Ecological drivers of seabird recovery after the eradication of introduced predators

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I regard the mutton-bird islands as the perfect dream-haven—a paradise set in the blue waters of the southern-most part of the Pacific Ocean, with the trees' foliage in places bowing and dipping to pay homage to the sparkling waters lapping the shores of nature's bounteous gift

-T.V. Saunders 1968
Extended Abstract

Eradication of introduced mammalian predators to restore island ecosystems has become increasingly common, with over 800 successful projects around the world. Historically, introduced predators depleted populations of many native species, leading some, especially seabirds, to extinction or local extirpation. Island restoration is dependent on seabird population recovery, due to these birds’ indispensable role as ecosystem engineers. However, natural population responses are rarely documented and recovery dynamics are poorly understood. New Zealand holds the world’s highest diversity of seabirds and has completed more introduced predator eradication projects than any other country, making it an ideal location to study seabird population processes and island restoration. In this thesis I outline a model of seabird population growth, test the importance of key ecological variables in driving the recovery of burrow-nesting seabirds (order: Procellariiformes) on islands in New Zealand, and examine a possible method of enhancing population recovery. Finally, I summarize an effective post-eradication monitoring scheme that could provide information to improve the model of seabird population growth and facilitate priority setting for New Zealand’s seabirds.

My thesis begins by constructing a generic conceptual model of seabird colony growth to identify key predictor variables relevant to recovery and re-colonization (Chapter 2). I tested the importance of these variables in driving seabird population responses after introduced-predator eradication on islands around New Zealand. The most influential variable affecting re-colonization of seabirds was the distance to a source population, with few cases of re-colonization without a source population ≤ 25 km away. Colony growth was most affected by metapopulation status; there was little colony growth in species with a declining metapopulation. I conclude that these characteristics can help guide the prioritization of newly predator-free islands for active management.

The distribution of burrow-nesting seabird colonies is thought to be partly regulated by the availability and quality of suitable breeding habitat, which may limit colony growth after predator removal. I used a Bayesian hierarchical modelling approach to examine how nest-site selection differs among recovering procellariiform seabird communities after eradication of Pacific rats (*Rattus exulans*; Chapter 3). I found that soil depth was the most
important predictor of burrow presence, abundance, and occupancy in plots among islands, with more burrows found in deeper soil. There was a striking linear relationship between burrow density and time since rat eradication \((P < 0.01, R^2 = 0.37)\) and birds showed weaker nest-habitat selectivity with increasing time since rat eradication \((P = 0.02, R^2 = 0.47)\). Results suggested that selection of particular nesting habitat may be more important in small recovering populations. Thus, colony expansion immediately after introduced-predator removal may be limited by nesting habitat quality, namely the availability of deep soil.

When selecting nesting habitat, colonial animals can also use social cues provided by breeding conspecifics. Conservation practitioners have used seabirds’ affinity for conspecific cues to establish colonies at abandoned sites using decoys or call playback. However, success rates of these projects have varied. In Chapter 4 I tested the attraction of three sympatric petrel species to social cues in the form of vocalization playback. I then examined whether the size of breeding colonies within 1 km of playback locations (found to be important in Chapter 2) affected the strength of attraction. Grey-faced petrels \((Pterodroma macroptera gouldi)\) were attracted to conspecific vocalization playbacks at all sites, fluttering shearwaters \((Puffinus gavia)\) were only attracted at two of three locations, and flesh-footed shearwaters \((P. carneipes)\) were not attracted at all. Response to playback increased with increasing densities of nearby breeding conspecifics (all \(P < 0.002\)). For some species, such as grey-faced petrels, vocalization playbacks may represent a cost-effective alternative to other restoration approaches. However, their effectiveness for individual species at different sites should be assessed before embarking on restoration initiatives.

Although the recovery of burrow-nesting seabird communities is complex, driven in part by nesting habitat and social cues, the ultimate outcome will be limited by underlying assembly rules. Assembly rules are mechanisms governing colonization and eventual community structure, including inter-specific competition and facilitation. To draw inference on how inter-specific interactions regulate petrel community ‘reassembly’ after eradication, I investigated species co-occurrence using null model testing (Chapter 5). Community structure of six petrel species on six islands in north-eastern New Zealand provided evidence that reassembly is influenced predominantly by inter-specific
facilitation. However, exclusion between petrel species increased as time since rat eradication increased, suggesting that interactions between species may be competitive at certain stages of recovery. I demonstrate how co-occurrence analysis can aid in understanding and managing recovery of communities, rather than single species, after predator eradication.

Density dependence is important for managing recovery because it governs the rate and dynamics of population growth. In Chapter 6, I demonstrate how both positive and negative density dependence operate during seabird colony expansion after rat eradication. Using Bayesian hierarchical modelling of burrow density as a proxy for relative abundance, I tested whether petrel colonies increase in density or area on islands after rat eradication. I found that mean burrow density increased (mean effect size 0.05; 95% credible intervals 0.01 – 0.11), burrows remained clustered (i.e. spatially structured), but colony extent increased with time since rat eradication, with colonies filling over 70% of the island’s surface by 25 years after eradication.

In Chapter 7, I outline a potentially effective petrel monitoring programme using a power analysis of simulated monitoring data based on burrow densities from Chapters 3-6. To detect levels of change in burrow density of interest to conservation managers with >80% power, I found that at least 80 plots of 3-m-radius on 15 islands must be monitored annually, with more plots required in less-preferred habitat (shallow slopes at low elevations). As large-scale changes continue to alter populations and conservation priorities for seabirds, data collected using robust monitoring approaches can be used to revise the model of population recovery and prioritize management interventions.

Finally, I discuss the broader ecological implications of my thesis (Chapter 8). This includes my finding that, despite the central dogma in seabird ecology that species are strictly philopatric, strong evidence supports metapopulation connectivity as a driver of population recovery. Furthermore, my data suggest that positive and negative density dependence operate during recovery, meaning that remnant colonies facilitate initial colony growth, whereas competition may eventually reduce growth or encourage the spatial spread of a colony. I synthesize these ecological drivers of recovery into a set of management recommendations for island restoration, and suggest future research directions.
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Chapter 1  General Introduction

1.1 Ecological restoration: a global challenge

Between one-third and one-half of the earth’s land surface has been transformed by human activity (Vitousek et al. 1997b). In addition, global exchange has facilitated the spread of species into regions they may never have reached without human intervention (Mooney and Hobbs 2000, Hobbs et al. 2006). The introduction of species by humans exacerbates the negative effects of human activities and is considered to be one of the most pervasive components of global change (Vitousek et al. 1997a, Simberloff et al. 2013).

Increasing incidence of anthropogenic environmental degradation has generated a pressing need to understand ecological restoration (Gårdmark et al. 2003). Ecological restoration is the process of assisting the recovery of a population or ecosystem that has been damaged or destroyed by humans (Jackson et al. 1995, Hobbs and Norton 1996, Hobbs and Harris 2001). As pristine areas become scarcer, global conservation paradigms have shifted focus: from safeguarding untouched ecosystems to repairing and re-assembling degraded ones (Halle and Fattorini 2004). Accordingly, ecological restoration represents a significant new challenge, which can be guided by ecological science.

Restoration ecology has been regarded as a new strategy to maintain biological diversity and ecosystem functioning (Jordan et al. 1988, Hobbs and Cramer 2008), a hope for the future (Dobson et al. 1997, Choi 2007), and, conceptually fundamental to this thesis, a “testing laboratory” of ecological theory (Temperton et al. 2004). Although the discipline of restoration ecology has grown dramatically in the past few decades, scepticism has generated a number of requirements for successfully meeting restoration goals (Choi et al. 2008). These include clearly delineated past and present reference conditions and a sound conceptual model of recovery based on ecology and science (Michener 1997, Eagan and Howell 2005).

1.2 Island restoration
Islands play an increasingly important role in conservation biology. They often act as refuges, housing remnant populations or ecosystems eliminated from the mainland (Currie et al. 2003, Eldridge et al. 2004), or as model ecosystems for examining biodiversity conservation, allowing discrete assessment of response to environmental stressors (Vitousek et al. 1995). Due to their isolation and, in many cases lack of human habitation, islands are thought to harbour some of the least disturbed ecosystems (McCauley et al. 2013). However, with both pre-historic and European exploration, humans either reached or colonized even the most remote island groups (Steadman 1995). With humans came exotic mammals. Europeans often deliberately introduced cattle (Bos primigenius), sheep (Ovis aries), goats (Capra aegagrus hircus), pigs (Sus domesticus), and rabbits (Oryctolagus cuniculus) as alternative food sources for indigenous peoples or marooned sailors. Incidentally, predatory cats (Felis catus), rats (Rattus spp.), and dogs (Canis lupus) were also introduced (Towns et al. 2011b). Rodents are especially successful island invaders, having spread to 90% of all island archipelagos (Towns et al. 2006, Jones et al. 2008).

Because animal communities on islands have high rates of endemism, little diversification, and often evolved in the absence of ground-based mammalian predators, the introduction of predators by humans has had devastating effects (Courchamp et al. 2003). For example, 93% of 129 bird extinctions in the past 500 years have been island species (King 1985, Birdlife International 2000). Furthermore, island birds constitute 67% of the world bird species currently threatened with extinction (Rauzon 2007).

Evidence of the negative impacts of introduced mammalian predators (hereafter ‘introduced predators’) has prompted concerted global efforts to restore islands by eradicating invasive species (Veitch and Clout 2002, Keitt et al. 2010). To date, 25 species of introduced predators have been removed from over 800 islands around the world (Donlan and Wilcox 2008, Bellingham et al. 2010, Keitt et al. 2011). These successes show no sign of slowing, as conservation practitioners improve techniques and leverage new technologies, allowing predator eradication projects to be successful on increasingly larger islands with more complex terrain (Howald et al. 2007, Lavoie et al. 2007, Veitch et al. 2011a).

Thus, island restoration is now at a turning point, in which conservation managers
can begin to re-assemble ecosystems across large areas of newly predator-free space. However, due to the financial and logistical constraints associated with island research, post-eradication recovery dynamics remain poorly studied and restoration targets remain ambiguous (Towns 2002, Jones 2010b, Jones 2010a, Jones et al. 2011). Generally, comprehension of how island species and ecosystems respond to introduced predator eradication lags far behind our knowledge of how to remove predators (Mulder et al. 2009). This knowledge gap is particularly important, not only because of the potential to highlight the advantages of expensive eradication campaigns, but also because eradications are large-scale ecological experiments, and examining the results can reveal fundamental insights into key regulators of island populations (Phillips 2010).

1.3 Seabirds and “seabird islands”

Seabirds are major drivers of island ecosystem functioning. Seabirds are defined as highly mobile birds that spend the majority of their lives in the marine environment, where they are apex predators (Sydeman et al. 1997, Veit et al. 1997, Brooke 2004). However, seabirds must return to land to breed, and often do so in dense colonies on oceanic islands (Schreiber and Burger 2001). In this way, seabirds provide an important link between marine and terrestrial ecosystems, delivering marine-derived nutrients to breeding islands through their guano (Anderson and Polis 1999, Sanchez-Pinero and Polis 2000). Furthermore, high densities of breeding seabirds cause physical disturbance to soil and trees during the construction, entry, and maintenance of nests (Bancroft et al. 2005a, Mulder et al. 2011a). Therefore, on breeding islands (“seabird islands”) seabirds act as bottom-up island ecosystem engineers, increasing soil fertility, changing soil density, enhancing local primary productivity, and altering plant and invertebrate community composition (Ellis 2005, Mulder et al. 2011a). Seabirds also provide important food sources for native predators, such as snakes, crabs, tuatara, predatory and scavenging birds, whales, and sharks (Walls 1978, Burger and Gochfeld 1994) and are traditional food items for humans (Anderson 1997, Pars et al. 2001, Montevecchi et al. 2007). Furthermore, because breeding success and survival reflect the availability of forage fish, seabirds are used increasingly as indicators of marine health (Parsons et al. 2008, Durant et al. 2009,
Cury et al. 2011). Consequently, the conservation of seabird populations is of the utmost importance to maintain a variety of terrestrial and marine ecosystem functioning.

