bait during their nightly movements. Although one female and one male mouse radio-tracked on the island had small core home ranges (0.15 ha and 0.18 ha respectively) and short mean (±SE) distances between fixes (8.8±1.7 m and 10.8±2.9 m), they showed both larger movements outside of their core home range (Table 3.6) and would therefore have come into contact with the poison grid. The effect of habitat on animal movements was quite striking; the average movement between fixes for two individuals from areas of more complex habitat were half that of those from more open areas of the island. A similar effect was noted on the Isle of May in Scotland where mice living in open, "featureless" areas had larger home ranges than those living in varied habitats with more cover available (Triggs, 1991). When mice and ship rats were both present on Browns Island in New Zealand mice were only caught in areas of dense ground cover (Ji et al., 1999).

3.5.2.1. Density

Estimates of mouse population density are rare in the literature (White and King, 2006) and most studies report indices of mouse abundance rather than density (Ruscoe and Murphy, 2005). In the course of this study I calculated mouse density using three sessions of CMR and also with a removal estimate. Removal estimates are notoriously difficult to work with (Russell et al., 2009a) but my combination of trapping data and data from detection devices allowed a precise estimation of animal density to be calculated. Mice on Saddle Island reached a peak density of 19.2 mice/ha in March and a low of 8.8 mice/ha in August. A

similar seasonal pattern of density fluctuation through the year has also been observed on two other New Zealand islands where mice were the only introduced rodent species present. Mouse densities on forested Allports Island in the Marlborough Sounds peaked at 17 mice/ha and fell to a low of 2.2 mice/ha in September (Murphy, 1989). The mouse population on Mana Island near Wellington peaked at 71 mice/ha in March and fell to 5.2 mice/ha in September (Pickard, 1984). The mice on Mana Island were trapped in a grassy shore area suggesting that grassy habitats may support higher mouse densities compared with forests. Comparing populations on different islands in different regions is difficult as local climatic factors may also influence mouse population size.

The distribution of chewed WaxTags and poison eaten at bait stations were similar; this suggests that animals remaining on the island following trapping were detectable by WaxTags and were susceptible to poison. At the time of eradication the population on Saddle Island was small and according to the removal estimate we removed most of the population through trapping. This was confirmed by low poison bait consumed from bait stations.

3.5.3. Lessons learned

This eradication attempt required a lot of effort and this exact method would probably not be used in a non-experimental context. Trapping the whole island for four nights significantly reduced the mouse population and therefore the level of poison application on the island may be considered over-engineering to allow me to absolutely sure that all mice were eradicated. The island was then monitored far more intensively than is usual in order to allow the island to be declared mouse free so the next stage of the research could go ahead. If I was presented with a similar island today I would aim to eradicate the mouse population using a 25 m grid of bait stations with additional poison spread on the cliffs. Instead of the bait station design used in this experiment I would use a 25 m grid of tracking tunnels so the same devices could be used as bait stations and as a monitoring device. Some trapping would be done at the beginning of the eradication to obtain genetic samples. I would expect to replace the bait in all bait stations at least once. Monitoring would initially be done with tracking tunnels then later I would use WaxTags and traps in case there were any mice on the island that were avoiding tracking tunnels. This combination of methods should effectively eradicate mice from a small island up to about 10ha.

3.6. Conclusions and recommendations

MacKay et al. (2007) suggested that mouse eradication failures may be caused by aspects of mouse behaviour. In this instance my eradication method of trapping followed by poisoning was successful and we have information about the population of mice prior to eradication that allowed me to address why the eradication succeeded. Some conclusions I have drawn from this study are:

- Habitat has a large effect on mouse home range size and their movement behaviour (Triggs, 1991). MacKay *et al*. (2007) suggested that mice in complex habitats may have small home ranges and here I present data confirming this prediction. In areas where ground cover was dense average movements between fixes and home range size were less. As part of eradication planning areas of complex habitat should be identified and eradication methods adapted to ensure all mice living in these areas have access to bait.
- Combining removal trapping and detection devices allowed an accurate density estimate to be calculated. It is recommended that genetic samples are collected before an eradication attempt to distinguish between failed eradications and reinvasions (Abdelkrim et al., 2007, MacKay et al., 2007) so if time and resources are available it is worth considering using a grid of snap traps to trap mice thereby providing genetic samples and data to accurately estimate population size.
- Trapping followed by poisoning is an effective method of mouse eradication on a small island. A 25m grid was adequate in this instance and five out of the six mice radio-tracked moved over 25m between fixes at least once during a four night tracking period.

Chapter 4. See how they run: potential mate-finding Allee effect avoidance in house mice

4.1. Abstract

The behaviour of individuals at low population density and the potential Allee effects exhibited in low density populations are important aspects of conservation biology, particularly in the management of invasive species. In order to successfully establish in new areas invaders must overcome the Allee effect. Understanding how invasive species such as the house mouse do this will allow better surveillance systems for mouse-free sanctuaries to be developed. Sixteen mice were experimentally released in pairs (one of each sex) at opposite ends of a newly mouse-free island to investigate mouse behaviour at low densities by simulating a new invasion with each release. Behaviours shown by released animals were compared to those shown by animals living in a moderate-density population on the same island prior to successful mouse eradication. Released animals showed significant increases in ranging behaviour that allowed them to come into contact with each other. Range areas were ten times larger than those in the established population and nightly movements were double. Comparing range overlaps between breeding and non-breeding seasons suggested the drive behind increased ranging was mate finding. The altered behaviour exhibited by released animals may be an adaptation to avoid Allee effects.

4.2. Introduction

The behaviour of individuals in a population is closely linked to population density (Taylor et al., 1978, Butler, 1980). Density dependent behaviour is therefore an important aspect of conservation biology with relevance to the management of the last remnants of rare and endangered species (Stephens and Sutherland, 1999) and the management of invasive alien species (e.g. Russell et al., 2008a). At low population density, individuals may suffer from reduced fitness and reproductive output due to a lack of conspecifics leading to further population decline: a phenomenon known as the Allee effect (Courchamp et al., 2008). Allee effects could therefore have significant implications for management of both endangered and invasive species management (Gascoigne et al., 2009). Low densities of invasive species commonly occur either at the end of an eradication attempt (e.g. Morrison et al., 2007) or during a new invasion (Thorsen, 2000). In both of these contexts it is important for conservation goals to be able to predict how the invasive animals will behave in order to

effectively track and remove them. Invading parasitoid wasps have been shown to not suffer Allee effects during a new invasion (Fauvergue et al., 2007) and other studies have suggested that the Allee effect plays a strong role in invasion biology (Davis et al., 2004, Taylor and Hastings, 2005, Johnson et al., 2006, Boukal and Berec, 2009). It is therefore likely that to successfully establish, a population invaders must overcome the Allee effect. Behavioural adaptations seem a likely avenue for this.

Human activities have transported many species far beyond their native ranges and invasive alien species now constitute one of the gravest threats to native biodiversity (Vitousek et al., 1997, Blackburn et al., 2009). For example, introduced rodent species are found throughout the world (Howald et al., 2007) and have severe negative impacts on ecosystems, particularly those on islands (Courchamp et al., 2003). Eradication of invasive rodents from islands is an important conservation tool (Phillips, 2010), but not all eradication attempts are successful and areas that have been successfully eradicated may be re-invaded (Russell et al., 2010b). Methods therefore need to be developed to detect, monitor and remove rodents at low population densities.

House mice *Mus musculus* are high risk island invaders (Dilks and Towns, 2002) and are frequently recorded as stowaways on ships (Cucchi, 2008) and other vehicles (Pocock et al., 2005, Baker, 1994) making their invasion risk unpredictable. Mice have significant negative impacts on native species and ecosystems (e.g. Newman, 1994, Angel et al., 2009, St Clair, 2011) and have proven to be the most difficult rodent species to eradicate from islands (Chapter 2, MacKay et al., 2007). Understanding how mice behave at low densities is therefore crucial for creating and maintaining rodent-free sanctuaries.

The effective study of individuals in low density populations presents unique challenges in natural situations meaning an experimental approach is necessary (Birke and Arthur, 1983, Gosling, 2001, Russell et al., 2010a). Sixteen mice were experimentally released in pairs (one of each sex) at opposite ends of a newly mouse-free island to investigate mouse behaviour at low densities by simulating a new invasion with each release. The pre-existing population of mice on the island had been studied prior to being eradicated in 2008 (Chapter 3, MacKay et al., in press), so the study was unique in being able to compare the ranging behaviour of released mice with the ranging of mice living at moderate densities in the pre-eradication population. Throughout this chapter the phrase "established population" identifies data gathered from individuals living in the pre-eradication population during 2008.

House mice have proven to be extremely successful colonizers worldwide (Bronson, 1979, Gabriel et al., 2010) so I expected released animals to exhibit behavioural adaptations to mediate mate-finding Allee effects. Accordingly, I hypothesized that released animals would show increased ranging compared to the established population on the island. Both male and female mice were released to investigate behavioural differences between males and females and the interaction between them. Releasing both sexes allowed me to investigate individual motivation for exploration of the island and I hypothesized that if search for companionship was driving exploration the animals would remain close together whereas if they were searching for food or better habitat they would remain apart. A single release of two male mice enabled me to interpret the possible social and breeding context of repeated releases of both sexes of mice. In studies of ranging behaviour in established populations of mice there is either no difference in range size between the sexes (Fitzgerald et al., 1981, Moro and Morris, 2000) or male mice have larger ranges, particularly during the breeding season (Lidicker, 1966, Krebs et al., 1995). Conversely, laboratory studies investigating behavioural sex differences suggest that female rats and mice explore more and move further in novel environments and have higher activity levels than males (Archer, 1975, Farabollini et al., 1987, Augustsson et al., 2005). Therefore female mice released into a novel environment may be expected to explore further and have larger ranges than males. Finally, from an applied perspective, these experimental releases allowed quantification of the effectiveness of detection through tracking tunnels and removal through snap trapping.

4.3. Methods

4.3.1. Study site

This study took place on 6 ha Saddle Island, New Zealand (36˚31'S, 174˚47'E; Figure 4.1). The island measures approximately 650m by 50-150m and is forested, with some small areas of open shrubs and grassland. Norway rats (*Rattus norvegicus*) were eradicated from the island in 1989 and house mice were detected shortly afterwards (Tennyson and Taylor, 1999). Mice were eradicated from the island through trapping and poisoning in 2008 (MacKay et al., in press) and the island had been free of all introduced mammals for three months at the beginning of this study. All trap stations on the island caught mice during the study of the existing population in 2008 suggesting that suitable mouse habitat was present across the whole island. A comprehensive 25 m grid of 62 stations was established on the island in 2007 (Figure 4.1). In 2009 this grid was used to place footprint tracking tunnels

(Brown et al., 1996). Tracking tunnels were placed on the island in September 2008 and remained there for the duration of the research.

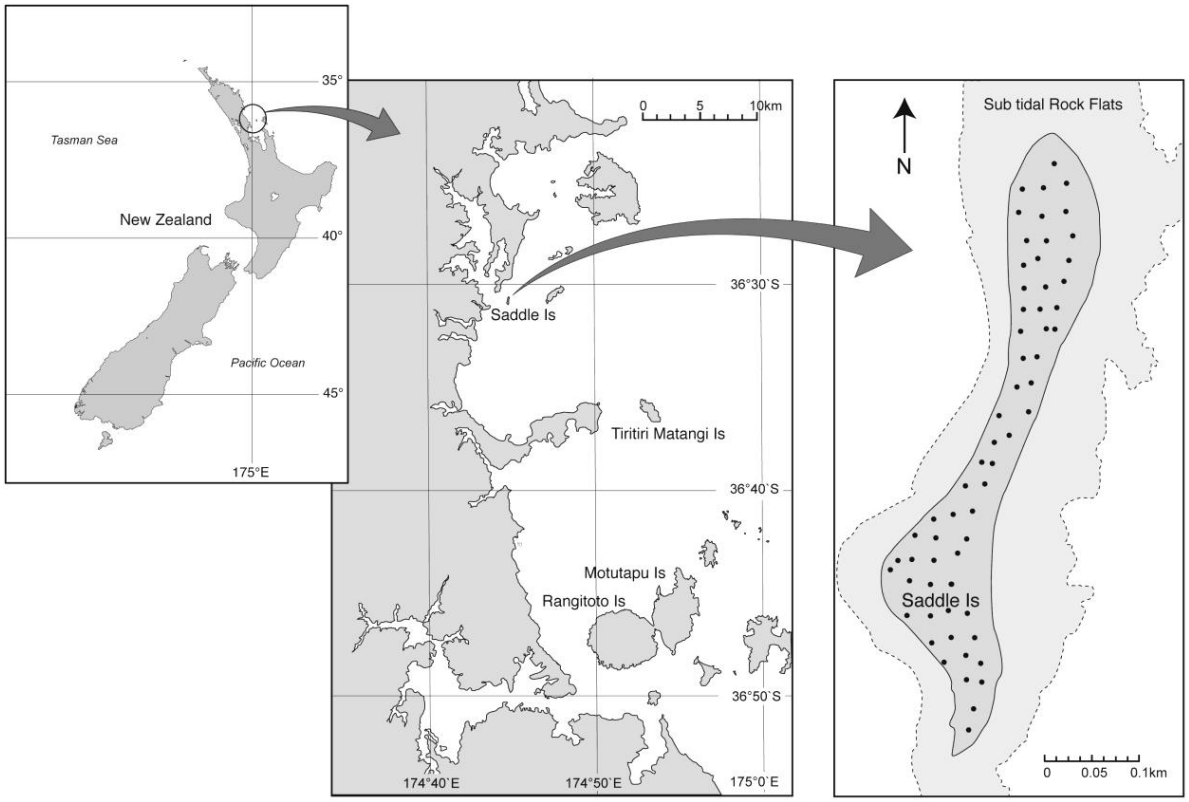


Figure 4.1 Location of Saddle Island and grid layout on the island

4.3.2. Mouse capture and handling

Fifteen house mice (seven females (F) and eight males (M)) were introduced onto the island in eight experimental releases between January and December 2009 (Table 4.1). The first male mouse died under anaesthetic so a lone female mouse was released as a pilot study. Data from this individual are used in comparisons of individual ranging behaviour but not in any animal interaction analyses. Two release sites (North and South, Figure 4.1) were chosen 400 m apart, at opposite ends of the island. Feral mice were captured at Tawharanui Open Sanctuary using Longworth live capture mouse traps (Longworth Scientific Instruments, Abingdon, UK; Chitty and Kempson, 1949) in areas of forest, grassland and dunes. Tawharanui is a mainland peninsula (Figure 4.1); approximately 16km north of Saddle Island) protected by a predator proof fence where rodents were eradicated through aerial brodifacoum applications in 2004 (Goldwater, 2007). Since then mice have been re-detected and are now the only rodent species resident and are found at densities exceeding 150 mice/ha (Goldwater, 2007). Each Longworth trap contained plastic fibre for bedding with peanut butter and oats on a carrot disk as bait. Captured mice were weighed to 0.5g

and sexed by visual inspection. Animals over 12g were marked with a numbered ear tag (National Band and Tag Co., Newport, Kentucky, USA) and transferred to single-sex housing cages (either MB1; North Kent Plastics or 1354G; Eurostandard type IV) in groups of 4-5 individuals. Animals weighing less than 12g were euthanized by cervical dislocation (following University of Auckland Animal Ethics Committee protocol). Captive mice were housed in an outdoor shelter at the University of Auckland and provided food and water *ad libitum*. Mice were kept in captivity for a mean of 15 days (range 11-24 days). The animals were maintained in captivity to ensure that females were not pregnant. The gestation period of mice is 18-21 days (Ruscoe and Murphy, 2005) so after 15 days we were certain that mice were not pregnant and this was confirmed by a veterinarian. The shorter captivity periods occurred over winter when mice do not normally breed in New Zealand (Ruscoe and Murphy, 2005) so pregnancy risk was low.

At the end of the captivity period a single male and female were selected for release based on weight and general appearance of health. The selected individuals were anaesthetised using isofluorane prior to veterinarian-supervised surgery in which a single toe was removed from both the left or right front and rear foot of the animals (two toes removed in total from each animal). Toe-clipping allows individual animals to be identified by footprints left in tracking tunnels (Fitzgerald et al., 1981). Prior to toe-clipping the animals were injected with rimadyl as an analgesic. After surgery the toe-clipped animals were returned to the holding cages to recover and were maintained in captivity for another 0-5 days before being transported to the island. On the day of release animals were again anaesthetised using isofluorane and were fitted with a single-stage whip aerial radio-transmitter (Model BD-2NC, Holohil Systems Ltd., Carp, Ontario, Canada). Transmitters were fitted by looping the aerial wire around the neck of the animal three times and crimping it to fasten it. Transmitters weighed 0.6 g so were equivalent to ≤5% of the animal's body weight for animals weighing ≥12 g. Animals in Releases 4 and 5 were not radio-tracked but were fitted with a dummy transmitter to ensure that all animals underwent the same experimental treatment. Two studies have investigated the effect of transmitter collars on mouse activity. Both used collars that were equivalent to 8-14% of the animal's body weight and both concluded that effects on mouse activity were small or non-existent (Mikesic and Drickamer, 1992, Pouliquen et al., 1990). On this basis, collars weighing ≤5% of the animal's body weight were deemed to not significantly affect movement or behaviour.

Table 4.1: Summary information for all released animals. *Too few tracking records were obtained to calculate a range area. #Tracking tunnels were used during radio-tracking to compare range area revealed by the two methods. ^These mice were left on the island to establish a population.