1.4 Threats to seabirds

With over 30% of species listed as threatened, the IUCN has ranked seabirds as the world’s most vulnerable group of birds (Birdlife International 2008). Seabirds interact with humans directly and indirectly in their marine and terrestrial habitats. At sea, seabirds suffer from mortality due to pollution, including ingestion of plastic debris (Ryan 1987b, a) and oil spills (Clark 1984), and by interacting with fisheries (Furness 2003). Human impacts are often more severe for seabirds on nesting islands because limited space and restricted habitat exacerbate anthropogenic factors (Burger and Gochfeld 1994). On breeding islands, seabirds are threatened by habitat loss and coastal development (Anderson and Keith 1980), overharvest (Vermeer and Rankin 1984, Duncan et al. 2002), climate change-induced sea level rise (Croxall et al. 2002, Baker et al. 2006), and the introduction of non-native predators (Atkinson 1985, King 1985, Courchamp et al. 2003). Introduced predators represent one of the most acute threats to seabird populations (Birdlife International, Donlan and Wilcox 2008). Because most seabirds have nested for millennia on islands free of mammalian predators, they lack behavioural and life-history adaptations to avoid and recover from ground-based predation (Atkinson 1985, Milberg and Tyrberg 1993). This has led to the extinction (e.g., Guadalupe Storm-petrel Oceanodroma macrodactyla; Jehl and Everett 1985), extirpation (McChesney and Tershy 1998), or severe reduction of seabird populations on islands where predators have been introduced (Towns et al. 2011b).

1.5 Seabird recovery and island restoration

Because of seabirds’ role as ecosystem engineers, population recovery after introduced predator eradication is central to the restoration of island ecosystems (Bellingham et al. 2010, Jones et al. 2011, Towns et al. 2012a). However, a number of
unique life-history and behavioural traits complicate the process of seabird population recovery. Seabirds are generally k-selected, with long life spans, low reproductive output, late age-at-first-reproduction, and long gestation periods, meaning that intrinsic rates of population growth are slow (Warham 1990, 1996, Schreiber and Burger 2001). Furthermore, although seabirds are physically able to move between breeding islands, behavioural constraints preclude more straightforward dispersal dynamics (Oro 2003, Matthiopoulos et al. 2005). For example, seabirds are thought to have high levels of philopatry (tendency for individuals to breed near their natal site; Ovenden et al. 1991, Stacey and Ligon 1991) and conspecific attraction (juvenile seabirds use conspecific social cues to signal safe nesting habitat; Kress 1998, Kildaw et al. 2005), meaning that immigration and new colony formation rates are potentially low.

Rates of seabird re-colonization at extirpated sites and population growth of remnant colonies after introduced predator eradication (“passive restoration”) have been variable. In some cases introduced predator eradication has resulted in dramatic population increases in remnant colonies (e.g. black oystercatcher Haematopus bachmani and pigeon guillemot Cephus columba after arctic fox Vulpes lagopus eradication in the Aleutian Islands; Byrd et al. 1997) or immediate re-colonizations (red-tailed tropicbird Phaethon aethereus and brown noddyl Anous stolidus after feral cat eradication from Ascension Island; Ratcliffe et al. 2010). More commonly, an increase in breeding success is observed after eradication, such as for Xantus’s Murrelet (Synthliboramphus hypoleucus) on Ancapa Island (Whitworth et al. 2005), shags (Phalacrocorax aristotelis) and razorbills (Alca torda) on Canna Island (Swann 2006), and petrels on Marion Island (Cooper et al. 1995) after rats and feral cat eradication.

There are some instances where eradication has not resulted in the re-colonization or recovery of native seabirds (e.g., common diving petrel Pelecanoides urinatrix on Mana Island, New Zealand 10 years after house mouse Mus musculus eradication; Miskelly and Taylor 2004). In these cases, further management (“active restoration”) is required to facilitate re-colonization and population recovery. Active restoration techniques for seabirds include chick translocation and social attraction (Griffith et al. 1989, Kress 1998, Parker 2008, Miskelly et al. 2009, Jones and Kress 2012). Translocation involves reintroducing populations by moving chicks from their natal colony.
to a restoration site and hand-rearing them to fledging, while social attraction aims to lure adult birds to breed at a restoration site using artificial social cues, such as vocal playbacks or decoys (Griffith et al. 1989, Kress 1998). However, much like passive restoration, active restoration project outcomes vary between seabird species and sites (Jones and Kress 2012). No current prioritization scheme exists to determine which sites would benefit most from active or passive restoration.

Generally, quantitative measures of seabird response after eradication are uncommon and a model of recovery has yet to be devised (Lavers et al. 2010). A lack of monitoring is most likely the result of unique logistical complexities associated with measuring seabird populations. Firstly, low reproductive output and late ages at reproduction suggest that the process of recovery will be slow, with lag periods before increases are observed requiring lengthy monitoring periods (Warham 1996). Furthermore, many seabirds nest on remote oceanic islands, nest in below-ground burrows or cavities, and attend nest sites at night (Brooke and Prince 1991, Hamer et al. 2002). Thus, not only must monitoring occur over long time periods, but breeding sites are expensive to reach and monitoring methods must overcome considerable logistical obstacles.

1.6 Island restoration in New Zealand

New Zealand represents an ideal location to examine island restoration and seabird population recovery after introduced predator eradication. New Zealand is the largest remote oceanic archipelago in the world (Bellingham et al. 2010). The archipelago holds the world’s highest diversity of seabirds, whose breeding ranges have been severely reduced by introduced predators; however, more successful introduced predator eradication projects have been completed than in any other country (Taylor 2000, Towns 2011).

With 24% of the world’s 350 seabird species breeding in New Zealand waters (42% of which breed nowhere else), New Zealand is the ‘seabird capital’ of the world (Taylor 2000). Furthermore, seabirds, specifically those in the order Procellariiformes (petrels) play a considerable role in the cultural identity of indigenous peoples (Māori). Since first arriving in New Zealand, Māori have harvested ‘tītī’ or muttonbirds (sooty shearwaters *Puffinus griseus* on the South Island and grey-faced petrels *Pterodroma*...
macroptera gouldi on the North Island), species that were an important source of food and trade (Lyver et al. 2008, Moller 2009). To this day, harvesting activities strengthen social cohesion and group identity (Taiepa et al. 1997).

Fossil records indicate that the mainland of New Zealand once housed an abundance of breeding seabirds (Holdaway et al. 2001). However, with the arrival of humans over 700 years ago, 577 of 735 islands around New Zealand were invaded by non-native mammals and seabirds were largely eliminated from the mainland (Holdaway et al. 2001, Wilmshurst et al. 2008). In response to the extinction or decline of many native birds, New Zealand conservation agencies began developing techniques for removing non-native mammals from islands (Parkes and Murphy 2003). By 1987, New Zealand was renowned internationally as a leader in eradication methods and managing islands for threatened species (Towns et al. 1997, Simberloff 2002). To date, over 15% of New Zealand’s invaded offshore islands have been cleared of introduced predators (Towns and Broome 2003, Dunlevy et al. 2011). This represents over 30,000 ha of newly predator-free space, including 30 projects which occurred over 25 years ago; and an enormous opportunity to examine the recovery of affected wildlife (Island Conservation 2011).

Currently, 27% of New Zealand’s seabird species are listed as ‘critically endangered’, ‘endangered’, or ‘vulnerable’ by IUCN standards, and the number of populations under threat increases annually (Taylor 2000, Wilson 2006). Despite the high threat levels for seabirds in New Zealand, research is chronically under-funded and knowledge gaps are vast (Moller et al. 2000, Wilson 2006). The prioritization of terrestrial biota in island conservation biology between the 1960s and 1980s meant that little emphasis was placed on the role of seabirds (Bellingham et al. 2010). However, more recently, a desire to restore island ecosystems, and the recognition of the role of seabirds as ecosystem drivers has been instrumental in putting the focus of ecological restoration research back onto seabirds (Atkinson and Towns 1990, Jones 2010b, Jones 2010a, Mulder et al. 2011a).

1.7 Thesis structure

1.7.1 Objectives and thesis roadmap
The goal of this thesis is to consider the general question, “how do seabird populations respond after introduced predator eradication and what ecological factors drive recovery?” These questions will be examined by addressing six objectives (Fig. 1.1):

Chapter 2) Summarize and test key predictor variables driving seabird response after introduced predator eradication from islands in New Zealand.

Chapter 3) Determine how nesting habitat preference affects the recovery of burrow-nesting seabird communities on a set of islands off New Zealand’s North Island.

Chapter 4) Examine the use of auditory social cues by petrel species and assess the use of auditory call playback as a method of actively enhancing petrel population recovery.

Chapter 5) Determine how inter-specific interactions affect the recovery of burrow-nesting seabirds on a set of islands off New Zealand’s North Island.

Chapter 6) Determine the density-dependent, spatio-temporal nature of petrel colony recovery after the eradication of introduced predators on a set of islands off New Zealand’s North Island.

Chapter 7) Outline an effective monitoring strategy for burrow-nesting seabirds, with the intention that post-eradication population response can be assessed more consistently in the future.

In Chapter 2, I outline a conceptual model of seabird recovery based on generic models of intrinsic population growth and metapopulation dynamics. From this conceptual model, I summarize the main ecological factors that could influence passive recovery. I then collate seabird recovery and re-colonization data from islands with introduced predators removed around New Zealand and test the effect of ecological factors on seabird population growth. Based on the influence of each factor, I make recommendations of species and sites where passive recovery is less likely and where active restoration should be prioritized.
Figure 1.1: Flow chart of thesis. Chapters within the grey box focus on burrow-nesting seabirds (order Procellariiformes) on islands off the north-eastern coast of New Zealand’s North Island. Chapters within the green box examine factors affecting passive colony recovery, while the chapter within the orange box examines a potential method of actively enhancing colony recovery.
In Chapters 3 to 6, I narrow my focus to changes in colony size of burrow-nesting seabirds (order Procellariiformes) on islands off the north-eastern coast of New Zealand’s North Island. Because little post-eradication data exist, I use a chronosequence or ‘space-for-time substitution’. In other words, I use a sample of islands with different times since Pacific rat (*Rattus exulans*) eradication, with rats still present, or where rats were never introduced as a proxy for temporal dynamics after eradication. I use islands within or directly adjacent to the Hauraki Gulf Marine Park for four reasons: 1) the Hauraki Gulf has been identified as an important area for seabird research, as little is known about population dynamics or basic habitat preferences for most seabird species (Taylor 2000, Gaskin and Rayner 2013); 2) islands in this region are of comparable climate, size, vegetation composition, and geology (Towns and Atkinson 2004, Whitehead et al. 2014); 3) islands offer a range of time periods after predator removal; and 4) some limited seabird data exist after predator removal (Taylor unpubl. data). Procellariiformes, or tubenose petrels, are ideal for island restoration research because the effects of introduced predators have been most pronounced in this order (Atkinson 1985, Warham 1990, Jones et al. 2008). Furthermore, because most species are burrow-nesting, and burrowing results in soil aeration and formation, petrels represent one of the most ecologically important groups of seabirds (Bancroft et al. 2005a).

In Chapters 3 to 5, I test the island-scale effects of three ecological factors, drawn from the conceptual model in Chapter 2: nesting habitat, inter-specific interactions, and inter-specific attraction). In Chapter 3, I examine nesting habitat preference in burrow-nesting seabird communities. I use a Bayesian hierarchical modelling approach to compare petrel burrow presence, abundance, and occupancy with a suite of abiotic and biotic habitat covariates. In this way, nest-site selection is assessed on each island, and compared with time since rat eradication. I test two predictions: 1) petrels on islands with less time since rat eradication will be more attracted to remnant colonies, thus nest-site selection will be more influenced by the presence of other nests, and 2) on islands with more time since eradication, crowding eventually forces recruits into new habitat, thus selection for preferred habitat will be weaker.

In Chapter 4, I examine another means by which burrow-nesting seabirds select habitat: using conspecific social cues. I take an experimental approach to examine the
attraction of three species of petrel to artificial social cues using vocalization playbacks. I use one of the most important factors from the conceptual model of colony growth in Chapter 2, the characteristics of a source population, to test sources of variation in attraction to vocalization playback. Finally, I discuss the possibility of using attraction to vocalization playback as a method to actively restore petrel populations.

In Chapter 5, I use co-occurrence analyses paired with nesting habitat preferences to determine whether different species exclude or facilitate the presence of others. I compare patterns of species co-occurrence between islands with differing amounts of time since rat removal to infer how inter-specific interactions shape petrel community reassembly after predator eradication.

In Chapter 6, I examine how petrel colonies expand in space over time after predator removal. To extrapolate whether colony growth is mediated by positive or negative density-dependence, I test whether nesting burrows (used as a proxy for relative abundance) increase in density, spatial clustering, or spatial extent after rat removal.

In Chapter 7, I use the information from my thesis to propose a monitoring programme prototype for burrow-nesting seabirds. I use inter- and intra-island variance from study islands to simulate data sets of different sampling intensities. I then calculate the power a range of sampling intensities to detect different rates of change in the relative abundance of petrels.

Finally, Chapter 8 presents a synthesis of my thesis findings into a series of recommendations to guide the monitoring and management of burrow-nesting seabirds after introduced predator eradication.

### 1.7.2 Structure

This thesis has been written as a series of papers with linked themes, intended for independent publication. Although there is some recurrency of introductory and methodological material throughout, slight modifications have been made in an attempt to minimize repetition. Manuscript format has been altered to maintain consistency. First person plural tense of co-authored papers has been changed to first person singular in the thesis. Chapter 2 has been published in Conservation Biology; Chapter 3 is in review by
Biological Invasions; Chapter 4 is in review by Emu; and Chapter 5 is in review by Animal Conservation. Appendix F (“Incidence of plastic fragments among burrow-nesting seabird colonies on offshore islands in northern New Zealand”) has been published in Marine Pollution Bulletin. The data in this paper were collected during thesis field work and are relevant to seabird conservation; however, because they were not related directly to this thesis’ aims, the study is included with appended material. Due to the large number of pages, appendices are included on a CD-ROM.
Chapter 2  Drivers of seabird population recovery on New Zealand islands after predator eradication

2.1 Introduction

Introduced predators have been implicated in two-thirds of animal species extinctions on islands (Atkinson 1985, Atkinson 1989, Jones et al. 2008). In contrast, recent progress with island restoration has made it one of the most successful collaborative global conservation initiatives (Howald et al. 2007). To date, 25 species of non-native predators have been removed from over 800 islands around the world (Donlan and Wilcox 2008, Bellingham et al. 2010, Keitt et al. 2011). These successes show no sign of slowing, as eradication of introduced predators on increasingly larger islands with more complex terrain becomes feasible (Howald et al. 2007, Lavoie et al. 2007, Veitch et al. 2011a).

After eradication, restoration of affected populations of native fauna can be active, where dispersal of wildlife is deliberately manipulated through techniques such as translocation or social attraction (Jones and Kress 2012), or passive, where populations of native animals are left to grow or re-colonize naturally (Scott et al. 2001). Seabird populations are particularly vulnerable to the impacts of introduced predators (Moors and Atkinson 1984) and may not re-colonize or recover passively due to species-specific social (Nocera et al. 2006) or life-history constraints (Doherty et al. 2004). Considering these unique traits, active restoration can help re-establish populations. However, passive restoration is far more widely used due to financial and logistical constraints associated with management on isolated oceanic islands. Although eradications have become more efficient and cost-effective, costs remain high on remote offshore islands (Martins et al. 2006, Ewen and Armstrong 2007, Aguirre-Munoz et al. 2008). There is currently no published research-based prioritization scheme to identify sites which will benefit most from passive or active restoration after predator eradication.

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Seabirds have low reproductive output (Wooller et al. 1992), exhibit natal and breeding site philopatry (Greenwood 1980), and are unable to adapt their behaviour to avoid predation by non-native predators (Wanless et al. 2007). Thus, populations are often extirpated or severely reduced on islands after predators are introduced (Towns et al. 2006, Rauzon 2007). When predators are eradicated, the same life-history traits that render seabirds vulnerable to predation can make population recovery slow or non-existent. Seabirds in island ecosystems often act as bottom-up ecosystem engineers by delivering marine-derived nutrients in their guano and, for burrow-nesting species, causing physical disturbance to soils through nest construction (Sanchez-Pinero and Polis 2000, Bancroft et al. 2005a, Ellis 2005). When seabirds are eliminated from islands, nutrients are no longer imported, changing ecosystem processes (Croll et al. 2005). Thus, seabird population recovery after eradication, although slow and complex, is generally essential for the recovery of island ecosystem functioning.

The New Zealand archipelago represents a rich source of information on predator eradication. In New Zealand, terrestrial fauna evolved in the absence of mammals, other than bats; thus, the introduction of mammalian predators by humans had disproportionately large impacts (Diamond 1990). With the arrival of humans, 577 of 735 islands around New Zealand were invaded by non-native mammals and most seabirds were extirpated from the mainland (Towns and Ballantine 1993, Parkes and Murphy 2003, Tennyson and Martinson 2006). However, more offshore islands have been cleared of introduced predators around New Zealand than any other country (over 15% of invaded islands), including a range of eradication projects completed >25 years ago (Dunlevy et al. 2011, DIISE 2014).

Despite a significant and ongoing investment in predator eradications in New Zealand, partly to benefit seabird populations, little research has been conducted to determine patterns of seabird re-colonization and recovery after eradication. The few studies that followed natural population responses of seabirds after predator removal had variable results (Gaze 2000, Veitch et al. 2011b). There is, accordingly, little understanding of the factors that may facilitate passive seabird recovery. Thus, a comprehensive review of post-eradication seabird population responses and the development of an overarching conceptual model to identify key factors in recovery would be useful for guiding
management and monitoring and could also be used to develop a framework for island conservation investment strategies.

Here, I outline a conceptual model of the ecological and demographic factors influencing seabird colony growth and re-colonization after predator eradication. I use this model to test empirically, with collated data from post-eradication surveys, which island and species characteristics most influenced seabird recovery. From these results I develop recommendations for passive restoration monitoring, with particular consideration of the potential for prioritizing active management and improving models of population growth.

2.2 Methods

For the purpose of this review, I define islands as sites surrounded by water and terrestrial sanctuaries surrounded by predator-proof fences. Population recovery refers to a local increase in the number of individuals at a colony after predator removal, as opposed to an increase in the metapopulation. Re-colonization refers to a species of seabird recorded breeding on an island after not having been recorded there within a decade prior to eradication.

2.2.1 Conceptual model overview

With few exceptions, pelagic seabirds breed in colonies on oceanic islands. Separation between breeding sites due to water barriers means that island populations can be considered metapopulations (Oro 2003, Oro et al. 2011). However, behavioural mechanisms associated with coloniality (e.g. philopatry and social attraction) mean that population dynamics are characterized by traits that may not conform to more straightforward metapopulation processes (Matthiopoulos et al. 2005). Furthermore, seabirds have low annual reproductive output, fecundity is low, and intermittent breeding is common (Warham 1990, Cubaynes et al. 2011). Thus, any model of population recovery and re-colonization at a newly predator-free site must incorporate both slow intrinsic rates of population increase and seabirds’ unique behaviourally driven metapopulation dynamics (Johst and Brandl 1997).
I developed a generic seabird colony growth model by combining standard matrix population models (Croxall and Rothery 1991, Caswell 2001) and a model of metapopulation processes on the basis of diffusion, range expansion, and re-invasion (Appendix A1; Lubina and Simon 1988, Sinclair et al. 2006). I considered the potential effects of release from the impacts of introduced predators on each parameter in the generic model (Table 2.1).

Table 2.1: Predictor variables that will hinder or facilitate colony growth after predator eradication, drawn from parameters of generic population growth models

<table>
<thead>
<tr>
<th>Process\textsuperscript{a}</th>
<th>Symbol</th>
<th>Description</th>
<th>Variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intrinsic</td>
<td>$S^A$, $S_{t-1}^{Pr}$</td>
<td>Annual survival rates of adults (A) and pre-breeding birds (Pr)</td>
<td>Type of predator eradicated</td>
</tr>
<tr>
<td></td>
<td>$S_{AFR}^J$</td>
<td>Survival of immature birds to age at first return (AFR)</td>
<td>Environmental stochasticity</td>
</tr>
<tr>
<td></td>
<td>$P^{ret}$</td>
<td>philopatry</td>
<td>Unknown</td>
</tr>
<tr>
<td></td>
<td>AFR</td>
<td>age at first return</td>
<td>Time since eradication, species specific mean</td>
</tr>
<tr>
<td></td>
<td>Skip</td>
<td>proportion of breeding-age birds not breeding</td>
<td>Environmental stochasticity, species specific mean</td>
</tr>
<tr>
<td></td>
<td>BS</td>
<td>breeding success</td>
<td>Size of predator eradicated, species specific mean</td>
</tr>
<tr>
<td>Extrinsic</td>
<td>$N_{pt}$</td>
<td>number of prospectors</td>
<td>Status of species’ metapopulation</td>
</tr>
<tr>
<td></td>
<td>Ds</td>
<td>distance to a source population</td>
<td>Distance to source population</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>habitat quality</td>
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<td></td>
<td>C</td>
<td>intra- and inter-specific social cues</td>
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</table>

\textsuperscript{a}Intrinsic or site specific processes and extrinsic or metapopulation processes are outlined in Appendix A1.
2.2.2 Post-eradication population recovery

Any increase in intrinsic population growth after predator eradication depends largely on the magnitude of predation effects on adult and pre-breeder survival and breeding success, which will in turn affect the size, distribution, and age structure of a remnant seabird population (Appendix A1). Any positive response in demographic rates after predator eradication is often dictated by the relative sizes of the introduced predators and their seabird prey (Table 2.1) (Jones et al. 2008). Towns et al. (2011b) categorize introduced predators into large predators, such as cats, that consume seabirds of all age classes and small predators, such as rats, that commonly consume only eggs and chicks. Large predators can kill and hoard more seabirds than they consume at one time (Short et al. 2002). Not only do large predators depress adult and pre-breeder survival, but also, considering many seabirds are obligately bi-parental, a decrease in adult survival will translate into a decrease in breeding success. When large predators are eradicated from a colony, adult survival often increases (Keitt and Tershy 2003, Nogales et al. 2004), resulting in relatively rapid population increase due to the high sensitivity of population growth rates to changes in adult survival (Lavers et al. 2010). Small predators are more likely to influence breeding success (Towns et al. 2006, Jones et al. 2008). Thus, when small predators are eradicated, reproductive success often increases (Pascal et al. 2008), which has variable effects on colony growth (Finkelstein et al. 2010). When both large and small predators are present at a colony, interactions can be complex. If large (super) predators are eradicated before small (meso) predators, there may be unforeseen consequences due to mesopredator release. For example, cats eradicated before rats and mice can lead to inflated numbers and activity of rats and mice (Russell et al. 2009), which may be followed by increased predation on seabirds (Rayner et al. 2007c). This increase in predation can lead to more dramatic responses in reproductive success should the mesopredators be subsequently eradicated (Courchamp et al. 1999, Rayner et al. 2007c).