Release	Sex	Release date	Final capture date	Phase 1 Method and area (ha)	Phase 2 Method and area (ha)	Total range (ha)	Overlap %	Season	Shared TT	Distance apart at death
1	F	27/01/2009	05/02/2009	RT 0.89	TT 3.19	3.83	n/a	Breeding	n/a	n/a
2	F	06/03/2009	17/03/2009	RT 1.02	TT 3.75	4.51	31.26	Breeding	Yes	24m (p=0.0402)
	M	06/03/2009	17/03/2009	RT 0.54	TT 0.73	1.55	91.18			
3	F	04/05/2009	22/06/2009	RT 0.57	TT n/a*	0.72	32.83	Non-breeding	No	0m (p=0.0152)
	M	04/05/2009	22/06/2009[a]	RT 0.8	TT n/a*	2.31	10.23			
4	F	22/07/2009	04/08/2009	TT 0.96	TT 2.26	2.26	32.85	Non-breeding	No	69m (p=0.1978)
	M	22/07/2009	04/08/2009	TT 1.05	TT 1.64	1.91	38.75			
5	M	24/08/2009	05/09/2009	TT 1.04	TT 0.45	2.97	13.54	Non-breeding	No	507m (p=0.0178)
	M	24/08/2009	05/09/2009	TT 2.01	TT 2.28	2.29	6.17			
6	F	29/09/2009	07/10/2009	TT 2.8	TT 1.56	3.9	94.51	Breeding	Yes	18m (p=0.0207)
	M	29/09/2009	27/10/2009	TT 3.3	TT 3.57	3.59	78.14			
7	F	02/11/2009	11/11/2009	RT 0.85 TT 0.30#	TT 3.34	3.99	87.30	Breeding	Yes	18m (p=0.0207)
	M	02/11/2009	18/11/2009	RT 1.15 TT 0.67#	TT 2.63	3.81	89.35			
8	F	08/12/2009	02/07/2010^	RT 0.95	TT3.55	1.04	91.37	Breeding	Yes	33m (p=0.0491)
	M	08/12/2009	30/06/2010^	RT 0.76	TT 1.85	4.09	89.00			

4.3.3. Release and tracking

Animals were released within 8 hours of darkness on the beach just below the forest edge at the release site. M and F mice were released alternately at either the North or the South release site (Figure 4.2). Tracking took place in three phases. Phase 1 consisted of the first 3-5 nights on the island when locations were obtained through radio-tracking (RT) fixes or footprints in tracking tunnels (TT). Phase 2 was the next 4-5 nights when all animals were tracked using tracking tunnels only. The final phase varied in length (from between 1 and 40 days). During this final phase mice were located with TT or RT methods and paired peanut butter baited snap traps (Victor Easy Set Mouse Traps, Woodstream Corporation, Lilitz, Pennsylvania, USA) were placed in tracking tunnels near where they were found to remove them before the next release. There was a mean gap of 25 days (range 5-51 days) between releases to allow scent remaining on the island to dissipate (Gsell et al., 2010). The body of Male 6 was recovered from a trap on 27th October 2010, five days before Release 7 began. The body was highly decomposed suggesting the animal died not long after traps were set on 7th October 2009. Excluding this value the shortest period between body recovery and the subsequent release was 14 days (Table 4.1).

A TR4 receiver (Telonics, Mesa, Arizona, USA) and a Yagi 3-stage folding antenna (Sirtrack Electronics, Havelock North, New Zealand) were used for radio-tracking. Mice were located by tracking to within 2-3 m and a GPS location was recorded. Fixes were obtained once an hour for each animal during the night and a daytime den fix was also recorded.

When animals were tracked with tracking tunnels a peanut butter baited card was placed into each tunnel and left out for between three and five nights. Tracked cards were removed and prints later examined to determine which animal had passed through the tunnel. Fitzgerald et al. (1981) discovered that baiting tracking tunnels lead to increased movements in some of their study animals. In order to test the accuracy of TT tracking compared to RT the tracking tunnels were baited during radio-tracking in Phase 1 of Release 7 and the revealed ranges were examined.

Two male mice (rather than a male and a female) were released in Release 5 to test if animals were found close together for social reasons (independent of sex) or because of mate attraction.

4.3.4. Breeding season

Releases took place throughout 2009 during breeding and non-breeding seasons (Table 4.1). In the established population on Saddle Island pregnant females were trapped in January and March but not in May (MacKay et al., in press) and at Tawharanui small juvenile mice (≤7 g) were caught in September so breeding must have begun earlier that month or in late August (Goldwater, 2007). On Mana Island near Wellington, New Zealand, mouse breeding began in September (Efford et al., 1988). Therefore we defined the non-breeding period as May-August and this covered Releases 3-5 (Table 4.1).

4.3.5. Established population ranging data

Mice in the established population on Saddle Island were trapped on five occasions between January and August 2008. All captured mice were individually marked allowing them to be identified in subsequent trapping sessions. The capture locations of mice that were captured on six or more occasions (six F and eight M) were used to describe ranging behaviour in the established population. All of these mice would have been caught in at least two trapping sessions. In addition, six mice (four M and two F) were radio-tracked for four nights between July 17th and July 21st 2008. Mice were tracked using TR4 receiver (Telonics, Mesa, Arizona, USA) with a Yagi 3-stage folding antenna (Sirtrack Electronics, Havelock North, New Zealand). Most mice spent much of their time near the beach so one person located the animal by walking along the beach while the second person confirmed the location from the cliff face above the beach. When the mouse was between the trackers its location was recorded by recording a bearing and estimating the distance from a marked point on the beach. When a mouse ventured into the interior of the island both people tracked the animal and a similar distance and bearing was recorded from the nearest trap site. Marked locations were then revisited in August and mapped with a GPS. Four or five fixes at approximately 90-120 minute intervals during the night and one daytime den site fix were obtained for each mouse over four nights of tracking. Some night fixes were missed due to adverse weather conditions. Daytime den fixes were confirmed using the telemetry receiver without an antenna to maximise accuracy. At night, so as to minimise disturbance to the animals, they were not approached as closely as during the day. Despite this, the mice tracked were seen on a number of occasions during tracking confirming the accuracy of night fixes (MacKay et al., in press). Most of the radio-tracked mice were also caught before July and four were caught in August. These capture locations were combined with RT data.

4.3.6. Statistical analyses

Minimum Convex Polygons (MCP) were used to describe animal ranges and were created using Ranges VII software (Anatrack Ltd., Wareham, Dorset, UK). MCPs were used because range outliers which would be excluded from analysis by more sophisticated home range estimators (such as kernel density estimators; Worton, 1989) are some of the most interesting points as animals extend their range.

Three MCP measures were calculated for each released animal – Phase 1; Phase 2 and Total Range. One MCP was calculated for each animal in the established population. MCP ranges were clipped using ArcGIS version 9.3 (ESRI, Redlands, CA, USA) to only include terrestrial habitat upon the island. Phase 1 and Phase 2 ranges for released animals were compared using a Mann-Whitney test to investigate whether or not mice increased their range size as they spent longer on the island.

Area of range overlap between each released pair of mice was calculated and presented as a percentage of each individual's total range. Randomization tests were used to determine if inter-trap distances for pairs of animals released were significantly different from those expected by chance alone. Random distances on the island were created by selecting two random trap sites and calculating the distance between them. This was repeated 10,000 times to create a null distribution of random distances across the island. The inter-trap distances for pairs of released animals were then compared to this null distribution using one-tailed tests when the pair was expected to be trapped closer together (M-F releases - sexual affinity) or further apart (M-M release - sexual aversion) respectively. Significance was assigned if the observed inter-trap distance was in the extreme 5% quartile. A two-way ANOVA was used to investigate differences in mean range between males and females in the breeding and non-breeding seasons and a Mann-Whitney U-test was used to compare range overlap in breeding and non-breeding seasons. In the established population ranges were calculated from trapping and radio-tracking data. A one-way ANOVA was used to compare the mean ranges shown by each tracking method.

Mean total range area of released males and females was compared to the mean range area of males and females in the established population using a two-way ANOVA. Between-fix movements were calculated for the six mice radio-tracked in the established population and eleven released mice that were radio-tracked during Phase 1 or Phase 3 (Table 1). Total distance moved during each tracking night was calculated and then averaged across the number of nights the animal was tracked for. Movements of established and released males and females were compared using a two-way independent ANOVA.

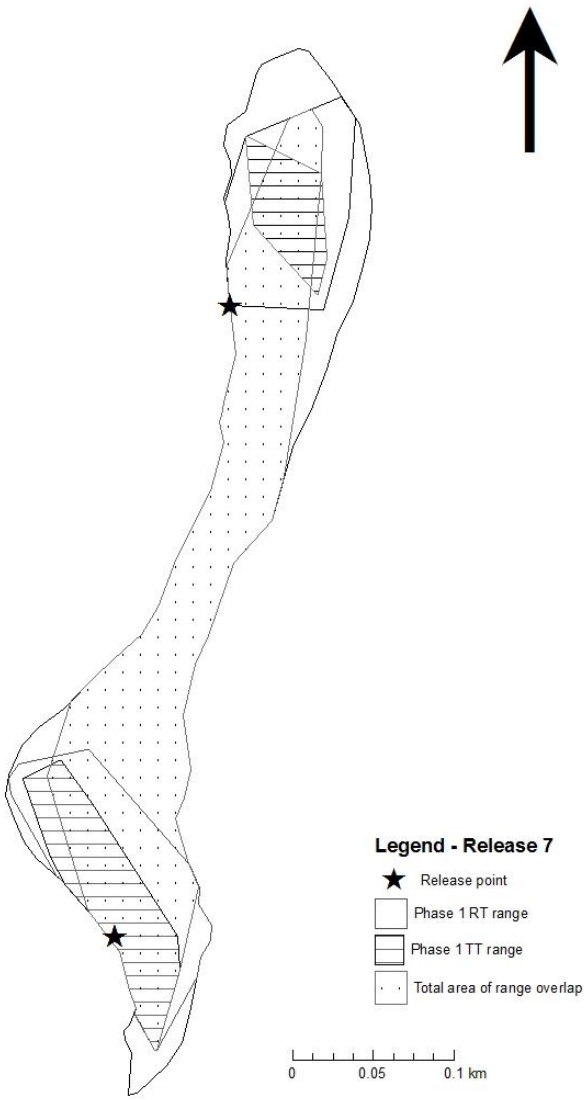


Figure 4.2 Release 7 tracking data showing Phase 1 TT and RT revealed ranges and the total area of range overlap between the male and female mouse released. The male was released at the south of the island and the female at the north.

4.4. Results

4.4.1. Movements

A total of 735 mouse locations were recorded during mouse releases comprising 291 RT fixes, 402 TT fixes and 42 den sites. RT revealed a larger range than TT during Phase 1 of Release 7 (RT mean (±SE) 1.00±0.15 ha; TT mean 0.48±0.18 ha) but all TT locations were within the RT range (Figure 4.2). This suggests that the mice were using tracking tunnels within their core range and that tracking methods are complementary, although TT ranges are likely underestimates of the true range covered by the mice.

Released animals showed a significant increase of 47% in range size (M and F combined, MANN WHITNEY, U=44.0, P=0.01) between Phases 1 (mean range 1.25±0.21 ha) and 2 (mean range 2.37±0.30 ha). Tracking methods were combined for this analysis. Phase 1 animals had a mean of 23.7 fixes per mouse and Phase 2 animals 16.1 fixes per mouse.

4.4.2. Range overlap

All released mice except one (M3) were detected using tracking tunnels. In four out of seven releases footprints of both animals were found in the same tracking tunnel (Table 4.1). These releases all took place during the breeding season. All simultaneously released mice showed some level of range overlap from 6-95% of each individual's total range. The mean overlap for M-F releases was 63.9% (n=5, SD=31.6) and for the M-M release it was 9.9% (n=2, SD=5.2). All released mice that were targeted with snap traps were trapped and their bodies recovered. Time between trap set and body recovery ranged from 1 to 39 days (Table 4.1).

4.4.3. Randomisation test

Results from the randomisation test showed that four out of the five M-F pairs were trapped significantly closer together than expected by chance alone, and the M-M pair were trapped significantly further apart than would have been expected by chance alone (Table 4.1). The final M-F pair of mice released (Release 8) were left on the island to establish a population (Helen Nathan, University of Auckland, unpublished data). These mice remained alive on the island for over 200 days before last being caught 33m apart, significantly closer than would have been expected by chance alone (Table 4.1). Animals released in the breeding season (September-April) had significantly larger ranges (ANOVA, $F_{(2,11)}$=16.902, P=0.002) than those in the non-breeding season (May-August) with no significant difference between the sexes (ANOVA, $F_{(2,11)}$=0.026, P=0.849). Mean range for breeding animals was 3.58±0.29 ha and mean range for non-breeding animals was 1.76±0.29 ha. Median range overlap for M-F releases was 89.2% (n=8, SD=20.6) in the non-breeding season and 32.8% (n=4, SD=12.6) in the breeding season: a significant difference (MANN-WHITNEY U=3.00, P=0.027).

4.4.4. Released/Established comparison

There was no significant difference between range sizes obtained through trapping or through radio-tracking and trapping in the established population (ANOVA, $F_{(1,10)}$=4.402, P=0.062) so ranges from the two methods were combined for analysis. Released animals covered over 10 times more area on the island than animals in the established population (Released mean range 2.85±0.31 ha; established mean range 0.26±0.03 ha) and there was a

significant difference between these ranges (ANOVA, $F_{(1,25)}$=157, P<0.001) but no significant difference between the sexes in either group (ANOVA, $F_{(1,25)}$=0.460, P=0.504). These figures include all location information from RT, TT and trapping methods (Figure 4.3).

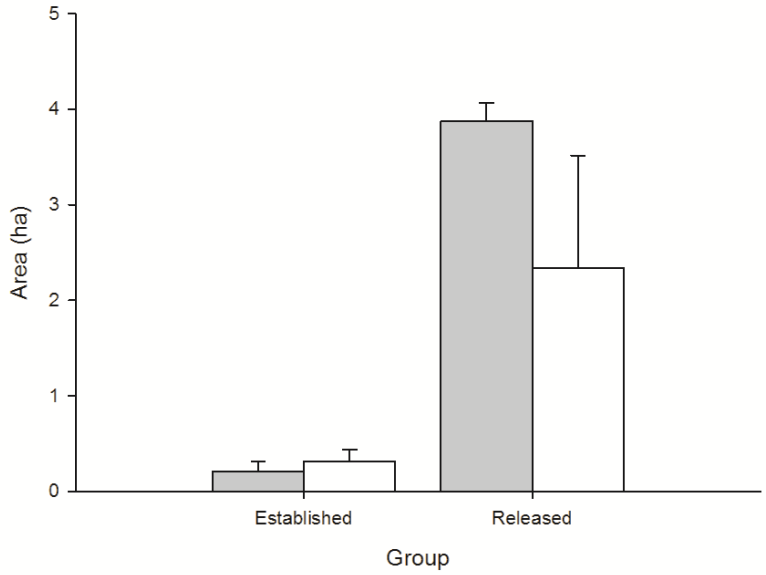


Figure 4.3 Mean area covered during tracking by males (open bars) and females (shaded bars) in the established population and released animals

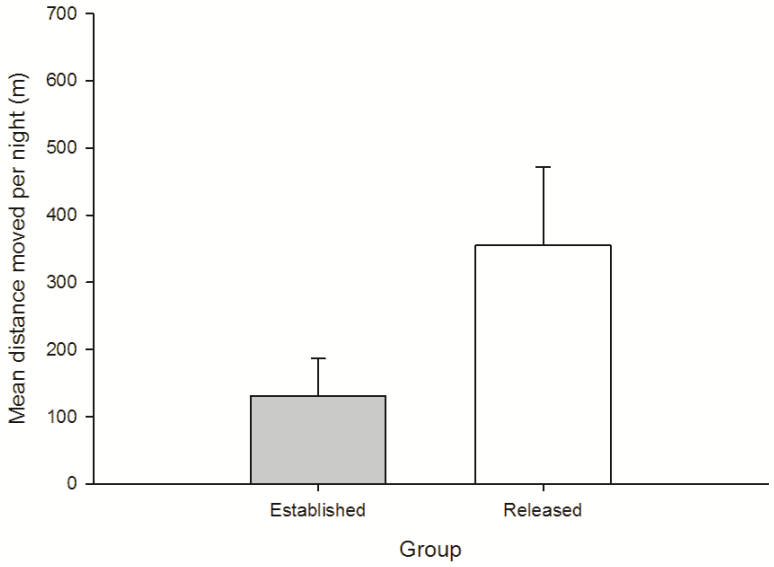


Figure 4.4: Mean distance moved per night by radio-tracked animals. Males and females were combined due to low sample size for females in the established population.

Average nightly movements for radio-tracked animals showed significant differences between the groups (ANOVA, $F_{(1,11)}$=11.926, P=0.005) but not the sexes (ANOVA, $F_{(1,11)}$=0.191, P=0.670; Figure 4.4). Average nightly movements for released animals were over double those of the established population (established mean 130.4±55 m, released

mean 288.6±96 m). All eleven radio-tracked released mice were recorded moving over 100m between fixes on at least one occasion. Only one out of six mice in the established population was recorded moving over 100m between fixes and only on one occasion.

4.5. Discussion

This is the first experimental investigation into the invasion behaviour of house mice on a rodent-free island. Uniquely, detailed information about individual mouse behaviour from the pre-eradication population on the same island was available for ecological comparisons. One of the main reasons house mice are such successful colonisers worldwide is their extensive behavioural flexibility (Berry, 1981). Mice are successful in both commensal and non-commensal habitats and are able to adapt their diet, social structure and behaviour to suit the conditions in the area where they live (Butler, 1980, Singleton and Krebs, 2007). This extensive level of flexibility makes it difficult to compare mouse ranging behaviour between studies, since ranging is dependent on habitat, the food availability within that habitat and population density (McNab, 1963, Lidicker, 1966, Taylor et al., 1978, Butler, 1980). This study removed landscape-level habitat variability thus allowing the investigation of the effect of low population density on mouse ranging behaviour and highlighting some of the reasons for the species' success as an invader.

In addition to knowing about the established population on Saddle Island there was also detailed information available about mouse behaviour in the source population at Tawharanui. Mouse densities recorded at Tawharanui in 2007 are the highest yet recorded in New Zealand (over 150 mice/ha) and mean home range lengths were under 10m (Goldwater, 2007). This allows me to be certain that the behavioural changes observed during mouse releases were a response to the novel environment rather than a relic of behaviour in the source population.

The differences in behaviour between mice in the established population and mice released onto the island are dramatic. Released animals doubled their nightly movements and showed a tenfold increase in range size. All released animals behaved in a similar way with larger nightly movements and overall ranges than animals in the previously established Saddle Island population or in the Tawharanui source population. It is probable that if the animals were released onto a larger island they would have ranged even further, as the largest range recorded in the literature is 8 ha (Chambers et al., 2000). These changes in ranging behaviour allowed the released animals to come into contact with each other, which would not have occurred if they had maintained the ranging behaviour exhibited in their

source population or settled into ranging behaviour patterns shown in the previous established population. It is unlikely that the animals were ranging in search of food as it can be assumed that the range sizes shown in the established population were sufficiently large for the animals to find adequate food. The motivation for increased exploration is therefore likely to be mate finding.

Evidence to support the mate finding hypothesis comes from interactions between the released pairs of animals. All pairs showed some level of range overlap, but the overlap between M-F pairs was larger than that shown by the M-M pair. Five out of six M-F pairs released on the island were trapped significantly closer together than would be expected by chance and the single M-M pair released were trapped significantly further away. Breeding season also had a significant effect on animal interactions. Range overlap between M-F pairs was significantly smaller in the non-breeding season and the M-F pair that were trapped furthest apart were released during the non-breeding season. The pairs of mice released during the breeding season were detected using the same tracking tunnel, although tunnels were operated for three to five nights so the tunnel visits may not have occurred at the same time. Additionally, there were no significant differences in ranging behaviour between male and female mice, contrary to what may have been expected based on laboratory studies of exploration (Archer, 1975, Farabollini et al., 1987, Augustsson et al., 2005). The overall picture these interactions paint is that both males and females respond to low population density by exploring widely searching for other animals. What the animals do when they find each other depends on the season – during the breeding season M-F pairs appeared to stay close together whereas during the non-breeding season they stayed further apart. Mice are therefore able to avoid mate-finding Allee effects by changing their ranging behaviour to allow them to find compatriots. This is likely to be a major factor in their success as an invasive species.

Areas that are free of mice and therefore at risk of (re)invasion are also at risk of invasion by functionally similar rat species. Cost-effective surveillance systems should therefore be designed to detect invasions by all rodent species. The invasion behaviour of ship and Norway rats (*Rattus rattus* and *R. norvegicus*) has already been studied (Russell et al., 2008a, Russell et al., 2010a, Innes et al., in press) and together with mice these are the species most likely to invade islands (Russell and Clout, 2005). Comparing the reported behaviour of ship and Norway rats with the results of this study shows some common patterns in the way rodents respond to a change from high density to low density situations. Norway rats were released onto three islands in New Zealand to test island biosecurity systems (Russell et al.,

2008a). The authors concluded that permanent surveillance systems were more effective than contingency responses and these systems should consist of an array of tested devices to counteract rat neophobia. More detailed analysis of the movements of Norway rats tracked on one of the islands showed that the animals ranged far further than animals in established populations and rapidly explored the whole 9.5 ha island over 3 weeks (Russell et al., 2010a). Ship rats were also released into a pest-free enclosure in New Zealand. These rats stayed relatively close to the release site before making large movements into the enclosure. These movements were longer than those shown by animals in the source population outside the fence (Innes et al., in press). Released mice on Saddle Island behaved in a similar way to ship rats after release – the area covered in Phase 2 was larger than Phase 1 so the animals increased their exploration after 3-4 nights on the island. All released rodents showed long range movements, which makes it possible to use a relatively sparse grid of devices for standard island surveillance. Approximately one station per hectare is adequate to detect invading rats and mice. A selection of device types should be used to avoid the possibility of individual invaders avoiding one type, e.g. from prior exposure. Permanently installed devices that can be used for both rodent detection and rodent removal are preferable for surveillance to avoid any neophobic response (Clapperton, 2006). Tracking tunnels are ideal for this as they can also be used as poison bait stations or trap covers. Tracking tunnels are rapidly colonised by invertebrates and become part of the island habitat to the extent that mice have been recorded running through them when there was no bait in the tunnel (pers. obs.). A final point concerns the use of "Judas" or "Delilah" animals, a technique where a radio-collared animal is released to assist in the detection of other individuals of the same species (e.g. McIlroy and Gifford, 1997). It has been suggested that this technique may have some use in attempts to remove rodent invaders (Russell et al., 2008b). On the second night of the pilot study release of a single female, this mouse was observed sitting on top of the dead male's cage at the camping area. The presence of two people less than 10 m away did not deter her from investigating the cage. This suggests that the use of radio-collared or caged mice may be worth investigating as an effective method of attracting and removing invading mice.

In summary, house mice released onto a mouse-free island show changes in ranging behaviour that appear to be adaptations to counter mate-finding Allee effects. Behavioural flexibility like this is likely to be a major reason for the success of house mice as a species with an introduced range spanning the globe. However, with correct management in place, changes in ranging behaviour may work against mice arriving in a mouse-free area by making them more detectable and more likely to come into contact with control devices.

Chapter 5. Phylogeography of New Zealand house mice in relation to control

5.1. Abstract

House mice were first introduced to New Zealand accidentally in 1824 and phylogeographic methods have shown that there have been many subsequent introductions from a diverse range of sources. Mice have significant negative impacts on native ecosystems in New Zealand and worldwide making their eradication a desirable conservation outcome yet they have proven to be the hardest rodent species to eradicate from islands for reasons which are unclear. This pilot study used a phylogeographic approach was used to identify the source population and subspecies of mice obtained from island and mainland sites in New Zealand with different mouse control regimes with the aim of identifying links between mtDNA D-loop haplotype and control outcome. D-loop haplotypes can be used to identify mouse subspecies and to make inferences about the original source population. Anticoagulant resistance is widespread and has a genetic basis therefore if New Zealand mice were sourced from populations showing resistance it may be present in New Zealand and affect eradication outcome. Two mtDNA D-loop haplotypes that had not previously been recorded in New Zealand were identified linking New Zealand mice to populations in Portugal and Iran. Control outcome results were inconclusive but several promising avenues for further research were identified.

5.2. Introduction

New Zealand was the last major land mass to be colonised by humans, around 730 years before the present day (Wilmshurst et al., 2008). Prior to the arrival of humans the only extant mammals present in New Zealand were 12 species of bats and pinnipeds (King, 2005) but now over 30 species of mammals have become established in New Zealand following both deliberate and accidental transport (King, 2005). With the exception of kiore (Pacific rat, *Rattus exulans*) and kuri (Polynesian domestic dog, *Canis familiaris*), which were transported by the ancestors of the Māori people (Craig et al., 2000), all these mammals arrived with European colonists within the last 250 years (King, 2005). The only evidence of non-volant terrestrial mammals in New Zealand prior to human-mediated introductions is a small number of fossilised bone fragments from an unidentified mouse-sized primitive mammal estimated to have lived 19-16 million years ago (Worthy et al., 2006).

The relatively recent arrival of invasive mammal species to New Zealand means it may be feasible to identify their original source populations through genetic analysis. As well as providing interesting historical information about human migration patterns (Matisoo-Smith and Robins, 2004, Matisoo-Smith et al., 1998) and past links between New Zealand and other countries (Wallis and Trewick, 2009), identifying potential source populations may provide information about how better to control the invasive species (Sakai et al., 2001). For example, the brush-tailed possum (*Trichosurus vulpecula*) is a major pest species in New Zealand and it is controlled in large areas using 1080 (sodium monofluoroacetate) poison (Clout and Ericksen, 2000). The possums released in New Zealand came from Eastern Australia and Tasmania (Cowan, 2005); if they had been sourced from Western Australia it would be likely that 1080 would not be effective as a control. Plants in Western Australia produce 1080 naturally (Mead et al., 1985) and possums from this region show reduced susceptibility to 1080 (King et al., 1978). Similar, as yet unknown, traits may exist in other introduced mammal populations in New Zealand.

Phylogeography is a discipline whereby genetic variation shown in populations is used to draw inferences about the original source of a population and its relationship with other populations of the same species (Avise, 2000, Bloomquist et al., 2010). The D-loop is a region of the mitochondrial DNA that has been extensively studied in mice (e.g. Prager et al., 1998, Prager et al., 1996, Gündüz et al., 2000) and has been used in a series of recent phylogeographic studies (e.g. van Vuuren and Chown, 2007, Jones et al., 2010). This marker is useful due to a high substitution rate in comparison with other mtDNA regions (Bachmann, 2001, Ballard and Rand, 2005). Mitochondrial DNA exhibits a general lack of recombination, fast mutation rate and maternal inheritance (Birky-Jr et al., 1989, Brown et al., 1993, Bachmann, 2001) which contributes to the potential use of mtDNA to identify source populations.

There are three main subspecies of house mouse that originated in different regions: *Mus musculus musculus* (Eastern Europe); *M. m. domesticus* (Western Europe) and *M. m. castaneus* (South-East Asia) (Lundrigan et al., 2002). Throughout the rest of this chapter the subspecies will be referred to by their subspecific classification alone, i.e. *musculus*, *domesticus* and *castaneus*. The species likely originated in India (Boursot et al., 1993) and followed different colonisation paths across Eurasia resulting in the three subspecies known today (Boursot et al., 1993, Din et al., 1996). House mice (hereafter mice) are highly commensal (Boursot et al., 1993) and this close association with humans lead to the species being spread throughout the world through long-distance colonisation events (Bronson, 1979, Pocock et al., 2005, Gabriel

et al., 2010). The mouse was first recorded in New Zealand following the wreck of an Australian ship in the far south of the country in 1824 (McNab, 1907) and by the beginning of the 20th Century they were found across the whole country (Ruscoe and Murphy, 2005). A recent phylogeographic analysis of mice in New Zealand revealed that the mouse population in the country is made up of all three subspecies, with *domesticus* as the most prevalent (Searle et al., 2009a). The mtDNA haplotypes present in New Zealand are very diverse and indicate multiple colonisations from different areas of the world (Searle et al., 2009a). Different subspecies of mice in New Zealand have also hybridised and individuals with mtDNA of one subspecies often have nuclear DNA of another (Searle et al., 2009a).

The samples processed by the prior phylogeographic study (Searle et al., 2009a) were collected on both the NZ mainland and outlying islands. Mouse populations on islands are known to cause significant damage to native species (Newman, 1994, Angel et al., 2009, St Clair, 2011) and eradicating populations from islands is an important conservation tool (Howald et al., 2007). However, mice have proven to be the hardest rodent species to eradicate from islands (Chapter 2, MacKay et al., 2007) and it is possible that different subspecies respond in different ways to control attempts. Behavioural studies in laboratories have found variation in the way laboratory mice bred from different subspecies respond to identical situations (Le Roy et al., 1998, Koide et al., 2000, Fernandes et al., 2004). Also, in behavioural trials of social interactions in wild mice, *musculus* individuals were more aggressive than *domesticus* individuals (Munclinger and Frynta, 2000), indicating that subspecies differences are not restricted to the laboratory setting. These behavioural differences may possibly mean that one subspecies is better able to survive eradication attempts than the others. In addition, there may be links between mtDNA D-loop haplotype and response to eradication. Although the D-loop is a non-coding region and is unlikely to have a direct effect on behaviour (Sbisà et al., 1997) mice from different mtDNA lineages, and therefore different source populations, may have other genetic traits that lead them to respond to control in different ways.

A key area of concern regarding the genetic background of mice is anticoagulant resistance (MacKay et al., 2007). Mice are able to detect 1080 in baits (O'Connor et al., 2005) and demonstrate intermittent feeding behaviour (regular visits to a food source where a small amount is consumed, Lund, 1988) which increases the risk of bait shyness being developed if a sub-lethal dose of toxin is ingested (Hickling et al., 1999, Howald et al., 2007), so anticoagulant toxins are normally used for control (Courchamp et al., 2003). The effects of anticoagulant toxins occur in such a way that mice do not associate them with the bait they

have ingested meaning bait shyness does not develop (Timm, 1994). Mice resistant to warfarin (a first generation anticoagulant) were first reported in Europe the late 1950s (Pelz et al., 2005) and warfarin-resistant populations of mice are now found throughout the world (Billing, 2000, Pelz et al., 2005). Second generation anticoagulants such as brodifacoum act rapidly and are now used in place of warfarin in most eradication and control programmes (Howald et al., 2007, MacKay et al., 2007), and early trials of brodifacoum as a toxin showed that warfarin-resistant mice were susceptible (Redfern et al., 1976). However, there have been reports of mice with resistance to second-generation anticoagulants such as bromodialone (Guidobono et al., 2010) and brodifacoum (Greaves, 1994). This is not as widespread as warfarin resistance (Greaves, 1994) but reported incidences of resistance to second-generation anticoagulant toxins are increasing (Murphy et al., 2003). There is a genetic basis to anticoagulant resistance (Pelz et al., 2005, Rost et al., 2009), so if New Zealand mice are descended from populations in areas where resistance is present this trait may be present in the New Zealand population.

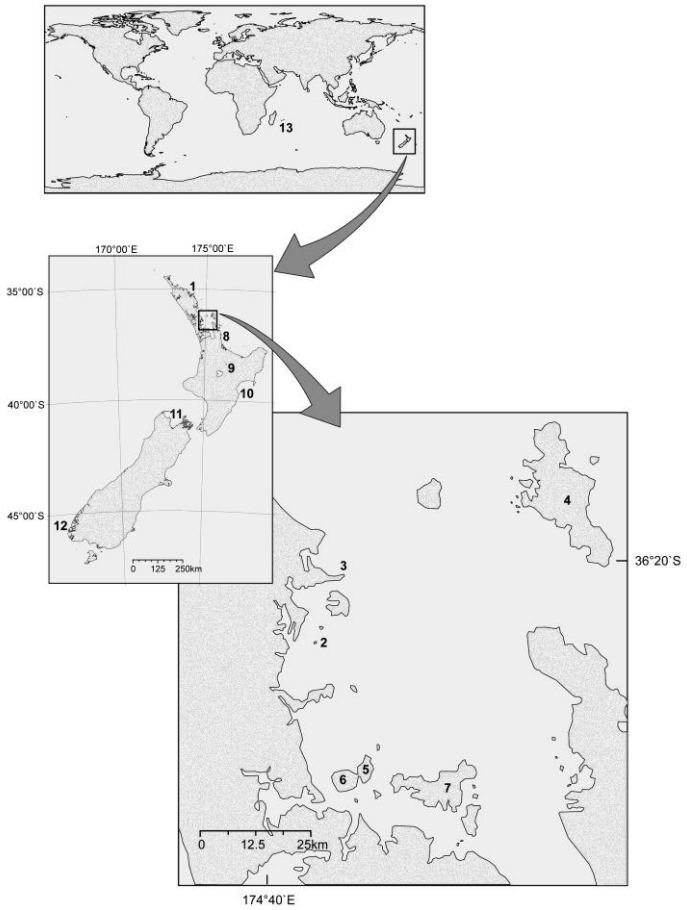


Figure 5.1: Mouse sampling locations. Numbers refer to map references in Table 5.1

Table 5.1: House mouse collection locations and control regime summaries. 'Map ref.' refers to the location numbers in Figure 5.1. All locations except number 13 are in New Zealand

Map ref.	Location	Island/Mainland	Control regime	Sample source
1	Bay of Islands Mainland	Mainland	No control	Supplied by J. Russell, University of Auckland
2	Saddle Island, Mahurangi	Island	Samples obtained prior to successful eradication	Collected for this research
3	Tawharanui, Rodney	Mainland	Failed eradication at fenced site, ongoing ground based poisoning	Collected for this research
4	Great Barrier Island, Auckland	Island	No control	Supplied by J. Russell, University of Auckland
5	Motutapu Island, Auckland	Island	Samples obtained prior to eradication attempt, outcome not yet confirmed	Supplied by R. Griffiths, Department of Conservation
6	Rangitoto Island, Auckland	Island	Samples obtained prior to eradication attempt, outcome not yet confirmed	Supplied by R. Griffiths, Department of Conservation
7	Waiheke Island, Auckland	Island	No control	Supplied by J. Russell, University of Auckland
8	Hauturu Island, Whangamata	Island	Failed eradication	Supplied by J. Russell, University of Auckland
9	Mokoia Island, Lake Rotorua	Island	Single invading mice trapped seven years after successful eradication	Supplied by T. Sachtleben, Department of Conservation
10	Cape Kidnappers, Hawkes Bay	Mainland	Ongoing ground based poisoning at fenced site designed to keep rats at low numbers, no targeted mouse control	Collected for this research by T. Ward-Smith, Cape Sanctuary
11	Adele Island, Abel Tasman	Island	Samples obtained prior to successful eradication	Collected for this research
12	Resolution Island, Fiordland	Island	No control	Supplied by A. Veale, University of Auckland
13	Reunion Island, Indian Ocean	Mainland	No control	Supplied by J. Russell, University of Auckland

This chapter describes a pilot study designed to analyse mtDNA D-loop sequences of mice (following the methods of Searle et al., 2009b) collected from a range of mainland and island sites in New Zealand with different conservation control regimes (Table 5.1). The aim was to identify the D-loop haplotypes, indicating subspecies and possible source population, present in the areas sampled and to investigate possible links between D-loop haplotype and either control outcome (eradication success or failure, if known) or areas of the world where anticoagulant resistance has been reported. If control outcome is related to D-loop haplotype, I would expect to find distinct haplotypes at the sites where eradications have failed. Conversely there may be no link; in which case haplotype distribution will have no relationship to the control status of an area.

5.3. Methods

5.3.1. Sample Collection

Mice were captured in snap traps and a small section of tail tip or other tissue was taken and preserved in 70% ethanol prior to analysis. Samples were supplied by colleagues or captured specifically for this research (Table 5.1).In order to maximise the range of locations processed, a maximum of three individuals were sequenced from each site. Sampling locations are shown in Figure 1. Samples provided by J. Russell (Table 5.1) were by-catch from his work on rats (*Rattus norvegicus* and *R. rattus*) in New Zealand and Reunion Island (Indian Ocean). The Reunion samples were included in this study as a geographical out group. Other samples were collected for this research or requested from colleagues working in relevant areas (Table 5.1).