An increase in intrinsic population growth after predator eradication will also depend on species-specific characteristics, such as age at first breeding and the number of eggs laid per breeding attempt, that will influence the rate at which potential new recruits are created. For many seabird species, age at first breeding is over 5 years and
only one or two eggs are laid (Warham 1990), resulting in long generation times and a subsequent lag between predator eradication and population growth. Thus, any response in intrinsic population growth is also related to time since predator eradication (Table 2.1). Seabirds have other unique, species-specific traits that will likely play a role in recovery after eradication, such as natal philopatry (Milot et al. 2008), intermittent breeding (Cubaynes et al. 2011), and a disproportionately high number and influence of pre-breeders and immature birds on population dynamics (Oro et al. 2006).

At higher population densities, intrinsic population growth is likely to be limited by negative density dependence (Pontier et al. 2008, Moller et al. 2009). The number of available nest sites may be limited due to competition between or within species, resulting in emigration or reduced breeding success (Table 2.1). If colonies are dense, removal of predators (or other sources of mortality, such as harvesting) may result in a decrease in breeding success and a net negative effect on colony growth (Moller et al. 2009). Conversely, if colonies are sparse, populations may be influenced by Allee effects and positive density dependence (Stephens et al. 1999). Removal of predators from a moderate-sized colony, where social attraction encourages prospecting individuals to settle, may lead to increased growth (Kildaw et al. 2005). However, it is currently unknown when net positive density effects become negative; thresholds are likely to be both species- and site-specific.

Extrinsic or metapopulation processes are particularly important for local re-colonization of breeding populations extirpated by predators. When a space becomes free of predators, the number of immature birds that prospect is likely to depend on the distance to a source population and the number of immature birds in a metapopulation (Appendix A1). The probability of an immature bird locating and prospecting a new site is greater at shorter distances to the natal colony and when more immature prospectors are available in an increasing or stable metapopulation (Table 2.1; Vuilleumier et al. 2007). Recruitment to a newly predator-free space is mediated by habitat quality and social cues (Crespin et al. 2006, Wilcox et al. 2006). If an island has been altered by anthropogenic disturbance (e.g. cleared for farming), recruitment may be less likely (Table 2.1). Arguably the most influential factors affecting recruitment in seabirds, however, are density-mediated social attraction, habitat copying, and competition for nest sites (Doligez et al. 2003, Parejo et al. 2006, Schippers et al. 2011). Thus, the population sizes of con- or hetero-specifics immediately following predator
eradication will either encourage (social attraction) or impede (competition) recruitment (Table 2.1).

2.2.3 Data collation

I collated information on pre- and post-eradication seabird populations around New Zealand from published and unpublished literature and interviews with island researchers. I scored seabird responses as a binary recovery or re-colonization or no observed recovery or re-colonization and developed a statistical model to test the relative effects of a set of key recovery factors identified in the conceptual model outlined above.

I constructed an updated list (final search, July 2012) of predator eradication projects on New Zealand islands based on Clout and Russell (2006), Towns et al. (2006), Bellingham et al. (2010), and Keitt (2011). I then searched for information about seabird population status pre- and post-eradication in Google Scholar and Web of Science. I searched for each island name and seabird* or bird* as keywords. I also reviewed New Zealand ecological journals Notornis and Tane and conference proceedings from Veitch and Clout (2002) and Veitch et al. (2011a). If no published information on a particular project was available, I contacted research personnel working on the island and asked the following questions: Is there any evidence (anecdotal, observational, or census data) of seabirds of any species re-colonizing or increasing in relative abundance on the island after predator removal? Were there any species that were expected to re-colonize or recover (i.e. they bred on the island historically or are known to prospect there), but never did? Are there any rock stacks, islets, or islands within approx. 10 km of the island with populations of seabird? If so, of what species are these populations?

To be included in further analyses, relative abundance of seabirds had to have increased, decreased, or remained unchanged at the colony site (too few studies documented changes in seabird reproductive success or survival after eradication); successful predator eradication had to have been > 3 years ago; and there had to have been no active restoration of seabirds. Furthermore, because of insufficient data on some taxa, from this point forward only species that lay one egg per year were considered.
2.2.4 Deriving predictor variables

I included factors as predictor variables that I identified as likely to affect intrinsic population growth, recruitment, or both, when developing the conceptual model (Table 2.1): island characteristics, species characteristics, and available data. Island characteristics were relative size of predators eradicated, time between seabird surveys and eradication, number of years predators were present on an island, the degree of habitat modification, distance to a source population, number of other seabird species breeding at the time of eradication. Although island size has the potential to affect seabird communities, i.e. smaller islands tend to have greater diversity of species per unit area (Estades 2001), island size was not included in my models because it was correlated with habitat modification and number of other breeding seabird species. Species characteristics were: age at first reproduction, population size at the time of predator eradication, and population status in New Zealand. I also used available data as a variable to control for different types of seabird data (anecdotal, observational, and quantitative) collected before and after eradication (details in Table 2.2).

2.2.5 Statistical analyses

For each seabird species on each island, I scored evidence of re-colonization or population recovery as 1 and a lack of evidence as 0 (Table 2.2). I found no evidence of negative responses. To assess whether recovery predictor variables (Table 2.1 and 2.2) explained seabird population responses on different islands, 17 a priori candidate generalized linear mixed models (GLMM) were considered in a model selection framework. Models had binomial error structure, log links, and Laplace approximations. I accounted for random variation between islands and species by including these as random variables in GLMMs. Interaction terms were not included because mixed models would be overparameterized (i.e., too many parameters and insufficient data points within each category) and thus cause non-convergence (Ginzburg and Jensen 2004). To ensure that resulting parameter estimates would be comparable, I standardized the data by subtracting the mean and dividing by two standard deviations (Schielzeth 2010). Statistical tests were run in R version 2.14.2 with the library lme4 (R Development Core Team 2012.).
Table 2.2: Predictor variables included in models of seabird response (defined as either ‘re-colonization’ or ‘colony recovery’) after eradication of introduced predators

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Scoring or Category</th>
<th>Description</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Response</td>
<td>Br&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0</td>
<td>No observed population recovery or re-colonization</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>Observed population growth or re-colonization after eradication</td>
<td></td>
</tr>
<tr>
<td>Relative predator size&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Cat&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Large predator</td>
<td>Cats, possums, stoats, pigs (superpredators)</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Small predator</td>
<td>Rats and mice (mesopredators)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Large and small</td>
<td>Both predators eradicated at the same time</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>predators</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesopredator release</td>
<td>Large predators removed before small</td>
<td></td>
</tr>
<tr>
<td>Years since predator eradication&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Con&lt;sup&gt;f&lt;/sup&gt;</td>
<td></td>
<td>Year from eradication to survey</td>
<td>This study</td>
</tr>
<tr>
<td>Years predators present on island&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Con</td>
<td></td>
<td>Not enough data</td>
<td>(Veitch &amp; Clout 2002)</td>
</tr>
<tr>
<td>Age at first breeding&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Con</td>
<td></td>
<td>Only available for a few species, others approximated based on family and mass</td>
<td>(Marchant &amp; Higgins 1990)</td>
</tr>
<tr>
<td>Population size at eradication&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Con</td>
<td>1</td>
<td>None</td>
<td>This study</td>
</tr>
<tr>
<td>Interspecific competition or facilitation&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Cat</td>
<td>1</td>
<td>None recorded</td>
<td>This study</td>
</tr>
<tr>
<td>Habitat modification&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Cat</td>
<td>2</td>
<td>Burned historically</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>Occupied by Maori (archaeological evidence)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>Stock grazing or mining</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>Farmed</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>Occupied by Maori and farmed by Europeans</td>
<td></td>
</tr>
<tr>
<td>Distance to source population&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Con</td>
<td>kms</td>
<td>Google Earth 6.2.2</td>
<td></td>
</tr>
<tr>
<td>New Zealand population status&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Cat</td>
<td>D</td>
<td>Decreasing metapopulation (Miskelly et al. 2008)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>I</td>
<td>Increasing metapopulation (IUCN 2012)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>S</td>
<td>Stable metapopulation</td>
<td></td>
</tr>
<tr>
<td>Available data&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Cat</td>
<td>1</td>
<td>Anecdotal</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>Observation of increase in relative abundance</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>Increase direct counts of birds or burrows</td>
<td></td>
</tr>
</tbody>
</table>
a Used in colony recovery analysis only.

b Used in both re-colonization and colony recovery analyses.

c Excluded from further analysis.

d Binomial variable

e Categorical variable

f Continuous variable
I ranked candidate models with Akaike’s information criterion (AIC) corrected for small sample sizes and overdispersion (QAIC\textsubscript{c}) (Burnham and Anderson 2002). The QAIC\textsubscript{c} weights (\(w_i\)) were used to evaluate model likelihoods. When the best supported model received a weight of less than 0.9, I used model averaging to generate parameter estimates, unconditional standard errors, and 95% confidence intervals, which were used with parameter likelihoods to estimate the effect size for each predictor variable (Johnson and Omland 2004).

I carried out three separate analyses, the first with all seabird responses (re-colonization and colony population increase) aggregated. This first analysis revealed that the predictor variable data type had low weight; thus, its effects were considered weak and it was removed from further analysis. The other two analyses separated re-colonization and colony population increase as response variables. Different predictor variables were used for each analysis depending on biological relevance (Table 2.2).

### 2.3 Results

I identified 92 islands from around New Zealand from which all non-native predators had been eradicated between 1936 and 2011 (Appendix A2). From this larger data set, I classified 132 seabird responses (evidence of re-colonization or population growth or no evidence) from 48 islands with predators eradicated. However, after screening results, data included responses of 103 seabird populations on 41 islands. Of these responses, 49 involved population recovery and 54 involved re-colonization.

When all seabird responses (re-colonization and colony growth) were combined into one analysis, the model that received the most weight included only distance to a source population as a predictor (Appendix A3). Model weights were < 0.5 for top models in all analyses (Appendix A3); thus, model selection exclusively was used to draw inference from my data set.

#### 2.3.1 Population growth
For models explaining colony growth, parameter estimates that received the highest summed Akaike weights included colony size before eradication and metapopulation status (Table 2.3).

Table 2.3: Summed Akaike weights ($w$), weighted parameter estimates ($w$PE), and unconditional standard errors ($SE_{\mu}$) calculated from all candidate models describing population recovery and re-colonization probability of seabirds around New Zealand after predator eradication. Bold parameter estimates had strong effects (i.e. SEs that did not bound zero)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$w$</th>
<th>$w$PE</th>
<th>$SE_{\mu}$</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Colony growth</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>1.82</td>
<td>1.63</td>
<td>3.2</td>
</tr>
<tr>
<td>Number of other spp. breeding</td>
<td>0.093</td>
<td>-0.02</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>Age at first breeding</td>
<td>0.19</td>
<td>-0.04</td>
<td>0.16</td>
<td>0.31</td>
</tr>
<tr>
<td>Population size</td>
<td>0.654</td>
<td><strong>-0.61</strong></td>
<td>0.55</td>
<td>1.07</td>
</tr>
<tr>
<td>Years since eradication</td>
<td>0.194</td>
<td>-0.12</td>
<td>0.24</td>
<td>0.48</td>
</tr>
<tr>
<td>Small predators$^a$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesopredator release</td>
<td>0.102</td>
<td>0.29</td>
<td>0.57</td>
<td>1.12</td>
</tr>
<tr>
<td>Large predators</td>
<td>0.102</td>
<td>-0.11</td>
<td>0.29</td>
<td>0.57</td>
</tr>
<tr>
<td>Large and small predators</td>
<td>0.102</td>
<td>1.56</td>
<td>379.93</td>
<td>744.66</td>
</tr>
<tr>
<td>Distance to source</td>
<td>0.261</td>
<td>-0.22</td>
<td>0.37</td>
<td>0.73</td>
</tr>
<tr>
<td>Habitat modification</td>
<td>0.095</td>
<td>0</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Decreasing metapopulation$^a$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Increasing metapopulation</td>
<td>0.74</td>
<td><strong>1.57</strong></td>
<td>1.37</td>
<td>2.69</td>
</tr>
<tr>
<td>Stable metapopulation</td>
<td>0.74</td>
<td><strong>1.35</strong></td>
<td>1.31</td>
<td>2.58</td>
</tr>
<tr>
<td><strong>Re-colonization</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>-2.94</td>
<td>8.69</td>
<td>17.04</td>
</tr>
<tr>
<td>Number of other spp. breeding</td>
<td>0.941</td>
<td><strong>13.28</strong></td>
<td>7.77</td>
<td>15.23</td>
</tr>
<tr>
<td>Age at first breeding</td>
<td>0.126</td>
<td>-0.12</td>
<td>0.16</td>
<td>0.32</td>
</tr>
<tr>
<td>Years since eradication</td>
<td>0.931</td>
<td>-2.7</td>
<td>5.27</td>
<td>10.32</td>
</tr>
</tbody>
</table>
Colonies with a smaller size pre-eradication were more likely to show detectable growth in size following eradication than larger colonies. Little colony growth was observed in large populations after predator eradication; colony growth was most likely in populations with 25-100 individuals (Fig. 2.1). Seabird colony growth after eradication was also more likely in species with increasing or stable metapopulations (Fig. 2.1).