5.3.1.1. Sampling locations

Eight of the thirteen sites sampled had been the target of mouse control (Table 5.1). Four sites (map refs 2, 5, 6 and 11, Figure 5.1) were sampled prior to successful a mouse eradication attempt therefore the haplotype present in these sites can be considered susceptible to control. Two sites were the target of failed eradication attempts. Mice at both Hauturu Island (map ref. 8) and Tawharanui (map ref. 3) were re-detected following poisoning. It is unclear whether the Hauturu mouse population represents a failed eradication or a reinvasion (Glassey, 2006). Tawharanui is a mainland peninsula protected by a predator-proof fence; eradication there probably failed due to rank grass sheltering mice from poison (Goldwater, 2007) but there could also be a genetic background to the failure. A single mouse was trapped on mouse-free Mokoia Island (map ref. 9) as part of

biosecurity monitoring, behavioural differences between subspecies could result in differential invasion likelihood. Cape Kidnappers (map ref. 10) is another mainland fenced site where mice are being controlled as a side-effect of rat control; the control regime is not designed to remove mice (Tamsin Ward-Smith, Cape Sanctuary, pers. comm.). The remaining five sites (map refs 1, 4, 7, 12 and 13) have no mouse control.

5.3.2. Molecular methods

DNA extraction and processing were undertaken at EcoGene Ltd., Auckland, New Zealand. DNA was extracted from mouse samples using the Corbett X-tractor Gene (Concorde, New South Wales, Australia) automated standard tissue protocol, following the manufacturers' instructions. DNA was eluted in 70 µl of elution buffer.

A 947 base pair (bp) part of the control region was amplified using the primers MouseCRF (TCTTCTCAAGACATCAAGAAG) (Robyn Howitt, pers comm.) and H00072 (TATAAGGCCAGGACCAAACCT) (Prager et al., 1993). The primer MouseCRF was developed specifically for this research due to problems with non-specific binding associated with other reported primers (Robyn Howitt, pers. comm.). PCR amplifications were performed in 25-µl reactions containing 1 µl of DNA extract from tissue, 1× PCR buffer with $MgCl_2$ (50 mM Tris/HCl, 10 mM KCl, 5 mM $[NH_4]_2SO_4$, 2 mM $MgCl_2$, pH 8.3), 0.4 µl BSA (10mg/ml), 200 µM of each dNTP, 0.2 µM each primer, and 1.25U of FastStart Taq DNA Polymerase (Roche Diagnostics, Auckland, New Zealand). Amplification conditions on a GeneAmp PCR System 9700 thermocycler (Applied Biosystems, Carlsbad, California, USA) were: initial denaturation at 95 °C for 4 min; 37 cycles of 45 s at 94°C, 45 s at 58°C, 1 min at 72°C; and a final extension of 10 min at 72°C.

Direct sequencing of purified products was carried out with BigDye™ Terminator Version 3.1 (Applied Biosystems) following the manufacturers' protocol. Sequences were analysed on an Applied Biosystems 3130xl genetic analyser using DNA Sequencing Analysis Software Version 5.3.1 (Applied Biosystems). Resulting DNA sequences were compared and edited manually using the programme Sequencher 4.6 (Gene Codes, Ann Arbor, Michigan, USA).

The sequences obtained were aligned and edited in MEGA 4.0 (Tamura et al., 2007) using the Clustal-W algorithm (Larkin et al., 2007). For each sample 933 bp of sequence was obtained between the positions 15,367 and 16,299 relative to the mouse mtDNA reference (NCBI accession number AY172335) published by Bayona-Bafaluy et al. (2003). Alignments were truncated to 894 bp between positions 15406 and 16299 to allow comparison with 141 sequences obtained from recent studies covering a wide geographic area allowing as many

source populations as possible to be examined using the phylogeographic approach. Accession numbers and geographic origin of the sequences are listed in Table 5.2. *M. m. musculus* (FM211645 and U47504) and *M. m. castaneus* (FM211642-FM211644, AJ286322 and EF108342) were included to allow identification of these subspecies if they were present.

Table 5.2: NCBI accession number and collection locality for all sequences compared to those collected in this study.

Accession numbers	Subspecies	Country of collection	Reference
AY172335	*domesticus*	Inbred lab strain	(Bayona-Bafaluy et al., 2003)
FM211596-FM211630	*domesticus*	UK	(Searle et al., 2009b)
FM211632-FM211641	*domesticus*	NZ	(Searle et al., 2009a)
GQ241989-GQ242005	*domesticus*	Madeira	(Forster et al., 2009)
GQ242006-GQ242020	*domesticus*	Portugal	(Forster et al., 2009)
U47431-U47497	*domesticus*	Western Europe	(Prager et al., 1996)
AJ286317-AJ286321	*domesticus*	Iran and Turkey	(Gündüz et al., 2000)
HQ241731, HQ241733-HQ241756	*domesticus*	Scandinavia	(Jones et al., 2010)
AJ286322	*castaneus*	Iran and Turkey	(Gündüz et al., 2000)
EF108342	*castaneus*	Inbred lab strain	(Goios et al., 2007)
FM211642-FM211644	*castaneus*	NZ	(Searle et al., 2009a)
FM211645	*musculus*	NZ	(Searle et al., 2009a)
U47504	*musculus*	Eastern Europe	(Prager et al., 1996)
AF074544-AF74545	*gentilulus*	Yemen	(Prager et al., 1998)

Fifty percent majority-rule consensus trees were created using the Bayesian algorithm MrBayes plugin (Ronquist and Huelsenbeck, 2003) in Geneious 5.3.4 (Biomatters, Auckland, New Zealand), with *M. gentilulus* sequences (AF074544 and AF074545) acting as outgroups (as in Rajabi-Maham et al., 2008). The model of DNA sequence evolution selected was the GTR+I+Γ model. Searle et al. (2009a, 2009b) ran model test procedures which selected this as the most appropriate for their data and as the sequences used in this study are mostly the same as those used by Searle et al. (2009a, 2009b), it is expected the sample in this study conforms to the same underlying model of evolution. Parameters were set following the methods described in Searle et al. (2009a, 2009b): two independent Markov chain Monte Carlo analyses were run, each with one cold chain and four heated chains with the incremental heating parameter set at 0.2. The analyses were terminated after 5 million generations and the first 30 percent of trees were discarded as burn-in (Searle et al., 2009b).

Trees were used to describe phylogenetic relationships between the sequences collected in this study and other published sequences in order to infer ultimate population of origin of the mice from the locations sampled in this study.

Nucleotide diversity for New Zealand *domesticus* samples was calculated using the Tamura and Nei model of nucleotide substitution (Tamura and Nei, 1993) in ARLEQUIN 3.5 (Excoffier and Lischer, 2010). ARLEQUIN was also used to calculate haplotype diversity for

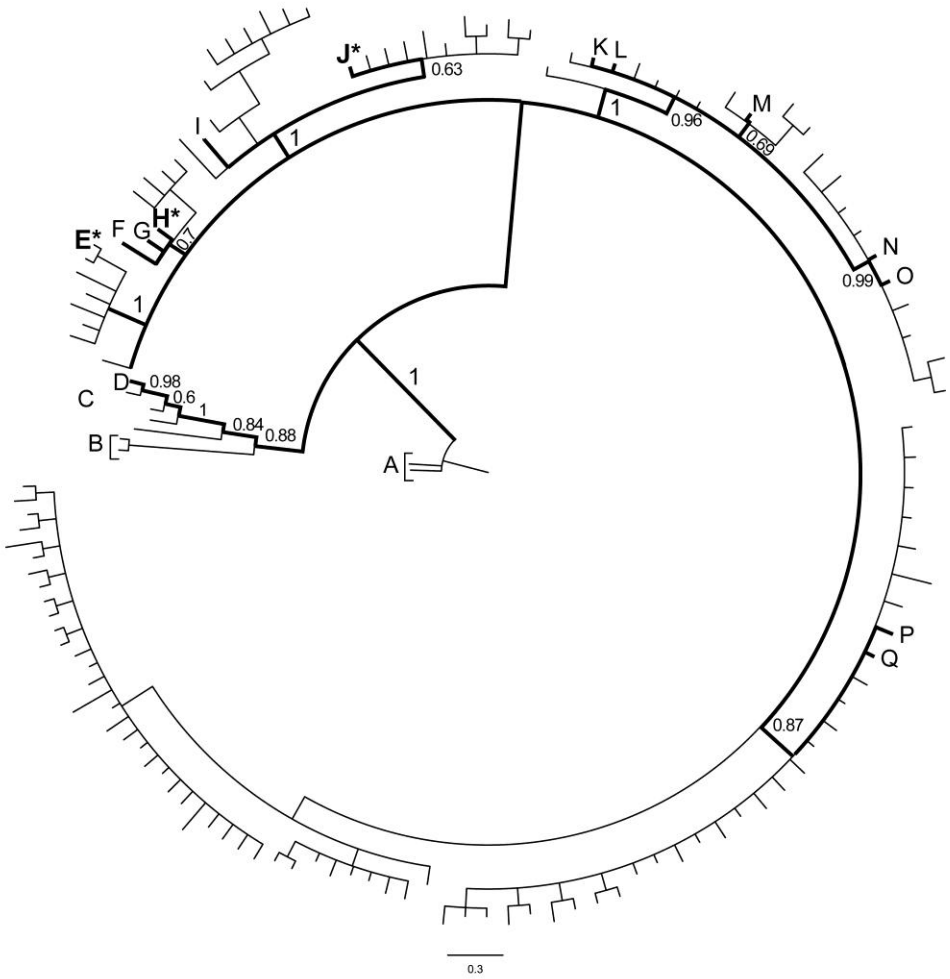
samples from this study and samples from this study combined with the samples from Searle et al. (2009a) for comparative purposes.

5.4. Results

Complete mtDNA D-loop sequences were generated for 23 New Zealand samples which represented six haplotypes (Figure 5.2). The samples from Reunion Island were sequenced successfully and represented a haplotype that was distinct from the New Zealand samples. Twenty four mice had *domesticus* D-loop sequences and one mouse from Resolution Island in Fiordland had *castaneus* mtDNA (casNZ.1). No *musculus* individuals were found.

New Zealand *domesticus* haplotypes were located in five regions of the phylogenetic tree (Figure 5.2), four of which were the same as reported in Searle et al. (2009a). Some of the haplotypes from this study confirmed previous findings. As found in the New Zealand mouse study by Searle et al. (2009a), domNZ.4 was the most abundant haplotype, with 15 out of 25 mice from seven locations possessing this haplotype (Table 5.1). This haplotype has also been recorded from Britain (BritIsl.5) and Germany (Searle et al., 2009b). Mice from Tawharanui were haplotype domNZ.9 which is part of a lineage known as the Orkney lineage (Searle et al., 2009b) and is also identical to a sample from Croatia (U47495, Prager et al., 1996). This haplotype was also previously recorded in Ashburton and Ruatangata by Searle et al. (2009a). One Cape Kidnappers mouse (Cape1) possessed haplotype domNZ.3 (Figure 5.2). This haplotype was previously recorded in nearby Napier and also in Britain and Germany (Searle et al., 2009a).

Two new geographical relationships for New Zealand mice were revealed by this study. Mice from Saddle Island had a haplotype previously undescribed in New Zealand (Mac.domNZ.1). This haplotype is the same as a sample obtained from Iran (AJ286321; Gündüz et al., 2000). The second sample from Cape Kidnappers (Cape2) represents the second haplotype (Mac.domNZ.2) discovered in this analysis that had not previously been found in New Zealand. This haplotype is closest to a sample from Portugal and is located in a separate clade to any other New Zealand samples (Figure 5.2). Reunion Island had a *domesticus* haplotype (Mac.domREU.1) identical to one collected in Lisbon, Portugal (GQ242006, Forster et al., 2009). The *domesticus* D-loop haplotypes recorded in this study are illustrated in Table 5.3. The final haplotype found in this study was casNZ.1 from Resolution Island. Mice with *castaneus* DNA are found throughout southern New Zealand (Searle et al., 2009a).



Reference	Label
A	*M. m. gentilulus*
B	*M. m. musculus*
C	*M. m. castaneus*
D	casNZ.1
E	Mac.domNZ.2
F	domNZ.7
G	domNZ.6
H	Mac.domNZ.1, AJ286321
I	domNZ.8
J	Mac.domREU.1, GQ242006
K	domNZ.2
L	domNZ.1
M	domNZ.3
N	domNZ.5
O	domNZ.4, BritIsl.5
P	domNZ.10
Q	domNZ.9, U47495

Figure 5.2: Phylogenetic tree for *M. m. domesticus* after Bayesian analysis (Section 5.3.2). Posterior probabilities are displayed for branches leading to haplotypes found in this study. An asterisk indicates a haplotype first recorded in New Zealand or Reunion in this study. Table 5.2 lists the sequences used to construct the phylogeny

Haplotype diversity of the New Zealand *domesticus* samples (n=22) was 0.55±0.12 and nucleotide diversity of the same samples was 0.005±0.003. Combining samples from this study with the samples from Searle et al. (2009a) produced a haplotype diversity of 0.63±0.05 and a nucleotide diversity of 0.005±0.003. Searle et al.'s (2009a) samples alone had haplotype and nucleotide diversities of 0.64±0.05 and 0.004±003 respectively.

5.5. Discussion

These data on mouse genetic diversity provide further evidence of the diverse origins of New Zealand house mice and both confirm the patterns previously described by Searle et al. (2009a) and reinforce the strong historical linkage between New Zealand and Britain. Four of the six New Zealand *domesticus* haplotypes found were identical to those previously reported from New Zealand and have also been found in Britain, Ireland, Germany and Croatia (Searle et al., 2009a). However, two new connections were discovered suggesting linkages between New Zealand mice and those in Portugal and Iran. Nucleotide and haplotype diversity values were similar to those obtained by Searle at al. (2009a) and suggest that the additional samples from this study are reflective of the underlying *domesticus* diversity present in New Zealand phylogenies.

5.5.1. Phylogenies

Two *domesticus* haplotypes not previously known to New Zealand were found in this study. The first (Mac.domNZ.1) was found on Saddle Island where the mouse population had been present on the island for at least 20 years (Tennyson and Taylor, 1999) prior to being eradicated in 2008 (Chapter 3, MacKay et al., in press). Based on microsatellite genotyping, allelic diversity within this population was low compared to mainland sites in Australia and a significant genetic bottleneck signal was detected (Chapter 6). The haplotype found on Saddle Island differed both to the nearest sampled population at Tawharanui and also from the most common haplotype (domNZ.4) by 6 bp (Table 5.3). Within the global phylogeny the haplotype is the same as a sample from a port in Iran (Gündüz et al., 2000). Quite how mice with an Iranian D-loop haplotype arrived at a small island in New Zealand is unclear, but possibly the haplotype is present elsewhere in Europe or New Zealand and has not yet been sampled. Most visitors to Saddle Island launch their boats from one of three nearby launching points (pers. obs.) and although mice have been reported to be good swimmers (Singleton and Krebs, 2007), all known mouse incursions have been human-mediated (Russell and Clout, 2005) making boat transport the most likely invasion pathway. Mainland trapping of areas around boat launch sites may uncover the same haplotype and suggest a

possible source population. Bayesian assignment methods (Corander et al., 2008, Russell et al., 2010b) could then be used on the microsatellite data from Chapter 6 and samples from potential source population to identify where Saddle Island mice initially came from. However, if this haplotype was restricted to the Saddle Island population it may no longer be present in New Zealand, given that the population is now extinct (MacKay et al., in press).

Table 5.3: *domesticus* D-loop haplotypes found in this study. Sample AY172335 is the reference sample from Bayona-Bafauly et al. (2003) and indels are numbered with reference to this sample. A dot indicates that the sequence is identical to the reference sequence

	154	502	518	519	530	533	536	664	673	677	679	688	682	704	902	915	999	1602	2025	2257	2273
AY172335	T	T	T	C	A	C	A	C	C	T	C	T	T	A	C	C	A	A	G	A	T
Mac.domNZ.1	A	.	.	.	.	.	.	.	.	C	T	C	.	.	T	.	.	.	.	.	C
Mac.domNZ.2	A	C	.	.	.	.	.	C	T	.	T	.	.	T	T	T	T	.	A	G	C
domNZ.3	.	.	.	.	.	.		T	.	.	.	.	.	.	.	.	.	.	.	.	.
domNZ.4	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
domNZ.9	A	.	C	T	G	.	.	.	T	.	T	.	.	.	T	.	.	.	A	.	C
Mac.domREU.1	A	.	.	.	.	T	T	.	.	.	T	.	C	.	T	.	.	C	.	.	C

The second new haplotype found in this study (Mac.domNZ.2) came from Cape Kidnappers in Hawke's Bay. The two mice from this site were caught within a few metres of each other (Tamsin Ward-Smith, Cape Sanctuary, pers comm.) but their mtDNA haplotypes were located in completely different regions of the phylogenetic tree (Figure 5.2). Cape1 was identical to domNZ.3 and was part of a lineage that includes most New Zealand haplotypes (Figure 5.2). Cape2 differed from the first by 10 bp (Table 5.3) and is located in a separate lineage to all other New Zealand samples (Figure 5.2). The closest, but not identical, haplotype to Cape2 comes from Lisbon, Portugal (GQ242020; Forster et al., 2009). Cape Kidnappers was the only site sampled in this study that had multiple haplotypes present. Samples from Great Barrier (n=3) and Waiheke (n=2) Islands were collected at sites up to 10km apart yet all had the same haplotype. However, sampling for this research was opportunistic so there is a good chance that other haplotypes present at sampling sites may have been missed.

The haplotype present on Reunion Island also has Portuguese origins, having previously been found in Lisbon (Forster et al., 2009). Historical accounts state that the first people to

land on Reunion Island were Portuguese sailors in the early sixteenth century (page 9, Allen, 1999) so the link between Reunion and Portugal is not surprising.

The single *castaneus* mouse found in this study came from Resolution Island in Fiordland. *Castaneus* is the dominant subspecies found throughout the south of the South Island of New Zealand (Searle et al., 2009a) and the presence of this subspecies on Resolution Island suggests the island was colonised by animals from Fiordland or Southland rather than from elsewhere in New Zealand or beyond.