Figure 2.1: Relationship between proportion of colonies (± SE) at which subsequent increases in abundance were recorded in New Zealand and (a) size of existing seabird colonies at the time of predator eradication and (b) species’ metapopulation trend (D, decreasing; S, stable; I, increasing; dashed line indicates null proportion of recorded colonies increasing in abundance)
2.3.2 Re-colonization

When re-colonization events were the focal post-eradication response, time since predator eradication, distance to a source population, and the number of similar species breeding on the island received considerable summed Akaike weight (> 0.9, Table 2.3). Parameter estimates and standard errors bounded zero for time since eradication, indicating this effect was weak (Table 2.3). Re-colonization was negatively related to the distance to a source population. When the nearest source population was ≥ 25 km, the proportion of observed re-colonization events fell below 50% (Fig. 2.2). Re-colonization was positively related to the number of other species breeding on an island (Fig. 2.3a). The number of successful re-colonization events was greater on islands with ≥2 other breeding species. Because I suspected the relationship between re-colonization and the number of other breeding species may have been related to island size (Estades 2001) and habitat (i.e. habitat copying; Parejo et al. 2006), I corrected for these factors post hoc. When number of species was corrected for island area ([1 + number of species]/island area), I detected no difference in the number of successful re-colonization events (Fig. 3b). When the number of species was corrected for habitat modification (= [1 + number of species]/[ habitat modification category] Table 2.2), standard errors did not overlap (Fig. 2.3c), indicating that re-colonization was more likely on islands with more seabird species in less modified habitat.
Figure 2.2: Relationship between proportion of seabird species that re-colonized islands in New Zealand after predator eradication and distance from source populations (dashed line indicates null proportion of recorded seabird species increasing in abundance)
Figure 2.3: Relationships between observed re-colonization by previously occurring seabird species following introduced predator eradication and (a) number of ecologically similar seabird species breeding on an island; (b) number of breeding species corrected for island size (IS) and (c) number of breeding species corrected for habitat quality (H)
2.4 Discussion

The number of successful island pest eradication projects has increased rapidly in the past few decades, with hundreds of islands around the world cleared of introduced predators. Many of these eradication projects aim to benefit affected seabird populations; however, this is the first wide-ranging review of seabird population responses after predator removal and of the crucial factors that may impede or facilitate this recovery. Although the available data were relatively sparse, my analyses allowed the identification of trends in seabird population responses to predator eradication that will be valuable in planning restoration interventions and subsequent monitoring.

Re-colonization by an extirpated species depends largely on extrinsic factors, i.e. the newly predator-free site must be prospected and colonized by new recruits. Two factors had strong effects on the likelihood of re-colonization: distance to a source population and local diversity of other seabirds. More re-colonizations were observed on islands with a source population within 25 km. Seabirds are less likely to set up new colonies near the edge of a metapopulation (Schippers et al. 2009). For example, in a marked metapopulation of Audouin’s Gull (*Ichthyaetus audouinii*), recruitment probability decreased exponentially with distance from a source population (Oro and Pradel 1999). The low probability of re-colonization events at a large distance from source populations suggests strong metapopulation connectivity among nearby populations of New Zealand seabirds. Furthermore, re-colonizations were observed on islands with a greater diversity of seabird species with less habitat modification. The most likely ecological explanation for this result is the “heterospecific habitat copying hypothesis” (Wagner et al. 2000), whereby when choosing their breeding site animals key into the presence and performance of heterospecifics with similar ecological needs, as demonstrated in numerous colonial bird species (Parejo et al. 2005, Parejo et al. 2006, Buxton and Jones 2012a). Thus, new recruits of an extirpated species may be using the presence of other ecologically similar species on an island as a cue to safe breeding habitat and near-by feeding grounds.

An increase in the relative size of a remnant colony of seabirds after predator eradication is a much more complex process, involving a combination of intrinsic
population dynamics and extrinsic factors. The main complication is that any colony remaining after eradication may be highly disrupted, with altered demographic rates and habitat use. This could result in an unstable age structure and habitat copying into suboptimal areas, i.e. an evolutionary trap (Cushing and Saleem 1982, Igual et al. 2007). Furthermore, if a colony was decreasing in size at a fast enough rate before eradication, the removal of predators may only slow the rate of decline rather than reverse the trend (Moller 2006). Results suggest that the likelihood of detectable colony growth after eradication is negatively related to pre-eradication population size. There were fewer cases of colony growth in very large populations (>5000 individuals; Fig. 2.2), which may indicate any combination of: (a) negative density dependence, where limited resources near carrying capacity resulted in little population growth at a large population size (Moller et al. 2009), (b) predators were swamped and having a relatively insignificant effect (Lyver et al. 2000), or (c) growth could not be reliably detected when a population was large to begin with. However, I also found few cases of colony growth in very small colonies (<25 individuals; Fig. 2.2) which may indicate positive density dependence, e.g. Allee effects and weak social attraction, that is preventing growth at small population sizes (Stephens et al. 1999, Doligez et al. 2003). Results suggest that mid-sized seabird populations could have a higher probability of recovery under a passive post-eradication management scheme. Colony growth after eradication was also more likely in species with an increasing or stable metapopulation. This suggests that metapopulation status could indicate the potential for a colony to grow. If the metapopulation is declining due to extrinsic pressures, the newly predator-free colony is also likely to be vulnerable to decline because of the same pressures. In addition, a declining metapopulation would provide fewer immature birds to prospect and recruit to the newly predator-free space. The former situation is perhaps less likely, as classic metapopulation theory stresses the variability and high turnover of local populations (Hanski 1998, Oro 2003). I found that a small number of species with declining metapopulations recovered locally after predator eradication (Fig. 2.2). Thus, although a low probability of passive restoration is expected for species in decline, local dynamics may override the metapopulation’s trend to some degree.

In this study, age at first breeding had no effect on colony growth. This result was unexpected, considering seabird species with earlier ages at first breeding would be
expected to have a higher per capita growth rate (Aubry et al. 2009) and hence have greater potential to grow after predator eradication. There are numerous reasons for the lack of a detectable effect of this variable. For example, I may not have included a large enough range of ages at first breeding, which is unlikely because species from Common Diving Petrels (*Pelecanoides urinatrix*) (average first breeding, 2 years) to Sooty Shearwaters (*Puffinus griseus*) (average first breeding 7 years) were included. Also, age at first breeding is highly variable, depending on environmental conditions and density dependence (Votier et al. 2008) and thus may not be a reliable predictor of recovery. Furthermore, intrinsic factors, such as age at first breeding may be swamped by immigration. Indeed, none of the variables that affect intrinsic population dynamics exclusively (age at first breeding, time since predator removal, type of predator removed; Table 2.1) were identified as being important, suggesting they may be less important than extrinsic forces and dispersal dynamics when seabird populations are recovering after disturbance.

In attempting to identify the ecological factors that influence colony growth and re-colonization of seabirds after eradication of introduced predators, I found many understudied parameters. Density dependence and habitat limitation (Kokko et al. 2004, Moller 2006), intermittent breeding (Cubaynes et al. 2011), annual survival rates of different age classes (Votier et al. 2008), natal philopatry (Steiner and Gaston 2005), and the relative importance of prospecting and recruitment (Becker and Bradley 2007) are likely to play fundamental roles in colony recovery, but are poorly understood for many species, notably procellariiforms. Furthermore, reliable estimates of population parameters (e.g. demographic rates) are unavailable before and after eradication for most species in New Zealand and globally. Thus, although the most plausible (and available) factors influencing post-eradication recovery were included in our models, they are not exhaustive, and much unaccounted variance is likely to remain.

In reviewing seabird recovery post-eradication in New Zealand, the lack of post-eradication monitoring studies is also of concern. Monitoring data existed for only 34% of species breeding on predator-eradicatated islands, and these were mostly procellariiforms. Furthermore, only 3.6% of species with pre-eradication count data had post-eradication count data, suggesting that it is not possible to compare pre and post-eradication counts reliably. Without robust outcome monitoring, it is impossible to evaluate the effectiveness
of expensive predator eradication programmes in restoring seabird breeding populations or as part of wider coastal ecosystem recovery projects.

My results indicated that natural post-eradication recovery of seabird populations was more likely on islands less than 25 km from source populations, with higher numbers of similar seabird species, with mid-sized populations at the time of eradication, and in species with a stable or increasing metapopulation. I suggest that managers prioritize passive restoration on islands and for species that meet these criteria. If sites do not meet these specifications, active management techniques should instead be implemented. If uncertainty about passive restoration is to be reduced, monitoring and modelling seabird recovery will be essential steps for decision making in island management.
Chapter 3  Release of constraints on nest-site selection in burrow-nesting petrels following invasive rat eradication

3.1 Introduction

According to the fossil record, burrow-nesting petrels (order: Procellariiformes) once nested in abundance throughout the New Zealand archipelago (Holdaway et al. 2001). However, with the arrival of humans, petrels were largely extirpated from the mainland due to the combined effects of disturbance, habitat alteration, and predation by introduced mammalian predators (Jones 2000, Taylor 2000). Globally, the most widespread of invading predators are rodents, which affect seabirds directly, through predation (Atkinson 1985, Burger and Gochfeld 1994, Jones et al. 2008), and indirectly, by altering vegetation at nesting sites (Campbell and Atkinson 1999, Grant-Hoffman et al. 2009). Rodents have invaded over 40% of islands in the New Zealand archipelago over the past 800 years, which has limited the availability of predator-free, unaltered nesting habitat (Towns et al. 2011b).

Over the past 50 years, rodents, along with other vertebrate predators, have been eradicated from over 90 islands in New Zealand, representing approximately 30,000 ha of newly predator-free nesting habitat (Clout and Russell 2006, Towns 2011). One of the main goals of eradication is to facilitate the re-colonization and colony expansion (hereafter “recovery”) of affected burrow-nesting seabird populations (Jones et al. 2011). Evidence suggests that some seabird species have recovered on a number of islands after predator eradication (Towns et al. 2006, Jones 2010a, Veitch et al. 2011b, Buxton et al. 2013b). However, the key factors driving patterns of recovery has received relatively little research attention (Chapter 2).

Nesting habitat selection and availability could play a significant role in seabird recovery (Major et al. 2011). Nest site placement is a key reproductive decision for long-

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lived seabirds and is partly responsible for population regulation (Cody 1985, Forbes and Kaiser 1994). Depending on species’ habitat requirements relative to availability, some sections of a newly predator-free island may not support recovery as well as others. Moreover, factors influencing nest locations are likely to differ among islands relative to predator invasion and eradication histories.