5.5.2. Control outcome

The rationale behind this pilot study was an investigation into possible relationships between mouse subspecies or mtDNA lineage and mouse control outcome. It is difficult to make firm conclusions about this due to the low numbers of samples processed and low levels of replication of different control regimes. Samples were obtained from two sites where mouse eradications failed (Hauturu Island and Tawharanui), two where eradications were successful (Adele and Saddle Islands) and two more where the eradication appears to have been successful (Rangitoto and Motutapu). Six further sites had no targeted mouse control (Table 5.1). The final site (Mokoia Island) has been mouse free since 2003 (MacKay et al., 2007) and the sample obtained from here was a single mouse trapped during routine monitoring of the island designed to detect reinvading rodents (T. Sachtleben, Department of Conservation, pers. comm.). The data presented here suggest there is no clear link between D-loop haplotype and control outcome. However, there are three promising avenues for further investigation – haplotype domNZ.4, the Orkney lineage and *M. m. castaneus*.

5.5.2.1. Haplotype domNZ.4

Fifteen out of 25 mice sampled for this research had mtDNA D-loop haplotype domNZ.4. As mentioned previously, this haplotype has previously been recorded throughout New Zealand and Europe. It has also been recorded in Australia (Gabriel et al., submitted) and the mice that were first shipwrecked on Ruapuke Island may have had this haplotype. The same haplotype is found throughout the British Isles and has also been recorded in German, Norway, Denmark and Cameroon (Searle et al., 2009b). Interestingly, one of the locations that this haplotype has been recorded in the British Isles is Birmingham. In 1986 mice in areas of Birmingham were reported to have developed a cereal aversion (Humphries et al., 2000). Laboratory experiments confirmed the aversion and found that it was passed on to

offspring, suggesting a genetic basis (Humphries et al., 2000). Nothing similar has been reported in New Zealand but Birmingham was a major centre of industrial activity during the time that Europeans were first settling New Zealand so the ancestors of the cereal-averse mice may have contributed to New Zealand's mouse population.

The genetic basis for anticoagulant resistance in mice has been linked to mutations in the VKORC1 gene (Rost et al., 2009, Pelz et al., 2005) but as yet no mtDNA sequence data exists for populations of mice that exhibit anticoagulant resistance. This gap in knowledge would be relatively easy to rectify through collaboration with the groups in Europe who are currently researching anticoagulant resistance. Also, there are no known populations of anticoagulant resistant mice in New Zealand (Bailey and Eason, 2000) to sample so it is difficult to make any other links with the currently available data suggesting the theory should be rejected.

5.5.2.2. Orkney lineage

The Orkney lineage (Searle et al., 2009b) has now been recorded at three locations in New Zealand – Ashburton and Ruatangata by Searle et al. (2009a) and Tawharanui in this study. Tawharanui is a fenced mainland site where a mouse eradication attempt failed (Goldwater, 2007) and ongoing control has failed to keep mouse numbers low. There is evidence that mice from the Orkney lineage are more aggressive than mice from other lineages in behavioural trials (Ganem and Searle, 1996), but no other behavioural information about the lineage in New Zealand is available. Tawharanui provides an excellent arena for further research both into the behaviour of Orkney lineage mice in feral New Zealand populations and the possible presence of poison resistance or bait aversion within the population.

5.5.2.3. *M. m. castaneus*

All but one mouse sequenced were *domesticus* so identifying the effect of mouse subspecies on control outcome is challenging. No mouse control has been attempted on Resolution Island but recently mice were re-detected on Pomona Island in Lake Manapouri two years after an eradication attempt (K. Broome, Department of Conservation, pers. comm.). All mice sampled from this region have been *castaneus* and it is safe to assume the original population on Pomona Island were as well. Unfortunately, no genetic samples were taken prior to the eradication meaning no samples were available for phylogenetic analysis. The importance of obtaining genetic samples prior to an eradication attempt has been repeatedly emphasised in the literature as it makes it possible to determine whether new mice detected

are survivors or reinvaders through population assignment methods (Abdelkrim et al., 2005, Abdelkrim et al., 2007, MacKay et al., 2007, Russell et al., 2010b). It isn't clear why samples were not collected in this instance. Currently the mice that were re-detected on Pomona Island are considered to be re-invaders rather than survivors and a population assignment will be attempted using mainland mice to investigate this (K. Broome, pers. comm.). If the mice survived the eradication then this may have been related to mouse subspecies but two other mouse eradications in *castaneus*-dominated areas have succeeded recently so reinvasion is the more likely explanation.

5.5.3. Summary and conclusions

In summary, two new D-loop haplotypes have been found in New Zealand to add to the ten published by Searle et al. (2009a). The majority of mice sampled throughout the country belonged to the same *domesticus* haplotype previously found widely throughout New Zealand (domNZ.4). No *musculus* individuals were found and the single *castaneus* sample came from the region where *castaneus* is known to be the dominant subspecies.

This pilot study was limited by small sample size which makes it difficult to draw conclusions about links between D-loop haplotype and control outcome. However, some areas for future research have been identified. Conservation efforts in New Zealand are heavily reliant on the use of anti-coagulant toxins so any suspected signs of resistance need to be investigated. Anticoagulant resistance develops as populations are repeatedly exposed to poisons (Greaves, 1994, Billing, 2000) so sites where ongoing control of mouse populations is occurring rather than being eradicated need to be carefully monitored. Any research into poison resistance in New Zealand would be facilitated by a research programme encompassing studies of populations of rats and mice known to show anticoagulant resistance. The enclosed population of mice at Tawharanui could provide excellent research opportunities into the behaviour of Orkney lineage mice in relation to control. At the risk of repetition, genetic samples must always be taken prior to an eradication attempt to allow a full investigation into possible reasons for failure should the attempt not successfully remove mice.

Chapter 6. Population structure and colonisation history of house mice on a small island

6.1. Abstract

House mouse populations show a range of different models of social organisation depending on population density, food availability and breeding season. Social organisation can alter gene flow within a population and can lead to genetic drift and ultimately influence the evolution of a population. To complete the study of the mouse population on Saddle Island social organisation and population structure were described using a spatial method and a series of genetic techniques. Trapping data showed the population structure changing through the year in response to changes in population density and breeding season. Genetic methods suggested the population was divided into two genetically distinct subpopulations. The capture locations of individuals from the two genetically distinct groups were not geographically distinct and a more biologically plausible arrangement of subpopulations was created by combining genetic data, trapping data and knowledge about habitat and topography of the island.

6.2. Introduction

The house mouse (*Mus musculus*) is one of the best studied and most widely distributed mammal species in the world (Berry, 1981, Berry and Scriven, 2005). It is used as a laboratory model species (Morse III, 2007) and its genome has been mapped (Dietrich et al., 1996). Its commensal habits have resulted in the species being spread throughout the world by humans (Bronson, 1979, Pocock et al., 2005) and it exhibits enormous behavioural flexibility, allowing it to establish populations in most terrestrial habitats (Berry, 1981). Early studies of mice in granaries in Canada revealed that the populations were divided into small groups with little gene flow between them (Anderson, 1964). Since then, population structure and social organisation of the species have been the focus of large volumes of research using direct observation of individuals (Lidicker, 1976, Singleton and Hay, 1983), trapping (Singleton, 1983) and individual tracking methods such as radio-tracking or footprint-tracking tunnels (Fitzgerald et al., 1981, Krebs et al., 1995, Chambers et al., 2000). Genetic methods are also used to investigate how population structure affects gene flow (Anderson, 1964, Myers, 1974, Singleton, 1983) as structuring within a population can lead to genetic drift and ultimately influence the evolution of a population (Wright, 1940).

Population structure has proven to be far more flexible (Butler, 1980) than first suggested by Anderson (1964) and house mouse populations appear to broadly conform to four major models, as described by Krebs et al. (1995) and summarised in Table 6.1. In an interesting applied investigation into population structuring, Robertson and Gemmell (2004) showed that Norway rats (*Rattus norvegicus*) on South Georgia Island, sub-Antarctic are divided into isolated subpopulations separated by glaciers. The authors suggested that this will allow rats to be eradicated from South Georgia in stages rather than attempting to eradicate the whole population in one operation. Structuring within a mouse population may allow a similar approach to eradication to be adopted. Islands offer the opportunity to investigate social structure of naturally enclosed populations free from immigration and emigration other than births and deaths (Triggs, 1991). Small accessible islands allow more in depth population studies to take place as every individual on the island is potentially trappable (Triggs, 1991, Gliwicz, 1980).

Table 6.1: Models of social organisation in house mouse populations (Krebs et al., 1995)

Model	Defining features
I	Territorial system with exclusive home ranges that are defended against individuals of the same sex. Strong site attachment, e.g. Fitzgerald et al. (1981).
II	Not territorial but social dominance dictated by body size. Site attachment but overlapping ranges e.g. Krebs et al. (1995).
III	Nomadic, no site attachment apart from breeding females, e.g. non-breeding mice in Krebs et al. (1995).
IV	Clan structure with several reproductive individuals of both sexes in a small group of individuals e.g. Singleton (1983).

Table 6.2: Summary of trapping visits to Saddle Island, New Zealand. Density estimates were calculated within each session, high rates of tag loss made it impossible to combine sessions (MacKay et al., in press) .*CMR=capture-mark-recapture

Session	Month	Season	Number of mice captured	Estimated density (mice/ha)	Purpose
1	January 2008	Breeding	45	13	CMR*
2	March 2008	Breeding	92	19	CMR
3	May 2008	Non-breeding	63	11	CMR
4	August 2008	Non-breeding	51	9	Removal trapping

The aim of this chapter is to complete the study of the mouse population on Saddle Island by describing the population structure two methods outlined below. First, trapping data from four trapping sessions over an eight month period were used to look for signs of subgroups of individuals on the island. These trapping records cover both breeding and non-breeding seasons and a range of mouse densities (Table 6.2). Second, a range of genetic analyses were used to explore the genetic population structure on the island. Trapping records allowed the population structure to be described on four occasions whereas genetic data were only collected in the final trapping session. Comparing the results from the two

methods gives the opportunity to illustrate relationships between spatial population structure and genetic population structure. In addition to investigating population structure, genetic diversity and bottleneck signals were used to make inferences about the colonisation history of the Saddle Island mouse population.

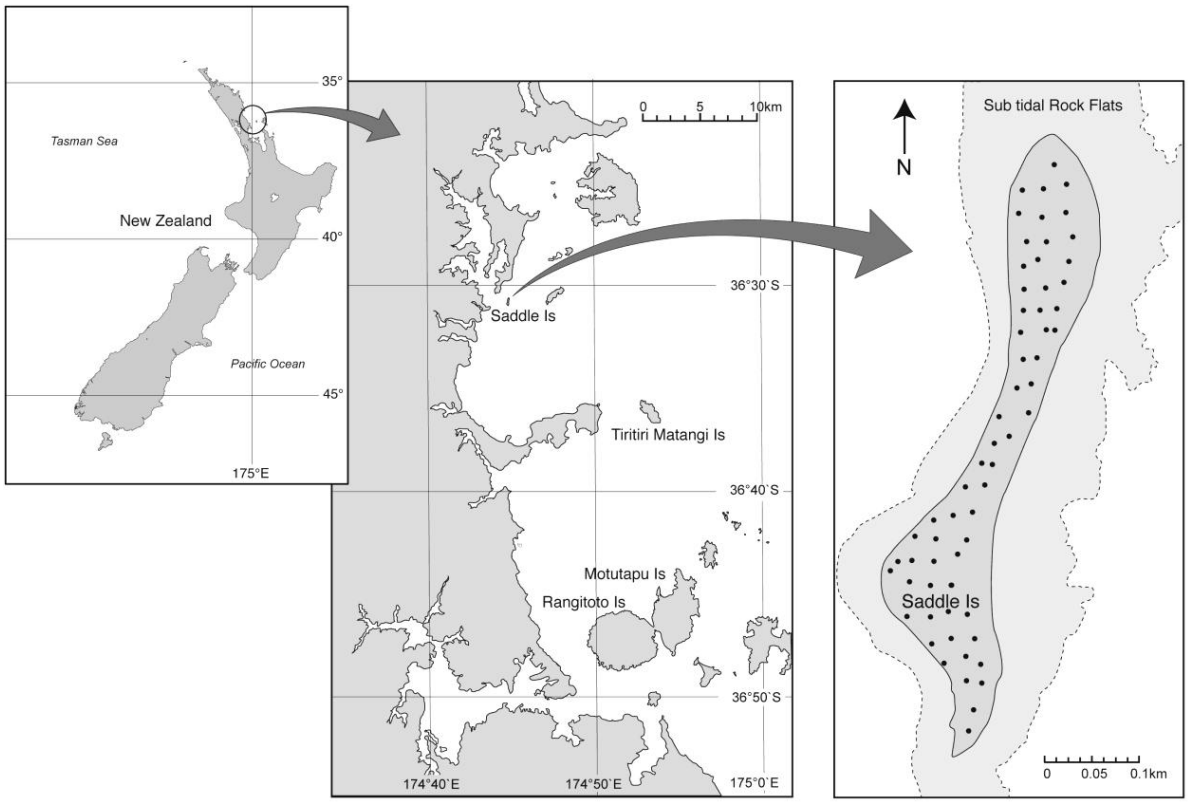


Figure 6.1: Location of Saddle Island and grid layout on the island

6.3. Methods

6.3.1. Study site and genetic sample collection

Saddle Island (36˚31'S, 174˚47'E;Figure 6.1) is a 6 ha forested island north of Auckland, New Zealand. Norway rats were eradicated from the island in 1989 and house mice were detected shortly afterwards (Tennyson and Taylor, 1999). A 25m grid of 62 stations was established in October 2007 and the geographic coordinates of all stations were recorded by GPS to 9 m accuracy. During 2008 (Table 6.2) mouse population densities and ranging behaviour on the island were described using live trapping and radio-tracking methods. All mice captured on the island in the three trapping sessions prior to removal trapping in August were sexed by visual inspection and marked with a numbered ear tag (National Band and Tag Co., Newport, Kentucky, USA) in each ear. This allowed recaptured mice to be identified within each trapping session for Capture-Mark-Recapture analysis (used to calculate mouse densities on the island, see Chapter 3). Ear tags also meant mice could be identified between

sessions allowing a capture location database to be created. This database was used to calculate mouse movements (Section 6.3.2.1). In August 2008, mice were successfully eradicated from Saddle Island using removal trapping and poisoning (Chapter 3, MacKay et al., in press). During the eradication 51 mice were trapped and a 2 cm section of tail was taken from each individual and preserved in 70% ethanol. No genetic samples were taken in any other trapping session.

The island has two high points at the north and south with a low flat saddle in between. Forest at either end of the island is wetter and denser than the forest on the central saddle and this combination of habitat and topography differences suggests that the mouse population may be divided into three groups at the North, the Central saddle and the South of the island.

6.3.2. Trapping methods

6.3.2.1. Deterministic probability analysis

Groupings of mice were identified using the deterministic proximity method of Pocock et al (2003). This method uses mouse capture locations and movement parameters calculated from trapping data and radio-tracking to identify potential subpopulations. In this case a subpopulation is a group of individuals where buffers drawn around each capture location overlapped. Mean mouse movements across the whole year were used to create a series of buffers around the capture locations of mice trapped in the four trapping session on Saddle Island (Table 6.2). Forty-two of the 51 mice (82%) caught in removal trapping in August had been trapped in previous trapping sessions and a second analysis was run for August including all previous capture locations for the mice caught in August (and therefore included in the genetic analyses as this was the trapping session that coincided with removal). This gave a picture of mouse range overlaps and possible interactions (assuming that individuals with overlapping ranges come into contact with each other) over the whole year to compare with the genetic population structure.

RANGES VII (Anatrack Ltd., Wareham, Dorset, UK) was used to calculate between-capture distances for all animals caught on two or more occasions between January and August 2008 to obtain a mean movement value for the population as a whole. These data were combined with movement parameters calculated using RANGES from radio-tracking data reported in MacKay et al. (in press) and a non-parametric Mann-Whitney U-test was implemented in SPSS (Somers, New York, USA) to test the combined movement data set for differences in

movements between the sexes. Combined distances were used to create buffers with diameters representing 50 and 90% of the mean of observed movements around each capture location. When mice were caught more than once within a session all capture locations were included in the analysis. Buffers were created in ArcGIS (ESRI, Redlands, CA, USA) and any overlapping regions buffers were combined allowing subpopulation divisions (i.e. discrete buffer regions not joined to other regions) were assessed by eye.

6.3.2.2. Territorial behaviour

Trapping records were also used to identify individuals which were site-attached. An individual was classed as site-attached if all of its between-capture distances were less than 90 m. This was based on average range length shown by animals in the Saddle Island population prior to eradication (unpublished data). Levels of range overlap between individuals were assessed using the pre-eradication Minimum Convex Polygon ranges calculated using RANGES VII (Anatrack Ltd., Wareham, Dorset, UK) and reported in Chapter 4.

6.3.3. Population genetics

6.3.3.1. Sample processing and genetic diversity

All samples were genotyped using nine microsatellite loci by EcoGene Ltd., Auckland, New Zealand. Primer details are in Table 6.3. DNA was extracted from mouse tail samples using the Corbett X-tractor Gene (Concorde, New South Wales, Australia) automated standard tissue protocol, following the manufacturers' instructions. DNA was eluted in 70µl of elution buffer. PCR amplifications were performed in 10-µl reactions containing 1µl of DNA extract from tissue, 1× PCR buffer with $MgCl_2$ (50 mM Tris/HCl, 10 mM KCl, 5 mM $[NH_4]_2SO_4$, 2 mM $MgCl_2$, pH 8.3), 200 µM of each dNTP, 0.4 µM of each primer, and 0.8U of FastStart Taq DNA Polymerase (Roche Diagnostics, Auckland, New Zealand). Amplification conditions on a GeneAmp PCR System 9700 thermocycler (Applied Biosystems, Carlsbad, California, USA) were: initial denaturation at 95°C for 4 min; 37 cycles of 30 s at 94°C, 30 s at 58°C, 45 s at 72°C; and a final extension of 40 min at 72°C. Primer D19Mit2 had the same conditions as above except annealing temperature was reduced to 53°C. The 5'-end of the forward primer of each pair was fluorescently labelled with either 6FAM, NED, VIC or PET dyes (Applied Biosystems, Table 6.3) and amplification products were separated using capillary electrophoresis (Applied Biosystems ABI PRISM 3130xl). Alleles were sized relative to an internal size standard (GS-500 LIZ) using GENESCAN 3.1 (Applied

Biosystems). The genotype profiles were analysed by eye and using the software GENEMAPPER Version 4.0 (Applied Biosystems). MICROCHECKER was used to assess the microsatellite data for evidence of null alleles, stuttering, or large allele dropout (Van Oosterhout et al., 2004).