Breeding bird densities are generally higher in better quality habitat (Rosenzweig 1981, Stenhouse and Montevecchi 2000). Abiotic and biotic factors that determine nesting site quality for burrow-nesting seabirds include: soil type, which must be soft enough to excavate, but strong enough to avoid collapse; canopy and understory vegetation, which adults must penetrate safely to reach their burrow; ground cover, which must be avoided or burrowed under; slope, which affects soil drainage; and aspect, elevation, and topography which affect the ease of take-off and landing (Burger and Gochfeld 1991, Springer 1991, Thompson and Furness 1991, Rodway et al. 1998, Bancroft et al. 2005b). In addition to biotic and abiotic habitat characteristics, social factors are expected to influence nest-site selection. Most seabirds are colonial animals, and large colonies are highly attractive to sexually mature birds searching for nesting sites (Wittenberger and Hunt 1985). Evidence suggests that colonies act as “information centers”, indicating high quality habitat (Forbes and Kaiser 1994, Doligez et al. 2003). Consequently, a potential nest site with relatively low quality habitat may be preferred if other breeding birds are present (Stenhouse and Montevecchi 2000, Oro 2008).

The presence of introduced predators can shape seabird nesting distribution by extirpating them from areas accessible to predators, thus limiting seabird nesting to refugia, such as cliffs or rocky tali (Drummond and Leonard 2010, Buxton et al. 2013b), or to habitats unsuitable for predators (Catry et al. 2007). Nest sites may also persist in extremely high density areas, where high numbers of birds are able to swamp the effects of predation (Lyver et al. 2000, Cuthbert 2002, Jones 2003, Regehr et al. 2007). When introduced predators are removed from an island, nesting habitat use will likely be governed by processes linked to the former presence of predators, until seabird populations begin to recover. As recovery proceeds and greater numbers of birds recruit into a newly-predator-free space, small remnant colonies are likely to be attractive initially (Danchin et al. 1998, Kildaw et al. 2005). As these sites become “saturated” through crowding, the
“ideal-free” and “ideal-despotic” models (Fretwell and Lucas 1969, Fretwell 1972) predict that competition will eventually force recruits into new habitat.

Here I examine nest-site selection by burrow-nesting petrels on six islands off the north-eastern coast of New Zealand that vary in the presence, absence, or time since eradication of Pacific rats (*Rattus exulans*). Research suggests that Pacific rats suppress seabird population size by reducing breeding success (Towns 2009). I measured burrow presence, abundance, and occupancy in plots placed along linear transects, to develop a nest-site selection model that addresses four questions. First, what habitat factors influenced nest-site selection? Second, after accounting for the effect of habitat, did the presence of other nests influence nest-site selection? Third, how did time since rat eradication and other island-specific (e.g. nesting habitat availability) variables affect nest-site selection? Fourth, as time since rat eradication increased, did the strength of selection for preferred habitat decrease? After rat eradication, petrels will likely be initially attracted to remnant colonies, until crowding eventually forces recruits into new habitat. Thus, I predict that nest-site selection will be more influenced by the presence of other nests on islands with less time since rat eradication. I further predict that on islands with more time since eradication, there will be weaker selection for preferred habitat.

3.2 Methods

Not all sites were expected to have burrows, and not all burrows were expected to be occupied. Consequently, inference on nest-site selection was made at three levels: (1) whether one or more burrow entrances were present; (2) the number of nests; and (3) the number of occupied nests. To maximise inference, I developed a Bayesian hierarchical model to incorporate these three levels. To assess the effect of social attraction to nest-site locations while controlling for habitat, I examined the spatial autocorrelation of model residuals at each of the three data-sampling levels. If residual autocorrelation existed, a spatial covariance error structure would be incorporated into the model (Banerjee et al. 2004, Wagner and Fortin 2005). I used the spatial scale and intensity of autocorrelation to indicate the distance and degree to which nest-site selection was influenced by the presence of other nests. To examine differences in nest-site selection with increasing time since eradication.
eradication, I examined model outputs from the first level of inference (the presence or absence of burrows). First, I compared the proportion of habitat covariates selected for with time since eradication, using generalized linear mixed models (GLMM), based on the assumption that a greater number of variables associated with burrow presence could indicate birds were being more selective. Second, to test the changing strength of nest-site selection with increasing time since eradication, I compared model fit across islands.

### 3.2.1 Study Area and Species

I assessed nest-site selection on five islands representing 0–24 years of recovery after Pacific rat eradication and one island that was never invaded by rats. Korapuki (18 ha), Kawhitu (100 ha) and Ohinau (32 ha) had Pacific rats and European rabbits (*Oryctolagus cuniculus*) eradicated in 1987, 1991, and 2005 respectively, and Taranga (470 ha) had Pacific rats removed in 2011; while Ruamaahuanui (21 ha) never had predators introduced and Mauitaha (22 ha) is still inhabited by Pacific rats. All islands are within 7–13 km of New Zealand’s North Island, within the Hauraki Gulf, and have similar climate and geology (Fig. 3.1). Furthermore, all islands have similar disturbance and habitat modification histories, with extensive burning and terracing by Māori (Sladden and Falla 1928, Edgar 1962). However, all islands have been protected as nature reserves and have remained relatively undisturbed since the mid-19th century.

I considered nesting habitat selection of seven species of burrow-nesting seabirds in the order Procellariiformes: grey-faced petrel (*Pterodroma macroptera gouldi*), fluttering shearwater (*Puffinus gavia*), flesh-footed shearwater (*Puffinus carneipes*), little shearwater (*Puffinus assimilis*), common diving petrel (*Pelecanoides urinatrix*), sooty shearwater (*Puffinus griseus*), and Pycroft’s petrel (*Pterodroma pycrofti*). Limited available information suggests that burrows of all species tend to be sympatric, with no heterospecific separation of physical habitat characteristics, and different species sometimes occupying burrows of others (Hicks et al. 1975, Pierce 2002). I surveyed islands when all petrel species were at some stage of the breeding cycle (courtship, laying, incubation, or chick rearing): Taranga and Mauitaha in late November–December, 2011.
and September–October, 2012; Ohinau, Kawhitu, and Korapuki from October to December 2012 and Ruamaahuanui in November 2010

### 3.2.2 Habitat surveys

To distribute habitat surveys across the entire surface of our study islands, I recorded habitat variables in plots placed randomly along evenly spaced transects. A mean of 35 transects (31 on Mauitaha to 61 on Taranga; Buxton et al. 2013a) ran from coast to coast, perpendicular to the long axis of each island, resulting in a distance of 10-40 m between transects depending on island size (Fig. 3.1). Because of the steep terrain on Taranga, transects were shorter and constrained by proximity to existing tracks. The transect method was not employed on Ruamaahuanui because of high burrow density and thus high risk of burrow collapse. Instead, I used surveys from existing plots that had been allocated randomly as part of a previous study (Whitehead et al. 2014).

I surveyed between one and six 3 m-radius circular plots at randomly-assigned distances along each transect. Each plot center was marked with a handheld Global Positioning System (GPS 60CSx Garmin, Kansas, USA) and a metal stake and the boundaries delineated using a transect tape. Within each plot I counted all seabird burrows where the midline of the entrance fell within the plot limits and assessed occupancy using an infrared burrow camera (burrowscope; Sextant Technology Ltd., Wellington, New Zealand). I also recorded key habitat variables selected based on studies of other burrow-nesting seabirds (Catry et al. 2003, Schulz et al. 2005, Rayner et al. 2007b, Charleton et al. 2009, Scott et al. 2009) and on preliminary surveys of our study sites. These were:

1) Aspect: slope direction, measured using hand-held compass pointed towards the nearest coast from the plot center;

2) Slope: measured using a hand-held inclinometer from the highest point of the plot to the lowest (down-slope) point;

3) Topography: class (ridge, face, gully, or terrace) and elevation, read using a handheld GPS;
Figure 3.1: Distribution of habitat plots along search transects on study islands off the northeast coast of the North Island, New Zealand. On Taranga, transects were restricted to cut tracks due to rugged terrain; no transects were placed on Ruamaahuanui due to the high density of burrows. Black line indicates 100 m scale. Distance between islands relative to each other is not to scale.
4) Soil depth: measured using a 1 m stainless steel rod at the center point of the plot. The rod was driven into the soil as far as possible until an obstruction was hit (or until the rod was buried). If the rod was blocked by a root at a shallow depth or a burrow was at the center of the plot, the spike was moved 30 cm away in a random direction until the obstacle was avoided.

5) Soil strength: measured using a penetrometer (New Zealand Soil Bureau Inc. Wellington, New Zealand) at the center of the plot;

6) Ground Cover: the percent cover in five categories (< 1% = 1, 1-25% = 2, 25-50% = 3, 50-75% = 4, 75-100% = 5) was estimated for the following: bare ground (exposed substrate), rock (defined as larger than 5-cm diameter), and vegetation under 135 cm height;

7) Stem count: species and number of stems between 2.5 and 10 cm in diameter at chest height (dbh);

8) Canopy species and percent cover: visual percent cover was estimated in five categories (described in 6) for each main canopy species (tree species > 5 m).

3.2.3 Statistical analyses

I used two-way indicator species analysis (TWINSPAN) prior to modelling to reduce the 25+ canopy and stem species into simple vegetation classes. This is a divisive clustering method that separates vegetation into classes based on the abundances and associations between plant species (Hill 1979, Whitehead et al. 2014). By combining data from plots on all islands, I was able to define seven canopy classes and five stem classes comparable among islands. Next, all categorical covariates (aspect, topography, canopy and stem classes) were transformed into dummy variables by setting one class as a reference class with a coefficient of zero (Hardy 1993). Finally, I computed a Spearman’s correlation matrix to assess multicollinearity among explanatory variables. I omitted one of each covariate randomly when correlation coefficients ($r_s$) were $\geq$ 0.5. I did not include interaction terms, because models would be over-parameterized and thus be unlikely to converge (Ginzburg and Jensen 2004).
To ensure that resulting parameter estimates would be comparable, all variables were scaled by subtracting the mean and dividing by one standard deviation (Schielzeth 2010).

All statistical analyses were performed in R version 2.14.2 (R Development Core Team 2012.).

### 3.2.3.1 Hierarchical modeling approach

To examine the relationships between burrow presence, abundance, and occupancy with habitat covariates I adopted a Bayesian hierarchical framework (Fig. 3.2), implemented with Markov chain Monte Carlo (MCMC) methods. I used Bayesian inference as it allows for parameter uncertainty, which can be substantial when modeling patchy and spatially-varying processes, such as habitat preference (Banerjee et al. 2004). Because I was interested in similarities and differences in nest-site selection among and between islands, I selected a hierarchical approach, which is ideal for aligning complex data from various sources (Ellison 1996, Cressie et al. 2009).

I used MCMC, Gibbs sampling, and Metropolis algorithms to generate posterior parameter distributions (Gelman et al. 2004). Posterior distributions from MCMC functions, given the data and priors, yielded medians and 95% credibility intervals (CI) for each habitat parameter. Because little information was available about habitat selection of burrow-nesting seabirds between islands, I used non-informative prior distributions (Gelman and Hill 2007). To ensure convergence and minimize autocorrelation between chains, I ran 2500 iterations with a burn-in of 10000 and a thinning rate of 40.

I used packages MASS and mvtnorm to write model code (Appendix B1; Venables and Ripley 2002, Genz et al. 2012).

### 3.2.3.2 Modelling burrow entrance density

Plots were placed randomly along transects, resulting in the inclusion of large amounts of plots with no burrow entrances. I therefore used a zero-inflated Poisson (ZIP; Martin et al. 2005) model with two states: a state in which burrows were present at a site and a state in which burrows occurred with varying levels of abundance (Fig. 3.2; Welsh et al. 1996).
This approach allowed the estimation of the probability that a burrow was absent in a particular habitat, and if it was present, estimate the mean number of burrows (Dagne 2004). The model took the form:

\[ Pr(Y_{jk} = y) = \varphi_{jk}\delta_{jk} + (1 - \varphi_{jk}) \frac{\lambda_{jk}^y e^{-\lambda_{jk}}}{y!} \]

where \( Y_{jk} \) was the number of burrows, \( \lambda_{jk} \) was the Poisson mean number of burrows, \( \varphi_{jk} \) was the Bernoulli probability of no burrows, and \( \delta_{jk} \) denoted a point mass at 0 (i.e. equals 1
when \( Y_{jk} = 0 \) in plot \( j \) on island \( k \). Eq. 1 can be broken down depending on the value of \( Y_{jk} \):

\[
(Y_{jk} = 0) = \varphi_{jk} + (1 - \varphi_{jk})e^{-\lambda_{jk}}
\]

\[
(Y_{jk} = y) = (1 - \varphi_{jk})\frac{\lambda_{jk}^y e^{-\lambda_{jk}}}{y!}, \quad y > 0.
\]

The Bernoulli probability of the absence of burrows \( (\varphi_{jk}) \) and the Poisson mean number of burrows \( (\lambda_{jk}) \) were linear predictions of covariates:

\[
\text{logit} (\varphi_{jk}) = \sum_{l=1}^{L} \alpha_{kl}W_{kl}, \quad 2
\]

\[
\ln(\lambda_{jk}) = \sum_{l=1}^{L} \alpha_{kl}W_{kl}, \quad 3
\]

where \( W_{kl} \) were individual environmental covariates \( l \) for models on island \( k \), and \( \alpha_{kl} \) were the associated parameter estimates. The \( \alpha_{kl} \) came from a prior distribution with mean \( M_{al} \) and variance \( \sigma_{\alpha l}^2 \):

\[
\alpha_{kl} \sim \text{Normal}(M_{al}, \sigma_{\alpha l}^2) \quad 4
\]

\[
M_{al} \sim \text{Normal}(0,000) \quad 5
\]

\[
\sigma_{\alpha l}^2 \sim \text{InverseGamma}(0.1, 0.1). \quad 6
\]

Posterior distributions were interpreted by generating median \( \alpha_{kl} \) values with 95% CI for each habitat variable on each island for both \( \varphi_{jk} \) (probability of a burrow being absent) and \( \lambda_{jk} \) (mean number of burrows).
3.2.3.3  Modeling burrow occupancy.

Observed measures of burrow occupancy are likely to be associated with an unknown detection probability (Hamilton 2000), but I assumed the detection probability to be non-variant over habitat conditions. I modeled the number of “occupied” burrows \( X_{jk} \) among present burrows \( Y_{jk} \) in each plot \( j \) on each island \( k \) as a binomial process:

\[
X_{jk} \sim \text{Binomial}(\psi_{jk}, Y_{jk}), \quad Y_{jk} > 0
\]

where \( \psi_{jk} \) was the probability of finding a bird in a burrow in plot \( j \) (note: \( \psi_{jk} \) is equal for all burrows in plot \( j \)). Similar to Eq. 2, the probability of an occupied burrow \( \psi_{jk} \) was modeled as:

\[
\text{logit}(\psi_{jk}) \sim \sum_{l=1}^{L} \alpha_{kl} W_{kl}
\]

where \( W_{kl} \) were the environmental covariates \( l \) for models on island \( k \), \( \alpha_{kl} \) were the associated parameters, and prior distributions of \( \alpha_{kl} \) were similar to Eqs. 4-6. Posterior distributions for each habitat variable on each island were interpreted by generating median \( \alpha_{kl} \) values with 95% CI.

3.2.3.4  Model selection.

To reduce the number of variables in a final multivariate model, I first ran a series of univariate models, with each habitat covariate included separately. To compare between habitat variables, I calculated deviance information criterion (DIC), a relative model fit statistic:

\[
\text{DIC} = p_D + \bar{D},
\]
where the mean deviance $\bar{D}$ was averaged over all MCMC simulations and penalized for the effective number of parameters $p_D$ (Spiegelhalter et al. 2002). The number of parameters is not clearly defined for multilevel models and is unstable, even from simulations that have converged (Gelman and Hill 2007). This requires caution when interpreting DIC values, which I therefore supported with visual interpretation of diagnostic plots in assessing model fit (Wheeler et al. 2010).

Similar to Akaike’s information criterion (AIC), the preferred model is one with the minimum DIC value. Thus, to construct biologically plausible multivariate models, I selected habitat covariates with a combination of the lowest DIC values and those whose 95% CI did not overlap zero on at least one island.

### 3.2.3.5 Spatial autocorrelation.

A variogram of multivariate-model residuals for each island was constructed to determine if adjacent plots were more similar than those separated by large distances (i.e. spatial autocorrelation; Legendre 1993). Distance classes were calculated from the eastings and northings of plot centers (geoR package; Ribeiro and Diggle 2001). I interpreted the distance (if any) at which residuals were no longer autocorrelated as the “range”, or distance class on the x-axis, at which a “sill”, or asymptote, is reached. If a sill in the semivariance was not reached within a range of 20 m (suggesting spatial autocorrelation up to 20 m), I calculated global and local Moran’s I values, which generated p-values to determine if model residuals are more or less similar than expected by chance at certain distance classes (spdep package; Bivand et al. 2013).

### 3.2.3.6 Post-hoc comparison of nest-site selection among islands.

To examine how selectivity for nesting habitat differed with time since eradication and other island factors, I compared outputs from the Bernoulli burrow absence model component ($\varphi_{jk}$; Eq. 2) using binomial GLMM (lme4 package; Bates et al. 2012). For each of the habitat covariates on each island, I used 95% CI from the posterior parameter distributions of univariate and multivariate models to construct a binary dependent variable. Parameter estimates of habitat covariates whose 95% CI did not overlap zero were scored as 1, as this likely indicated that petrels “selected” or “avoided” this particular habitat. Conversely, habitat covariates whose 95% CI overlapped zero were scored as 0, as
this likely indicated no selection or avoidance. This resulted in a dataset with a sample size of 108 for the univariate model (6 islands * 18 covariates) and 36 for the multivariate model (6 islands * 6 covariates). I tested the effect of the following independent variables on the probability of habitat covariates being selected or avoided: (1) number of years since Pacific rat eradication (where Ruamaahuanui, which never had predators introduced, was set to 100); (2) the historical presence of European rabbits; (3) the mean value of each habitat covariate on each island center-scaled among islands, and; (4) the coefficient of variation (standard deviation/mean) of each habitat covariate on each island. Categorical island and habitat variables were included as random factors. I assumed that a greater number of habitat covariates whose CI did not overlap zero indicated that birds were being more selective.

3.2.3.7 Comparing model fit.

I assessed model fit following the procedure described by Kesler and Haig (2005) and Bourgeois and Vidal (2007), by comparing the predicted probability of burrow presence between occupied and unoccupied plots. Predicted probabilities of burrow presence were calculated by taking $1 - \phi_{jk}$ (Eq. 2) from the top multivariate ZIP model. If unoccupied plots had similar predicted probabilities of burrow presence to occupied plots, this suggested that suitable nesting habitats remain unoccupied, or rather, the island had not been fully re-colonized (Anderson et al. 2013). Conversely, if occupied plots had higher predicted values than unoccupied it suggested that breeding birds were nesting in, and potentially saturating, preferred habitat types before using plots with lower predicted values. To quantify model fit I calculated area under Receiver Operating Characteristic curves (AUC) based on accuracy of predictions (PresenceAbsence package; Freeman and Moison 2008). AUC values vary between 0 and 1, with values ≤ 0.6 indicating a model performance no better than random, and values ≥ 0.7 considered useful (Oppel et al. 2012).

3.3 Results

Between 2010 and 2012 I surveyed a total of 597 habitat plots on 196 transects: 76 plots on Ruamaahuanui, 101 on Korapuki, 132 on Kawhitu, 100 on Ohinau, 120 on
Taranga, and 68 on Mauitaha. Burrow density was related positively to the number of years since Pacific rat eradication ($Z_1 = 9.883, P < 0.001$, Fig. 3.3). However, time since eradication explained less than 40% ($R^2 = 0.37$) of variation in burrow density between islands.

Figure 3.3: Mean density of burrow entrances on study islands off the northeast coast of the North Island of New Zealand with time since Pacific rat eradication. Mauitaha is still inhabited by Pacific rats; Ruamaahuanui (Nui) never had mammals introduced and all other islands ordered from left to right by increasing time since eradication. Error bars indicate standard error

3.3.1 Nest-site selection

I found two pairs of habitat covariates with correlation coefficients, $R_i \geq 0.5$ (slope and “face” topography category, $R = 0.56$; total canopy cover and total understory vegetation cover, $R = 0.50$). I removed “face” topography category and total understory vegetation cover from further analysis.
TWINSPAN analysis revealed seven canopy classes: pōhutukawa (*Metrosideros excelsa*), kanuka (*Kunzea ericoides*), kohekohe (*Dysoxylum spectabile*), nikau (*Rhopalostylis sapida*), tawa/taraire (*Beilschmiedia tawa / B. tarairi*), māpou (*Myrsine australis*), and māhoe (*Melicytus ramiflorus*); and five smaller stem classes (2.5-10 cm at breast height): māpou, māhoe, karamū (*Coprosma macrocarpa*), kawakawa (*Macropiper excelsum*), and karo (*Pittosporum crassifolium*). The canopy species nikau, kohekohe, and tawa/taraire and small stem species kawakawa and karo were observed on ≤3 islands in low abundance among plots and were thus removed from further analysis. The dummy variable for gully topography also occurred with low frequency among plots and was removed from further analysis.

Among islands, univariate ZIP models and observed occupancy models indicated that soil depth was the most influential factor determining the presence (1 - ϕ), density, and occupancy of burrows (Appendix B2), which all increased with increasing soil depth. I constructed 2 multivariate models (ZIP burrow count and observed occupancy model) using habitat covariates selected from these univariate models (see methods and Appendix B2).

In the top multivariate ZIP models, on at least one island, the expected probability of burrow presence (1 - ϕ) increased with a western aspect, slope, soil depth, rock cover, and the presence of māhoe and karamū stems (Fig. 3.4a); and burrow counts (Y_{jk}) increased with western and southern aspect, slope, soil depth, rock cover, and the presence of karamū stems (Fig. 3.4b). On most islands (Taranga, Korapuki, Ruamaahuanui), burrow count decreased with the number of stems, while on Mauitaha burrow count increased in the presence of large stems. On Kawhitu, burrow count increased in the presence of māhoe stems, while on Korapuki and Ruamaahuanui burrow count decreased with the presence of māhoe stems. Overall, more burrows were likely to be found on western aspects, steeper slopes, in deeper soil, with more rock cover, in the presence of māhoe stems. The top multivariate ZIP model predicting burrow presence had an AUC = 0.77 ± 0.02 and predicting burrow count had an AUC = 0.70 ± 0.02.

In the top multivariate observed occupancy models, on at least one island, probability of “observed” burrow occupancy (X_{jk}) increased with soil depth and māhoe in the canopy, and decreased with increasing rock cover, and with the presence of kanuka and
Figure 3.4: Median effect sizes and 95% credibility intervals of habitat covariates from multivariate models predicting a) petrel burrow presence or absence, b) abundance, and c) occupancy on six islands in northeastern New Zealand. Mauitaha is still inhabited by Pacific rats; Ruamaahuanui never had rats introduced and all other islands are ordered from left to right by increasing time since rat eradication. Habitat variables were selected based on low deviance information criterion values and credible intervals not overlapping 0 on ≥ 1 island from univariate models. Total values represent medians among islands (Mαl Eq. 5)
mapou stems (Fig. 3.4c). On most islands (Ohinau and Ruamaahuanui), the probability of burrow occupancy increased with western aspect, while on Kawhitu the probability of burrow occupancy decreased with western aspect. The top multivariate occupancy model had an AUC = 0.74 ± 0.03.