Table 6.3: Primer details for the nine microsatellite loci typed in this research. All primert were sourced from Mouse Genome Informatics, Jackson Laboratories, Bar Harbor, Maine, USA.

Locus	Forward primer (with fluorescent label)	Reverse primer	Accession#
D1Mit322	NED-CAAATTTACACCCATGTTGTGG	TCAATGGAGGGGAAGATCAG	MGI:704056
D2Mit338	VIC-TCACCAGCCTGAAAACACTG	TCTGGGTACAATCCTTAGTCCTG	MGI:703779
D3Mit41	VIC-AATTTCTTCCTGTTACACTGAGCC	CATGAGAGAACTCCTTCCATCC	MGI:703722
D5Mit95	NED-TGTTCTTGTCCATGTCTGATCC	AACCAAAGCATGAAACAGCC	MGI:703549
D10Mit20	6FAM-CACCCTCACACAGATATGCG	GCATTGGGAAGTCCATGAGT	MGI:706215
D11Mit29	PET-TTGAGGCATGAGGGGATTAG	TTTCCGTCATTGCTAAAGGG	MGI:702038
D12Mit4	PET-ACATCCCCAGCTCTTGTTTG	AAACCAAACCAAAGAAGCTTAGG	MGI:700703
D17Mit51	6FAM-TCTGCCCTGTAACAGGAGCT	CTTCTGGAATCAGAGGATCCC	MGI:705389
D19Mit2	NED-TGTTGATAGTGCAAGGTGCG	CAAGGGGCCATACCTAGTGA	MGI:700607

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Departures from Hardy-Weinberg equilibrium (HWE) were tested for at each locus over the whole population using GENALEX 6.4 (Peakall and Smouse, 2006). Linkage disequilibrium within the population was examined for each locus pair using 10,000 permutations and a Bonferroni correction for multiple comparisons in ARLEQUIN 3.5 (Excoffier and Lischer, 2010). Genetic diversity of the mouse population was described by calculating the number of alleles and observed and expected heterozygosity at each locus using GENALEX (Munshi-South and Kharchenko, 2010).

6.3.3.2. Genetic bottleneck detection

Most populations of invasive species are founded by small number of colonists (Thorsen, 2000, Russell and Clout, 2005, Clapperton, 2006) so the genetic diversity of mice on Saddle Island is likely to be lower than mainland populations. Genetic variation within an existing population can be used to identify signs of population bottleneck (Cornuet and Luikart, 1996, Luikart et al., 1998b) and two methods of population bottleneck detection were used on data from Saddle Island. The first method (sign test) looked for heterozygosity excess in the population and determined whether or not this excess is significantly larger than would be expected at mutation-drift equilibrium (Piry et al., 1999, Cornuet and Luikart, 1996). Significance was tested using a Wilcoxon test as this is considered the most powerful and robust method when fewer than 20 loci are used (Piry et al., 1999). The second method (mode-shift indicator) relies on allele frequency distributions to detect a recent bottleneck. In a stable population it is assumed that rare alleles are more common; after a bottleneck event

intermediate allele classes become better represented (Luikart and Corneut, 1998, Luikart et al., 1998a, Luikart et al., 1998b). Both these analyses were performed using BOTTLENECK 1.2.02 (Piry et al., 1999). The two phase model (TPM) was used for all tests. This model combines two mutational models: the infinite alleles model (IAM) and the stepwise mutation model (SMM). The TPM allows the proportion of IAM to SMM to be adjusted to suit the data (Piry et al., 1999). For this study the proportion was set to 90% IAM and 10% SMM based on previous research (Piry et al., 1999, Russell et al., 2009b).

6.3.3.3. Population structure

Mice caught on the island in August were assigned to one of three groups (North, Central and South) depending on their capture locations. These groupings were based on habitat and topographical features of the island described in Section 6.3.1. Pairwise F_{ST} values were used to measure genetic differentiation between groups using the nine loci microsatellite genotypes (Hartl and Clark, 1997). These values were calculated in GENALEX using 10,000 permutations of the data with a Bonferroni correction for multiple comparisons to assess significance. In addition to defining *a priori* groupings, a Mantel test was performed in GENALEX to test the isolation by distance hypothesis, i.e. the assumption that mice that were captured further apart were less closely related to each other than mice trapped closer together. Two matrices were created; one of the genetic distance between all pairs of individuals and the other of geographic distance; and tested to determine whether or not there was a statistically significant relationship between the two (Smouse et al., 1986, Smouse and Long, 1992).

6.3.3.4. Population assignment

Following on from the initial traditional examination of population structure on Saddle Island, Bayesian (Rannala and Mountain, 1997) and likelihood (Paetkau et al., 1995) population assignment methods were used in GENECLASS2 to test the genetic distinctiveness of the pre-defined groups used in previous analyses. The probability of each individual belonging to each group was calculated using 10,000 simulated individuals using the re-sampling algorithm of Paetkau et al. (2004). This algorithm reduces the number of resident individuals that are excluded from their home population during the analysis therefore creating a more robust population assignment (Piry et al., 2004).

6.3.3.5. Clustering

A Bayesian method (Corander et al., 2008) was used to detect genetically diverged groups of individuals on the island using the spatial clustering of individuals function in BAPS 5.4. Capture locations for each individual were included in the analysis and the best supported number of clusters (*K*) on the island was estimated using the log marginal likelihood values of the best partitions and the distribution of posterior probabilities for different *K* values (Munshi-South and Kharchenko, 2010). Spatial distribution of the individuals assigned to different clusters was mapped using ArcGIS and buffers around capture locations were created both including and excluding previous captures prior to August (see Section 6.3.3.4). Pairwise F_{ST} values were calculated between the groups revealed by this analysis.

6.4. Results

6.4.1. Trapping methods

A total of 431 movements were recorded comprising 294 between-capture distances and 137 between-fix distances obtained through radio-tracking. Four males and two females were radio-tracked; overall, movement data were collected from 51 males, 67 females and one unsexed juvenile, including the radio-tracked individuals. 130 movements were 0 m indicating that the mouse was trapped or located in the same place (Figure 6.2). Movements of 0 m were removed from analysis and buffer distance calculations only included movements that were greater than 1 m. Removing 0 m movements will have biased the mean movement estimate upwards resulting in a more conservative buffering method as subpopulations would need to be more distinct with a higher mean movement value than with a lower one. There was no significant difference in movements between the sexes (MANN-WHITNEY U=4552.5, two-tailed *P*=0.538). Female mean between location-movement was 34.7±1.6 (SE) m and male mean was 36.7±2.4 m. Buffers were drawn at radii of 18 m and 32 m reflecting 50% and 90% of the mean movement of 36 m respectively.

The deterministic probability analysis of trapping records from January showed evidence of three subpopulations on the island which were termed North, Central and South (Figure 6.4). Buffers around these subpopulations remained distinct using the 50% buffer but there was minor overlap at the 90% level. These divisions fitted with *a priori* expectations (Section 6.3.1) as to where population divisions may have occurred on the island based on detailed knowledge of topography and habitat on the island.

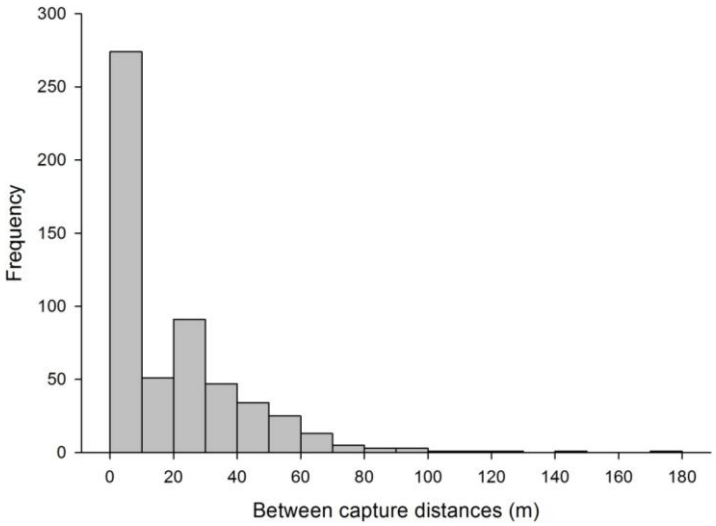

Figure 6.2: Distribution of between-capture distances

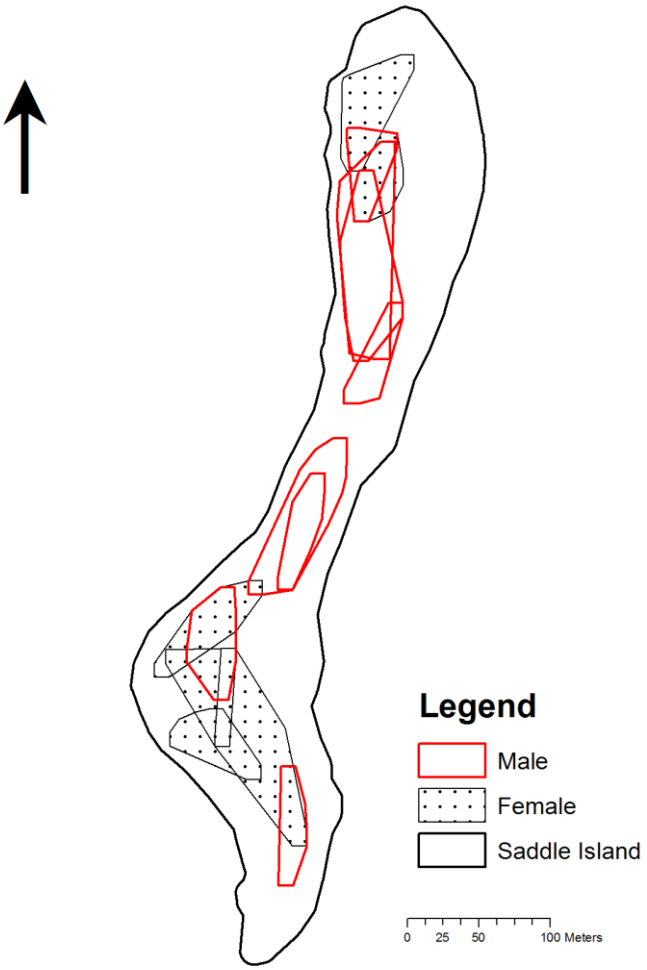

Figure 6.3: Pre-eradication MCP ranges calculated from trapping and radio-tracking data collected on Saddle Island in 2008

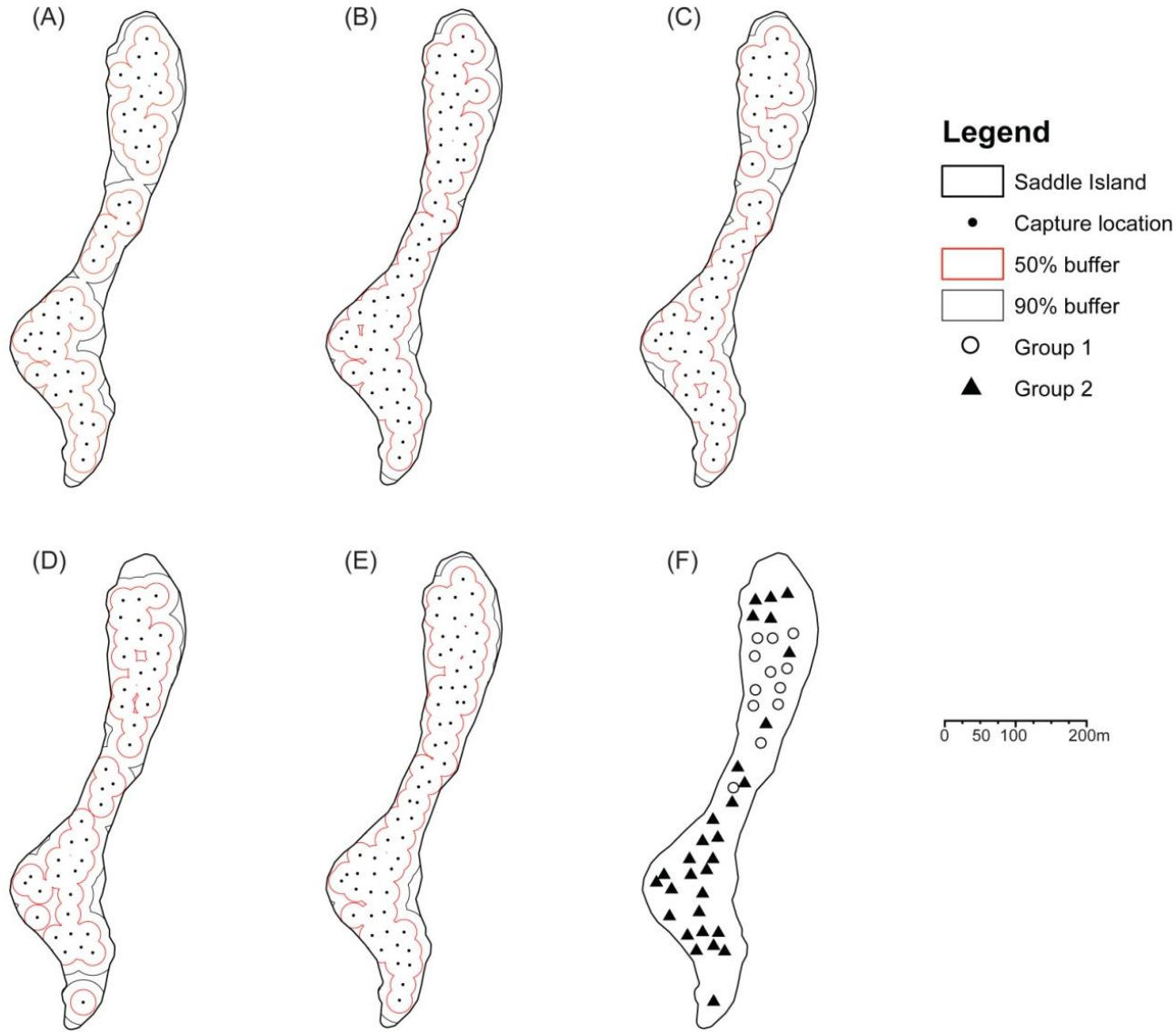

Figure 6.4: Deterministic probability analysis and Bayesian clustering results. Panels A-D represent trapping records from January-August (Table 6.2) and Panel E shows August trapping data combined with previous capture histories (Section 6.3.2.1). Panel F shows the capture locations of individuals assigned to genetically distinct groups by Bayesian clustering analysis (Section 6.3.3.5).

Subpopulations evident in January did not persist and in March the 50% buffer produced a continuous network across the island. This coincided with an increase in density from 13 to 19 mice/ha (Table 6.2). May trapping records revealed possible subdivision of the population into two groups using the 50% buffer but this division was removed by the 90% buffer. August captures again revealed two possible subpopulations with the 50% buffer but this division was removed by the 90% buffer. The division between these possible subpopulations were similar to those observed in January and May (Figure 6.4). All sign of population division was removed when previous capture locations for the mice trapped in August were included in the analysis with the 50% buffer creating a continuous network of range overlaps and therefore potential interactions.

The population showed high levels of site-attachment with only four (three males and one female) of 119 individuals (3%) ranging further than 90m between captures. One male moved 175 m between the March and May trapping sessions, another male moved 124 m in one night in March and one female moved 112 m over two nights in January. At the other end of the spectrum, 24 mice were trapped in multiple sessions in the same trap and one of these was trapped in the same trap in four different trapping sessions.

There was substantial inter- and intra-sexual range overlap observed from trapping and radio-tracking (Figure 6.3). Ranges were obtained for eight males and six females and all but two of these mice (one of each sex) were alive in March meaning there was temporal overlap of ranges despite the data being collected over an eight month period.

6.4.2. Population genetics

All nine loci were successfully amplified for all 51 individuals genotyped. MICRO-CHECKER found no evidence of null alleles, stuttering or large allele dropout. Locus D5Mit95 deviated significantly from Hardy-Weinberg equilibrium ($Chi^2(10)=20.944$, $P=0.021$) so it was excluded from analysis due to heterozygosity excess. All locus pairs were in linkage equilibrium across the population.

Genetic variation at the eight remaining loci was low with an average of 3.63 (±1.19 SE) alleles per locus and expected heterozygosity of 0.52 (±0.11 SE, Table 6.4). There was a clear bottleneck signal evident in the population: a significant heterozygote excess was detected (WILCOXON $P=0.002$) using the sign-test method, however, the mode shift indicator did not reveal a shifted distribution in the allele frequency classes.

Table 6.4: Genetic characteristics of mice from Saddle Island estimated using genotypes at eight microsatellite loci. All locus pairs were in linkage equilibrium.

Locus	Allele size range	Number Alleles	Observed Heterozygosity	Expected Heterozygosity
D1	294-310	3	0.451	0.541
D2	129-139	3	0.569	0.519
D3	209-234	4	0.569	0.528
D10	202-230	6	0.627	0.612
D11	144-164	4	0.549	0.510
D12	193-209	4	0.686	0.701
D17	150-154	2	0.373	0.370
D19	176-192	3	0.412	0.408
Mean	n/a	3.625	0.529	0.524

Pairwise F_{ST} values between the pre-defined subpopulations indicated significant (P<0.01) moderate differentiation between the North subpopulation and both Central (F_{ST}=0.076) and South (F_{ST}=0.078) subpopulations but no significant differentiation (P=0.196) between the Central and South subpopulations (F_{ST}=0.010). The Mantel test revealed a significant but weak relationship between pairwise genetic and geographic distances (R^2=0.02, P<0.01). Population assignment in GENECLASS was unsuccessful with only c.50% of individuals correctly assigned using both the Bayesian (Rannala and Mountain, 1997) and the likelihood-based (Paetkau et al., 1995) approaches. Most individuals were assigned to the Central subpopulation by this method.

Bayesian clustering methods in BAPS divided the population on the island into two genetically diverged groups (Panel F, Figure 6.4). Twelve mice were assigned to Group 1 in the northern third of the island and the remaining 39 mice made up Group 2. Group 2 individuals had an odd geographic distribution: most individuals were found in the southern two thirds of the island but a few individuals were trapped in the far north and others within the range of Group 1 individuals (Figure 6.4). The 50% buffer indicated that there was extensive overlap between groups, particularly when previous capture locations were included (not shown). Between group differentiation was moderate (F_{ST}=0.08, P<0.001).

6.5. Discussion

The small size and easy terrain of Saddle Island meant it was possible to set traps across the whole island and potentially trap every mouse present. Four trapping sessions and radio-tracking of six individuals provided detailed movement data that were combined with individual capture histories to illustrate mouse range overlaps over an eight month period. Genetic samples were obtained from 51 of an estimated 53 mice on the island (MacKay et al., in press) allowing the genetic structure of the population in midwinter to be described.

Combining these data enabled a detailed description of the population structure of mice on the island to be made. In this section I will discuss the colonisation history, social organisation and population structure of mice on Saddle Island.

6.5.1. Colonisation history

Population history of mice on Saddle Island can be inferred from the genetic data collected (Ficetola et al., 2008). The mouse population on Saddle Island showed signs of a significant genetic bottleneck which is surprising considering that the population has been present on the island for at least 20 years (Tennyson and Taylor, 1999). The BOTTLENECK software was designed to detect recently bottlenecked populations and analysis is usually only successful for a few dozen generations following the bottleneck event (Cristescu et al., 2010, Luikart et al., 1998a, Piry et al., 1999). Population bottlenecks are known to have negative impacts on populations, for example, the bird fauna of New Zealand is characterised by a number of species that have experienced varying degrees of population bottleneck (Briskie and Mackintosh, 2004, Hale and Briskie, 2007). Species where the population had been reduced to less than 150 individuals experienced hatching failure around 25% of the time, over eight times more often than species that had not been through a genetic bottleneck (Briskie and Mackintosh, 2004). All individuals handled on Saddle Island appeared healthy and breeding didn't appear to be impacted despite the apparent severity of the bottleneck event (pers. obs.). Further clues about the population history come from allelic diversity.

Allelic diversity for all nine microsatellite loci sampled was low, with a mean value of 3.6 alleles per locus (Table 6.4). Five of the loci examined in this study were also genotyped by Sutherland et al. (2005) in a population in mainland Australia. The Australian population had a mean of 13.2 alleles per locus, over three times the diversity found on Saddle Island. The maximum number of alleles per locus in Australia was 16 (Sutherland et al., 2005) compared to six in this study. Genetic diversity may be reduced in small areas due to social structure affecting gene flow (Hardouin et al., 2010) therefore comparing Saddle Island to the Australian mainland could be problematic. However, Sutherland et al. (2005) trapped mice along a 100m fence line and found high allelic diversity within a small area suggesting the low diversity on Saddle Island is a genuine result of a population bottleneck. The low allelic diversity and significant bottleneck observed on Saddle Island suggest a very low number of initial colonists, possibly only a single pregnant female.

A study of feral mouse populations in the USA found that 20% of litters were sired by more than one male (Dean et al., 2006). Multiple paternity has been recorded in two feral rat

species in New Zealand (Miller et al., 2010), but has not yet been reported in mice. Theoretically a single pregnant female with four offspring each with a different male parental allele at each of the loci tested in this study could have started the population. A more likely explanation is that a pregnant female arrived at the island and at least one other male arrived at the same time. The third alternative is that the island has experienced repeated colonisation events. Saddle Island is frequently visited by boats (pers. obs.) and mice are considered high risk island invaders as they are known to be frequent stowaways on boats (Dilks and Towns, 2002, Cucchi, 2008) and they have been detected arriving on mouse free islands in New Zealand on at least fourteen occasions (Russell and Clout, 2005). This suggests that mice could potentially be brought to the island regularly, especially since during the course of this research two rats were detected on the island (MacKay et al., in press). However, there seems to be little immigration to the island. Between September 2008 and August 2010 there were no signs of mice on the island other than those deliberately released during an investigation into the invasion biology of mice (Chapter 4) and I believe these data suggest that the population on Saddle Island was founded by a very small number of colonists over 20 years ago and that the population has received little or no further genetic input since then. House mice are an extremely successful invasive species worldwide and their ability to form successful populations from small numbers of founders, as suggested here, must play a large part in this.

6.5.2. Social organisation

Mice that were caught on multiple occasions throughout the year showed a high level of site attachment, with 97% of individuals remaining close to their initial capture site. Ranges showed large levels of overlap and two male mice radio-tracked for four nights in July 2008 had ranges that overlapped almost completely and dens that were within a few metres of each other (Chapter 2). This suggests that mice on Saddle Island maintained home ranges but did not defend them against either members of the same or the opposite sex. This form of social organisation corresponds to Model II described by Krebs et al. (1995) and is commonly seen in non-commensal mouse populations (Singleton and Krebs, 2007, Newsome, 1969). It is very different to the social organisation shown in the one other study of mouse social organisation in New Zealand. Fitzgerald et al. (1981) found that mice in the Orongorongo Valley were highly territorial and mice excluded others of the same sex from their ranges (Model I, Krebs et al., 1995). Densities in this study were far lower (0.55-3.3 mice/ha) than those seen on Saddle Island and this difference is likely to have caused the difference in social organisation (see Section 6.5.3).

6.5.3. Population structure

A combination of trapping records and genetic analysis were used to describe population structure on the island. Deterministic probability analysis revealed that the mouse population on Saddle Island had a flexible population structure influenced by population density. In January there were three subpopulations on the island that merged into one when the population density increased in March. In May the population density was lower than that recorded in March (11 mice/ha vs. 13 mice/ha in January) and no pregnant females were captured, suggesting breeding had ended (MacKay et al., in press). Trapping records in May showed a slight divide between mice in the northern third of the island and the rest of the island using the 50% buffer but not the 90%. In August the population was at its lowest point with an estimated density of 9 mice/ha (Table 6.2). The 50% buffer in this instance showed signs of a similar population structure to that observed in January. However, when previous capture locations for all the mice caught in August were included in the analysis all signs of population structure vanish. The mice trapped in August were shown to have ranged widely enough in the preceding months to allow members of different subpopulations to potentially have come into contact with members of others. This level of population mixing could have resulted in no genetic population structure being found, i.e. the whole island was acting as one population. Alternatively, genetic divisions in the population may persist despite population mixing suggested by trapping records.

Initial investigation into genetic population structure using pre-defined subpopulations based on *a priori* groupings (Section 6.3.1) and confirmed by January trapping data was not very informative. F_{ST} values revealed that the North population was moderately differentiated from the South and Central populations but there was no difference between the South and Central populations. This was backed up by a very poor population assignment result using GENECLASS. The conclusion from this initial investigation was that the social organisation suggested from January trapping did not have an effect on the genetic structure of the island.

The Bayesian clustering analysis divided individuals into two genetically diverged subpopulations (Panel F, Figure 6.4). The F_{ST} value for the populations indicated they were slightly more diverged from each other than the previous subpopulations and population assignment in GENECLASS resulted in 82% of individuals being correctly assigned. However, the geographic distribution of the groups was not related to any logical topographic or habitat divisions. Bossart and Prowell (1998) suggest that population structure should be associated with geography in the interpretation of genetic evidence.

With this in mind, I believe that the population on Saddle Island consists of two subpopulations: one in the Northern third of the island and the other occupying the rest of the island. Although there is definite evidence of genetic exchange between the subpopulations, there is also strong evidence for structuring. In all months except March trapping records suggested a separate Northern subpopulation. F_{ST} values between the preliminary Central and South populations were non-significant indicating they were acting as a single population. Clustering analysis identified a subpopulation in the North of the island (Figure 6.4) but the individuals assigned to both populations were mixed together. I believe that in this case geography outweighs genetics and that the island is divided into two subpopulations with some gene flow between them.

6.5.4. Summary and Conclusions

The aims of this chapter were largely descriptive – to describe the population structure of mice on a small island, and to describe a possible colonisation history for the population. Trapping data revealed changes in population structure through the year. The mice that were included in the genetic analysis had capture histories that revealed a network of overlapping ranges and potential interactions. The extent of overlapping ranges suggested the population was behaving as a single unit and that there would be no population structure revealed by genetic analysis. This was not the case and genetic analysis divided the population in two meaning that despite the extent of overlapping ranges and potential interactions there was still non-random mating resulting in population structuring (Berry and Jakobson, 1974). Combining methods allowed a far better description of population structure and social organisation to be made than would have been possible with one method alone.

The ability of mice to breed successfully and establish a population after arriving in a new area is clear from their wide distribution on islands (Pocock et al., 2005). Results from the genetic analyses reported here imply that the mouse population on Saddle Island was established by a low number of founders. Species which are able to establish a population from low numbers of colonising individuals require special management (Ficetola et al., 2008) as the arrival of low numbers of individuals could quickly result in a widespread population. This highlights the importance of effective quarantine and surveillance measures for maintaining mouse-free areas (Russell et al., 2008a, Oppel et al., 2010). Surveillance methods must be able to detect and remove all invaders before they have a chance to breed and become established.

Chapter 7. General conclusions

7.1. Research summary

The overall aim of this research was to investigate key aspects of house mouse behaviour in relation to eradicating them from islands. Population densities and individual ranging behaviour of mice on islands had not previously been studied in detail, possibly because mice tended to be overlooked relative to rats (Simberloff, 2009), so investigating these was a key priority (Chapter 3). It also became clear after reviewing all reported mouse eradication attempts (Chapter 2) that nothing was known about how mice behave at very low population densities, such as at the tail end of an eradication attempt or during a new invasion, and an experiment was designed to study this (Chapter 4). Chapter 5 used phylogeographic methods to identify where mouse populations in New Zealand may have originally come from and to investigate the possible impact this may have on mouse control and genetics and trapping were combined in Chapter 6 to investigate population structure and mouse colonisation history on a small island.

The results of this research have relevance both to preventing new invasions of mouse-free areas and the eradication of existing populations (Hulme, 2006). I will discuss these separately here before combining all my findings into a series of management recommendations. Specific discussion of results has already been covered in each chapter.

7.1.1. Mouse invasion biology

Knowing how invasive species behave when they arrive in a new area is essential to effectively manage new invasions (Dilks and Towns, 2002, Russell et al., 2008a, Russell et al., 2010a), yet research into this stage of the invasion process is rare (Byers et al., 2002). The worldwide distribution of house mice (Rowe, 1973, Ruscoe and Murphy, 2005) highlights how successful this species is as an invader (Pocock et al., 2005). However, the way mice behave after invading new areas was unknown so the experiment reported in Chapter 4 represents the first systematic investigation into mouse invasion biology. This experiment was unique due to the large amounts of behavioural data that were available for comparison, allowing the true novelty of behaviours shown by released animals to be appreciated. The released animals were sourced from a high density mouse population

where mice had small home ranges (Goldwater, 2007). Upon release onto Saddle Island their ranging behaviour changed significantly and the ranges of the released animals were ten times larger than the ranges shown by animals in the original population (eradicated in August 2008, Chapter 3) on Saddle Island. Released animals also moved twice as far in a night as the animals in the previously established population did. Previously reported investigations of the invasion behaviour of rat species (Russell et al., 2008a, Russell et al., 2010a, Innes et al., in press) have only released males, due to concerns about populations becoming established. In this research both males and females were released allowing exploration of possible reasons for the observed behavioural changes. There was no significant difference in behaviour between male and female mice. This was unexpected, but reassuring, as sex-related differences in behaviour would add an extra layer of complexity to the design of island surveillance systems. Differences in levels of range overlap between released animals in breeding and non-breeding seasons suggest that exploration of the island was driven by the search for companionship and the low level of overlap observed between two males that were released suggests that the search for companionship is really a search for a mate. The results of this experiment strongly suggest that mice show behavioural adaptations that allow them to effectively seek out other mice and therefore avoid mate-finding Allee effects. Evidence from Chapter 6 regarding the genetic diversity of mice in the established population of mice on Saddle Island suggests that mice are able to successfully found a population from a low number of colonising individuals. This was backed up by work carried out on Saddle Island in 2010. The final pair of mice released on Saddle Island in December 2009 were not removed to allow mouse colonisation dynamics to be investigated as an M.Sc. research project. Forty-one mice were removed from the island during August 2010 demonstrating that mice can establish a population from only two founders (H. Nathan, University of Auckland, unpub. data).

7.1.2. Eradication

My review of reported mouse eradication attempts up to 2007 painted a relatively bleak picture (Chapter 2). Nearly 40% of mouse eradication attempts worldwide had failed compared with only 5-10% for invasive rat species (Howald et al., 2007). Some failures were explicable due to operational problems such as a malfunctioning bait spreader on St. Paul Island (Micol and Jouventin, 2002). Other failures, such as Hauturu Island (Glassey, 2006), may be attributable to mouse reinvasion following a successful eradication – something which is difficult to distinguish from eradication failure without the use of population

genetics. For other failed eradication attempts there seemed to be no obvious operational reason, suggesting that failures were influenced by aspects of mouse biology. A review of the updated database was a little less bleak. The failure rate changed from 38% to 33% and there is evidence that mouse eradication attempts are getting more effective since only 9% of eradication attempts started in 2007 or later have failed.

The first step in determining why mouse eradication attempts fail was to gather baseline population data from mice living on an island. A small (6 ha) island north of Auckland was chosen for its accessibility and lack of threatened species following a long history of colonisation by Norway rats (*Rattus norvegicus*) and mice (Tennyson and Taylor, 1999). The mouse population on the island was studied throughout 2008. Three accurate density estimates were calculated through Capture-Mark-Recapture trapping in January, March and May and mouse home range size and movement parameters were calculated in July using radio-tracking. A final density estimate was calculated in August when the mouse population was eradicated using removal trapping and a 25 m grid of poison bait stations containing brodifacoum wax blocks (Chapter 3). Genetic samples were collected during the eradication and the analysis of these was described in Chapter 5 and Chapter 6. The island was intensively monitored following the application of poison and the eradication was declared successful in December 2008.

For an eradication attempt to succeed all individuals on the island must come into contact with the chosen kill device (usually traps or poison). There were concerns that mice may have very small home ranges or show limited ranging behaviour, resulting in not all individuals coming into contact with traps or poison. The ranges and movements reported in this study were in the middle range of those reported previously, but even the animals with the smallest recorded movements still ranged widely enough to come into contact with traps and poison. Results from Chapter 4 show that mice exhibit increased ranging behaviour in response to low density and Lidicker (1966) reported a similar effect from a population of mice on an island in the USA. It is possible that eradication survivors will show similar behaviour, thus increasing their chances of coming into contact with kill devices. However, a sudden reduction in population density of mice in an area may trigger a neophobic (fear of new objects, Barnett, 1988) response in any survivors. Rodents living in close proximity with humans show increased levels of neophobia as a result of repeated control attempts (Kronenberger and Médioni, 1985, Clapperton, 2006) and there is evidence that captive wild mice can also develop neophobia (Wolfe, 1969, Connor, 1975). Survivors of

an eradication attempt may therefore avoid traps, poison or monitoring devices (Brunton et al., 1993). It is unclear whether or not neophobia is inherited (Brunton et al., 1993); if it is not then offspring of survivors are likely to be detectable. This could explain why mice were not detected in a fenced enclosure in central New Zealand until 6 months after poison applications aimed at eradicating mice and a range of other mammal species were completed (Speedy et al., 2007), and may also be a factor in other failed eradication attempts. This response is part of the wide repertoire of innate mouse behaviours and as such is likely to be impossible to predict or control for.

The main toxin used in mouse eradication attempts is brodifacoum (Howald et al., 2007, MacKay et al., 2007) and a range of studies have confirmed that mice are susceptible to this toxin (Redfern et al., 1976, Rowe et al., 1978, O'Connor and Booth, 2001, Cleghorn and Griffiths, 2002, O'Connor et al., 2005, Morriss, 2007). Mice with resistance to anticoagulant toxins have been recorded in many localities (Lund, 1984, Greaves, 1994, Bailey and Eason, 2000, Billing, 2000, Pelz et al., 2005, Rost et al., 2009, Guidobono et al., 2010) and this resistance has a genetic basis (Pelz et al., 2005, Rost et al., 2009) meaning it could be present in mouse populations that are being eradicated. In Chapter 5 I used a phylogeographic approach to trace the origins of mice from islands and mainland sites with different conservation control regimes with the aim of searching for links to areas with reported anticoagulant resistance. No conclusive links were found, but resistance could become an issue in sites where mice are controlled with frequent anticoagulant applications rather than eradicated (e.g. Billing, 2000).

7.1.3. Conclusions

The data presented here suggest that well planned mouse eradications should be successful and highlight the impressive invasion potential of mice. I did not find any evidence of behavioural or genetic characteristics that would influence eradication success. However, the behavioural flexibility of mice makes it very difficult to be completely sure of this. Every population may have one mouse that is able to survive. Small numbers of eradication survivors or new invaders on an island are highly likely to find each other and successfully breed and establish a population. Therefore it is critically important that an eradication kills 100% of individuals and that invasions are detected and halted early. Recommendations for managers based on this work are listed in Section 7.3.

7.2. Mice and rats

It is important to remember that mice are not simply small rats. They show significant differences in behaviour and physiology that are relevant to control programmes (Clapperton, 2006). The LD_{50} (poison dose required to kill 50% of tested individuals) of brodifacoum for mice is well over twice that of Norway rats (O'Connor and Booth, 2001) meaning that mice are substantially less susceptible to the toxin. Levels of neophobia differ between the species (Barnett, 1988) and this can affect the response to toxic baits (Clapperton, 2006). More concerning is the ability of rats to suppress mouse populations and there have been a number of islands where mice were only detected following a rat eradication (Caut et al., 2007). Mice were not detected on Saddle Island until Norway rats were eradicated from the island in 1989 and it is not clear whether they arrived after the eradication or were coexisting with the rats (Tennyson and Taylor, 1999). A similar situation has been reported on other islands and has been termed the "competitor release effect" (Caut et al., 2007). From an eradication planning perspective it is important to know what species are present on the island. Often it is very difficult to trap mice when there are rats present (e.g. Witmer et al., 2007), but targeted trapping of areas where mice may be present may be successful. In my own experience of rodent trapping in areas where both rats and mice were present, I mainly caught mice in grassy areas and rats in forested areas. Failed eradications are financially costly and each failure increases the risk that future operations will not be supported. If there is any suggestion that mice may be coexisting with rats every effort should be made to confirm or deny their presence and eradication methods should be adapted accordingly. Encouragingly, it appears that mice and both ship and Norway rats show similar invasion behaviour meaning that one well-planned surveillance system should detect all three species (Chapter 4).

7.3. Management recommendations

The negative impacts of mice on ecosystems are arguably as severe as those of rats and therefore every effort should be made to eradicate them from islands where feasible. Although the high failure rate for mouse eradication attempts may seem daunting, with proper planning and implementation mice can be eradicated from islands. The increased success rate since 2007 (largely driven by the expertise of the Island Eradication Advisory Group) shows this. The invasion risk posed by mice is high and important mouse-free islands should therefore have effective surveillance systems that will allow mouse

incursions to be detected rapidly. Some management recommendations drawn from my research follow.

1. Collect genetic samples from at least 10 mice before the eradication attempt and store in 70% ethanol. Should mice be detected following the eradication attempt genetic samples will allow a distinction to be made between a failed eradication and a reinvasion.
2. Install permanent monitoring stations before the eradication attempt begins. Tracking tunnels are ideal for this purpose. Ensure some monitoring stations are placed in areas such as rank grassland where mice can find ample food and may be present in high numbers. Permanent monitoring devices become part of the island environment therefore avoiding any neophobic effects. If the eradication is successful, identify periods when rats or mice are likely to be dispersing or the island is frequently visited and target monitoring for these times. Rats and mice range widely when introduced to a new area meaning that sparse detection grids targeting likely landing points may be effective.
3. Ensure you know which species are being eradicated. If there are any suspicions that mice and rats are coexisting try to confirm the presence of mice by trapping areas where they may be present.
4. If feasible, consider applying extra poison to areas where mice may be present in high numbers.
5. Eradicating rats and mice in the same operation requires careful planning. Three aerial poison applications were used on Rangitoto and Motutapu in order to ensure that mice had access to poison (Griffiths, 2008). If two aerial applications are planned, delaying the second application longer than the 7-10 days which is currently recommended (Golding, 2010) may increase mouse access to poison. All 28 ship rats radio-tracked during a poison operation on Anacapa Island, California, USA died within 14 days of the poison application (Howald et al., 2010). A gap of at least 14 days between poison applications if mice and rats are present on the same island could be advisable.

If monitoring devices detect mice, consider the use of "Judas" or "Delilah" animals (McIlroy and Gifford, 1997) to detect and remove survivors or invaders. A female mouse released on Saddle Island was observed sitting on top of a cage containing the body of a male mouse suggesting, this technique may be worth further research.

7.4. Future perspectives

This research explored a range of factors that may influence the success of mouse eradication attempts. Along the way some limitations of the methods used were noted and some avenues for further research were identified.

A relatively high rate of ear tag loss during CMR trapping on Saddle Island (Chapter 3) meant it was impossible to accurately estimate survivorship. Each trapping session also had to be analysed separately as a result of animals not being identifiable between sessions thus violating one of the assumptions of closed capture analysis (3.3.5.1). Two alternative methods of animal marking may have been more effective – ear punching and PIT tags. Ear punching marks (Cruickshanks et al., 1991) are more permanent than ear tagging as they cannot be ripped out as easily. This marking method also allows a small genetic sample to be collected from every mouse that is handled. Analyses of population structure on the island would have been more powerful if genetic samples were available from every trapping session rather than just from the August 2008 eradication trapping. PIT tags are small transponders which are inserted under the skin of the mouse (Gibbons and Andrews, 2004). They are uniquely numbered and allow an animal to be identified permanently with a minimal amount of handling. They are an expensive option but definitely worth considering for long term studies.

The phylogeographic analysis reported in Chapter 5 could be improved if D-loop haplotypes from mice with known anticoagulant resistance were available for comparison. Mice from Tawharanui should be tested for mutations in the VKORC1 gene that are known to confer anticoagulant resistance (Rost et al., 2004, Pelz et al., 2005, Rost et al., 2009) in case sustained exposure to brodifacoum has contributed to selection for these mutations (Greaves, 1994). The capacity to identify mutations in the VKORC1 gene has been developed in New Zealand for ship and Norway rats (E. Murphy, Department of Conservation, pers. comm.) and including mice in this research should be a high priority.

Analysis of population genetic data from Saddle Island suggested that the original population was founded by a small number of individuals (Chapter 6). Combining individual genotype data with estimates of population growth rate obtained from Saddle Island during a colonisation experiment in 2010 (H. Nathan, University of Auckland, unpub. data) will allow the number of founders of the population to be estimated using a simulation

method described by Ficetola et al. (2008). Levels of multiple paternity of mouse litters in New Zealand are unknown and could be quantified by trapping pregnant mice in the breeding season and genotyping mothers and embryos following the methods of Miller et al. (2010).

Section 7.2 described some of the problems associated with managing rats and mice on the same island. There are many possible interactions between the species which could be studied in order to improve management; one of the most interesting for me is whether or not a mouse incursion can be detected on an island where there is a rat population and whether or not a mouse population can establish in the presence of rats. Goat Island, Leigh, New Zealand (Russell et al., 2009b) could be a good location for experiments of this nature.

7.5. Closing thoughts

The goal of this research was to identify possible reasons for why nearly 40% of mouse eradication attempts worldwide had failed and to produce recommendations to improve future eradication attempts. This applied, management-focussed goal provided plenty of scope for important ecological research with worldwide implications. My in depth study of the mouse population on Saddle Island prior to eradication was the first of its kind, and the information gathered regarding population densities, individual movements and population genetics will be invaluable for future eradication planning. In the introduction to this thesis I commented on the high levels of behavioural flexibility shown by mice. My unique experiments investigating the invasion biology of mice highlighted just how behaviourally flexible the species is and how this flexibility contributes to the species' success as an island invader. The management recommendations resulting from this research should be incorporated into eradication planning and in theory, well-planned and well-implemented eradication attempts against mice should result in success.

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Appendix 1. House mouse eradications database

Table 1: Islands where house mice have been successfully eradicated. The methods listed are: A=Aerial, B=Bait stations, H=Hand broadcast, T=Trapping. Toxins listed are: BM=Brodifacoum, BE=Bromadiolone, DE=Diphacinone, FN=Flocoumafen, PE=Pindone, WN=Warfarin. Countries listed are: AUS=Australia, FRA=France, ICE=Iceland, MAU=Mauritius, NZL=New Zealand, POR=Portugal, ROS=Republic of Seychelles, UK=United Kingdom. Entries in bold type were added to the database in the February 2011 update (Section 2.6). * = date confirmed after a 2 year confirmation process, # = Method not confirmed, assumed to be bait stations. $Mice have since reinvaded.

Island	Area (ha)	Country	Date started	Methods	Toxin	Date completed	Reference
Beacon	1.2	AUS	1997	B	PE, BM	1997	(Burbidge and Morris, 2002)
Bridled	22	AUS	1997	B	PE, BM	1997	(Burbidge and Morris, 2002)
Montague	**80**	**AUS**	**2007**	**A**	**BM**	**2007***	**I. Wilkinson pers. com**
Varanus	80	AUS	1997	B	PE, BM	1997	(Burbidge and Morris, 2002)
Surprise Island	24	FRA	2001	H	BE	2006	F. Courchamp, pers. comm.
Flatey Island	50	ICE	1971	B#	WN	1971	(Moors et al., 1992)
Flat Island	253	MAU	1998	B	BM	1998	(Bell, 2002)
Ile aux Sables	8	MAU	1995	B, H	BM	1995	(Bell, 2002)
Ile Cocos	15	MAU	1995	B, H	BM	1995	(Bell, 2002)
Rasa Island	60	MEX	1994	B, T	BM	1994	(Tershy et al., 2002)
Adele	**87**	**NZL**	**2007**	**A**	**BM**	**2009***	**(Golding, 2010)**
Allports	16	NZL	1989	B	FN	1991*	(Brown, 1993)
Blumine	377	NZL	2005	A	BN	2007*	M. Aviss pers. comm.
Browns	58	NZL	1995	A	BE	1997*	(Veitch, 2002a)
Coal	**1100**	**NZL**	**2008**	**A**	**BM**	**2010***	**A. Cox, pers. comm.**
Enderby	710	NZL	1993	A	BM	1995*	(Torr, 2002)
Fisherman	**4**	**NZL**	**2007**	**A**	**BM**	**2009***	**(Golding, 2010)**
Mana	217	NZL	1989	A, B	BM, FN	1991*	(Hook and Todd, 1992)
Mokoia	135	NZL	2001	A, H	BM	2003*	(Armstrong et al., 2001)
Motuihe	179	NZL	1997	A	BM	1999*	(Veitch, 2002b)
Moturemu	5	NZL	1992	B	BM	1994*	I. McFadden pers. comm.
Motutapere	45	NZL	1994	A, B	BM	1996*	P. Thomson pers. comm.
Motutapu (Marlborough)	2	NZL	1989	B	FN	1991*	(Brown, 1993)
Mou Waho	140	NZL	1995	A, T	BM	1997*	(McKinlay, 1999)
Ohinau	43	NZL	2005	A	BM	2006	J. Roxburgh pers. comm.
Papakohatu	0.7	NZL	1996	B, T	BM	1997	(Lee, 1999)
Pickersgill	103	NZL	2005	A	BM	2007*	M. Aviss pers. comm
Pomona$	**262**	**NZL**	**2007**	**A**	**BM**	**2009***	**(Shaw and Torr, in press)**
Rimariki	22	NZL	1989	B	BE	1991	(Veitch and Bell, 1990)
Rona	**60**	**NZL**	**2007**	**A**	**BM**	**2009***	**(Shaw and Torr, in press)**
Saddle	**6**	**NZL**	**2008**	**T, B**	**BM**	**2008**	**(MacKay et al., in press)**
Tonga	**8**	**NZL**	**2007**	**A**	**BM**	**2009***	**(Golding, 2010)**
Whenuakura	2	NZL	1983	B	BE	1984	(Newman, 1985)
Selvagem Grande	200	POR	2002	B	BM, HS	2003	(Olivera et al., 2010)
Curieuse Island	**286**	**ROS**	**1996**	**A**	**BM**	**1998**	**(Hill et al., 2002)**
Denis	**143**	**ROS**	**2000**	**A**	**BM**	**1992**	**(Parkes, 2008)**
Frégate	219	ROS	2000	A	BM	2002	(Merton et al., 2002)
White Cay, Bahamas	15	UK	1998	B	BM	1998	(Hayes et al., 2004)

Table 2: Eradication attempts that have not resulted in the removal of mice. The methods listed are: A=Aerial, B=Bait stations, H=Hand broadcast, T=Trapping. Toxins listed are: BM=Brodifacoum, BE=Bromadiolone, DE=Diphacinone, FN=Flocoumafen, PE=Pindone, WN=Warfarin. Countries listed are: AUS=Australia, FRA=France, ICE=Iceland, MAU=Mauritius, NZL=New Zealand, POR=Portugal, ROS=Republic of Seychelles, UK=United Kingdom.

Island	Area (ha)	Country	Date started	Methods	Toxin	Date completed	Reference
INCOMPLETE							
Ile Chateau	250	FRA	2002	A	BM	n/a	M. Pascal pers. comm
Motutapu (Hauraki Gulf)	**1560**	**NZL**	**2009**	**A**	**BM**	**n/a**	**(Griffiths, 2008)**
Rangitoto	**2321**	**NZL**	**2009**	**A**	**BM**	**n/a**	**(Griffiths, 2008)**
STOPPED							
Silver	25	NZL	1997	B	BM	n/a	S. Thorne pers. comm.
Stevensons	65	NZL	1997	B	BM	n/a	S. Thorne pers. comm.
UNSUCCESSFUL							
Varanus	80	AUS	1993	B	1080	n/a	(Burbidge and Morris, 2002)
Fajou	120	FRA	2001	H, T	BE	n/a	M. Pascal pers. comm..
St. Paul	800	FRA	1997	A	BM	n/a	(Micol and Jouventin, 2002)
Tromelin	100	FRA	2005	B, H	BM	n/a	?
Haulashore	6	NZL	1991	B	BM	n/a	(Thomas and Taylor, 2002)
Hauturu	10	NZL	1993	B, H	BM	n/a	(Glassey, 2006)
Hokianga (Ohiwa)	8	NZL	2006	B	PE	n/a	D. Paine pers. comm.
Limestone (Matakohe)	37	NZL	1996	A	BM	n/a	(Ritchie, 2000)
Limestone (Matakohe)	37	NZL	1997	A	BM	n/a	(Ritchie, 2000)
Limestone (Matakohe)	37	NZL	1998	A	BM	n/a	(Brackenbury, 2001)
Limestone (Matakohe)	37	NZL	1999	B	BM	n/a	P. & C. Mitchell pers. comm.
Mokoia	133	NZL	1989	B	BM	n/a	(Owen, 1998)
Mokoia	133	NZL	1996	A	BM	n/a	(Dumbell, 1998)
Patiti (Banded)	12.8	NZL	2004	B	BM	n/a	(Bancroft, 2004)
Saddle (Te Haupa)	6	NZL	1993	B	FN	n/a	T. Wilson pers. comm.
Quail	81	NZL	2002	B, H	BM	n/a	(Bowie, 2002)
Quail	**81**	**NZL**	**2009**	**A**	**BM**	**n/a**	**M. Bowie pers. comm.**
Bird Island	101	ROS	1996	B, H	BM	n/a	(Merton et al., 2002)

Appendix 1 References

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Appendix 2. MARK models

The following three tables provide details about the models used for Capture-Mark-Recapture analysis in Chapter 3. "Behaviour" means a behavioural response to capture and "Time" means capture probabilities were different on different trapping days. "." is the simplest model where capture probability is constant with no heterogeneity. "Age" and "Sex" are individual covariates discussed in Section 3.3.5.1. Data are only displayed for models that were included in model averaging (Section 3.4.2).

Table 1: MARK models used in Session 1 analysis

Model	ΔAICc	Weight*	Parameters	Population Estimate	SE
Behaviour + Age	0	0.51319	3	72.2	21.8
Behaviour + Age + Sex	2.064	0.18284	4	71.9	21.6
Age	2.7624	0.12895	2	54.6	6.3
Time + Age	4.321	0.05915	6	52.5	5.7
Age + Sex	4.7001	0.04894	3	54.6	6.3
Behaviour + Time + Age	5.5398	0.03216	7	67.4	24.9
Time + Age + Sex	6.3353	0.02161	7	52.6	5.8
Behaviour + Time + Age +Sex	7.6691	0.01109	8	66.6	24.1
Behaviour	13.5761	0.00058	2	54.4	7.3
Behaviour + Sex	13.6849	0.00055	3	56.0	8.7
.	14.6043	0.00035	1	48.9	2.4
Sex	15.1526	0.00026	2	49.2	2.6
Time	16.4256	0.00014	5	48.1	2.4
Time + Sex	17.002	0.0001	6	48.3	2.5
Behaviour + Time	18.4887	0.00005	6	50.7	6.4
Behaviour + Time + Sex	18.9657	0.00004	7	52.3	8.5

Table 2: MARK models used in Session 2 analysis

Model	ΔAICc	Weight	Parameters	Population Estimate	SE
.	0	0.17232	1	108.0	5.7
Sex	0.1985	0.15603	2	108.8	6.0
Behaviour + Sex	0.5005	0.13417	3	119.5	15.6
Behaviour	0.6469	0.1247	2	116.5	13.5
Age	1.0829	0.10027	2	112.0	7.6
Age + Sex	1.5287	0.08024	3	112.9	8.0
Behaviour + Age	1.8552	0.06815	3	119.0	14.6
Behaviour + Age + Sex	1.9766	0.06414	4	122.0	16.7
Time	3.8547	0.02508	4	107.8	5.7
Time + Sex	4.075	0.02246	5	108.6	6.0
Time + Age	4.958	0.01444	5	111.8	7.6
Time + Age + Sex	5.4277	0.01142	6	112.7	8.0

Behaviour + Time	5.8715	0.00915	5	105.0	12.0
Behaviour + Time + Sex	6.1383	0.00801	6	108.7	17.3
Behaviour + Time + Age	6.9317	0.00538	6	104.1	9.9
Behaviour + Time + Age + Sex	7.5034	0.00405	7	106.1	12.3

Table 3: MARK models used in Session 3 analysis

Model	ΔAICc	Weight	Parameters	Population Estimate	SE
Behaviour	0	0.25313	2	69.1	4.3
Behaviour + Sex	0.5216	0.19502	3	70.0	5.1
Behaviour + Age	1.7041	0.10797	3	69.1	4.3
Behaviour + Age + Sex	2.1675	0.09441	4	70.0	5.1
.	3.0582	0.06048	1	65.1	1.6
Time	3.9607	0.03851	4	65.0	1.6
Sex	4.1206	0.03555	2	65.2	1.7
Age	4.3018	0.03247	2	65.1	1.6
Time + Sex	5.0594	0.02223	5	65.1	1.6
Behaviour + Time	5.2301	0.02042	5	67.4	4.9
Time + Age	5.243	0.02028	5	65.0	1.6
Age + Sex	5.2532	0.02018	3	65.2	1.7
Behaviour + Time + Sex	5.9189	0.01447	6	69.4	8.0
Time + Age + Sex	6.2295	0.01239	6	65.1	1.6
Behaviour + Time + Age	6.838	0.00914	6	67.5	5.0
Behaviour + Time + Age + Sex	7.5416	0.00643	7	69.4	8.1