3.3.2 Spatial autocorrelation

I found little evidence of spatial autocorrelation. For most islands, variograms of φ, λ, and Ψ residuals (Eqs. 2, 3, and 8) reached a sill at a range of ≤10 m (Appendix B3, Figs. B3.1, B3.3, B3.5) and Moran’s I values did not differ significantly from 0 (Appendix B3, Fig. B3.2, B3.4, B3.6), indicating no spatial autocorrelation at distances greater than 10 m. The majority of plots (~90%) were ≥10 m apart, thus I did not consider spatial autocorrelation to be a statistical issue in my analysis. I found weak evidence of spatial autocorrelation on Taranga and Mauitaha only. The φ and λ residuals on Taranga did not reach a sill until ~20 m (Appendix B3, Figs. B3.1, B3.3), while the Ψ residuals on Mauitaha did not reach a sill until ~30 m (Appendix B3, Fig. B3.5).

3.3.3 Nest-site selection among islands

I examined inter-island factors affecting the number of selected nesting habitat covariates using 95% CI from a multivariate burrow absence model (Eq. 2) and found a significant effect of the coefficient of variation (standard deviation/mean habitat variable; n = 36, Z₁ = −1.88, P = 0.05, adjusted R² = 0.64; Fig. 3.5a, Table 3.1). When coefficients of variation on an island were high (i.e., habitat was variable – high standard deviation and a low mean) fewer habitat covariates were selected for. When I examined factors affecting the number of nesting habitat variables selected for using 95% CI from univariate burrow absence models I found a significant effect of time since rat eradication (n = 108, Z₁ = −2.53, P = 0.021, adjusted R² = 0.47; Fig. 3.5b, Table 3.1). Fewer habitat covariates were selected for (higher proportion of covariates whose CI overlapped 0) at sites with more time since rat eradication. I found no effect of the historical presence of rabbits or the mean
value of each habitat covariate (habitat abundance) on the number of nesting habitat variables selected (all $P > 0.182$, Fig. 3.5c and d).

### 3.3.4 Model fit

On Ohinau and Mauitaha (Pacific rats removed in 2005 and Pacific rats still present, respectively; Fig. 3.6), I found that predicted probabilities of burrows being present were higher in plots with burrows present, suggesting that birds were nesting in specific habitat types on these islands. On all other islands there was no clear difference between predicted probabilities in plots with burrows present or absent, suggesting model habitat covariates did not influence nest-site selection. AUC values indicated better model fit on islands with less time since eradication (Mauitaha – rats present – 0.70 ± 0.07; Taranga – rats removed 2011 – 0.62 ± 0.06; Ohinau – rats removed 2005 – 0.70 ± 0.05; Stanley – rats removed 1991 – 0.53 ± 0.05; Korapuki – rats removed 1986 – 0.52 ± 0.06; Ruamaahuanui – rats never introduced – 0.54 ± 0.11), suggesting that as time since eradication increased, birds were more likely to nest in less preferred habitat.
Table 3.1: Model outputs from generalized linear mixed regression of the number of
nesting habitat variables selected for by burrow-nesting petrels (based on the
presence/absence component of univariate and multivariate Bayesian hierarchical nesting
habitat selection models) versus the number of years since Pacific rat eradication, the
center-scaled mean value of each habitat covariate, the coefficient of variation of each
habitat covariate on each island, and the historical presence of rabbits. $R^2_m$ indicates
marginal $R^2$ values; $R^2_c$ indicates conditional $R^2$. Asterisk indicates statistical significance.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Univariate models</th>
<th>Multivariate models</th>
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<tbody>
<tr>
<td></td>
<td>Parameter estimates ± SE</td>
<td>Z-value</td>
</tr>
<tr>
<td>Years since eradication</td>
<td>-0.04 ± 0.02</td>
<td>-2.41</td>
</tr>
<tr>
<td>Mean habitat covariate</td>
<td>0.30 ± 0.29</td>
<td>1.03</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>-0.02 ± 0.15</td>
<td>-0.13</td>
</tr>
<tr>
<td>Rabbits</td>
<td>0.75 ± 0.56</td>
<td>1.34</td>
</tr>
</tbody>
</table>
Figure 3.5: Post-hoc analysis of a nest site selection model on six islands in north-eastern New Zealand. I compared the proportions of habitat covariates “selected” (95% credible intervals not overlapping zero, scored as 1) or “not selected” (95% credible intervals overlapping zero, scored as 0) with a) the number of years since Pacific rat eradication, b) the coefficient of variation of each habitat covariate on each island, c) the mean value of each habitat covariate, and d) the historical presence of rabbits. Error bars indicate standard error.
Figure 3.6: Predicted probabilities from a model describing the effects of habitat variables on burrow presence \((1-\varphi)\) in plots with burrows present versus plots with no burrows on islands in north-eastern New Zealand with different times since Pacific rat eradication. Low predicted probabilities in plots with burrows absent (white dots) and high predicted probabilities in plots with burrows present (black dots) suggest saturation of preferred habitat.
3.4 Discussion

I examined burrow-nesting petrel nest-site selection on islands with different periods since Pacific rat eradication. Although the structure of the data and results were complex, with numerous interacting variables, results indicate that nest-site selection is island-specific, depending on both restoration history and habitat availability.

3.4.1 Nest-site selection among islands

For burrow-nesting seabirds, selection of appropriate nest habitat will affect burrow quality and thus influence reproductive success. Substrate characteristics, such as soil properties, can affect the excavation, stability, and thermal properties of a burrow (Dalsted et al. 1981, Stokes and Boersma 1991). I found that soil depth was the most important factor predicting the presence, abundance, and occupancy of burrows across all study islands. Soil depth is an important nesting habitat feature for many species of petrel, as they tend to construct long, multi-cavity burrows (Schramm 1986, Gaze 2000, Schulz et al. 2005, Charleton et al. 2009). Rock cover also arose as important in all models, with more burrows found in plots with large boulders present. Burrow collapse is less likely under boulders (Brandt et al. 1995), however, burrow occupancy was lower in plots with more rock cover, possibly due to the poor insulating properties of volcanic boulders (Brandt et al. 1995).

I found more burrows in steeper terrain. On slopes, burrows open horizontally, whereas on terraces, openings face upwards, allowing water to enter more readily (Stokes and Boersma 1991). Furthermore, because most petrels have high wing-loading, slope is thought to increase take-off and landing capability, by creating updrafts that increase lift (Schulz et al. 2005, Rayner et al. 2007b, Scott et al. 2009). However, I found little evidence that slope affected burrow occupancy. I speculate that slope may have a weaker effect on habitat selection on heavily forested islands, such as the islands in this study. Updrafts generated from wind striking a hill may be less effective at creating lift when large trees are present. Furthermore, to take advantage of lift, it would be necessary for birds to gain the necessary height and clearance to depart the colony by walking to large
rocks or clear areas, or by climbing trees. However, lift may still be an important feature in habitat selection, as I found a higher abundance and occupancy of burrows on the south and west side of islands, which face the prevailing south-westerly winds of northern New Zealand (National Institute of Water and Atmospheric Research). Slopes facing prevailing winds generate lift during take-off and drag during landing (Warham 1990).

Finally, burrow abundance and occupancy were related to canopy and stem species. Generally, I found more burrows in areas with karamū and māhoe stems and more occupied burrows in areas with māhoe in the canopy and without kanuka in the canopy and māpou stems. These associations could be due to a combination of the following factors: (1) all study islands were burned in recent history by indigenous Māori and evidence suggests that kanuka is a common pioneering species, whereas māhoe and karamū are secondary successional immigrants (Atkinson 2004). Thus, islands or sites with more māhoe and karamū may represent areas with more time to recover after fire disturbance, suggesting that the relationship between petrel burrows and plant species may be correlated (due to longer recovery times) rather than causative; (2) some species, such as kanuka, have thick, interlocking root systems which may be difficult for petrels to penetrate (Bergin et al. 1995); (3) plant species may be associated with soil properties; for example, māhoe grow exclusively in well-drained, fertilized soils, also preferred by burrow-nesting petrels (Dawson and Lucas 2011); and (4) the density of the canopy and understory may affect the accessibility of a nest site (Whitehead et al. 2014). For example, young māpou tend to form dense stands; thick understory could make it more difficult for petrels to safely reach burrows.

### 3.4.2 Social attraction and nest-site selection

Petrels are colonial animals, nesting in large social groups (Warham 1990). Evidence suggests that for colonial animals, “social attraction” is among the most important drivers of habitat selection, where the presence, density, and reproductive success of established breeders indicate habitat quality (Forbes and Kaiser 1994, Danchin et al. 1998, Kildaw et al. 2005). However, I found little evidence for spatial autocorrelation, or rather that the presence of other nests influences nest-site selection. This suggests that petrels are not
selecting habitat based on the presence of other birds (Bayard and Elphick 2010).
However, plots were generally separated by relatively large (>20 m) distances, compared
to distances separating burrows still considered to be in the same colony (~8 m; RTB pers.
obs.), which may have resulted in the lack of observed spatial autocorrelation. Although
not statistically significant, I found weak support for spatial autocorrelation on Mauitaha
and Taranga, islands with Pacific rats present and removed in 2011, respectively. The low
nest density and high habitat-mediated nest-site selection on these islands suggests that
birds may be clustering more in the presence of rats, a pattern which has been observed in
other seabird species (Cuthbert 2002, Regehr et al. 2007).

3.4.3 Effect of time since rat eradication

Although I lack the ability to assume a causal effect of time since Pacific rat eradication, I found a distinct pattern of increasing burrow density along the chronosequence of islands used as a proxy for colony expansion or “recovery” after disturbance (Fig. 3.4). Low burrow densities on Mauitaha (0.03 ± 0.01 burrows/m²), where Pacific rats are still present, and Taranga (0.05 ± 0.01 ), from where they were eradicated only 2 years prior to surveys, are comparable to those on other predator-invaded islands in New Zealand (e.g. 0.04 Cook's petrel *Pterodroma cookii* burrows/m² on Hauturu-Little Barrier Island; Rayner et al. 2007b). Burrow densities on Korapuki and Kawhitu (0.09 ± 0.01 and 0.08 ± 0.01), islands with over 20 years since rat eradication, were significantly lower than a predator free islands (e.g. Ruamaahuanui 0.23 ± 0.03 burrows/m², Ruamaahuaiti 0.21 ± 0.04, and Hongiora 0.76 ± 0.07; Whitehead et al. 2014). However densities were comparable with those on other islands with similar times since predator eradication (e.g. Moutohorā 0.07 ± 0.01; Whitehead et al. 2014). Although this relationship was striking, caution must be taken when inferring a causal relationship with Pacific rat removal (Craig 1983, Jones 2001). For example, 13 years after Pacific rats were removed from Middle Chain Islands, burrow density was 0.04 ± 0.01 burrows/m² (Whitehead et al. 2014). Current distribution of burrow-nesting petrels on restored islands is likely to be shaped by a set of interacting variables including: other introduced species
(e.g. European rabbits), habitat modification, history of human harvesting, historical distribution, and species-specific behaviour and biology.

### 3.4.4 Nest-site selection between islands

I found differences in nest-site selection between islands, including a negative relationship between the number of habitat covariates selected for and time since rat eradication (Fig. 3.5a). This suggests that as time passes after rat eradication and burrow density increases, birds may reduce selectivity of nest-site locations and occupy new nesting habitat.

I hypothesize that the presence of Pacific rats may have restricted petrel nest-site selection to patches of habitat where: (1) they could escape predation; (2) density was high before rat invasion (i.e. high quality habitat) and predation was swamped (Lyver, Robertson and Moller 2000; Regehr et al. 2007); (3) micro-habitat was used infrequently by predators; or (4) alternative food resources were available (Rayner et al. 2007). On islands lacking other predators, Pacific rats can move large distances, populations have been found in a range of habitat types (Moller and Craig 1987), and few micro-habitats lack rats completely (Newman and McFadden 1990). Thus, I find the first explanation the least likely. In many mainland colonies, petrel predation is inversely density-dependent, i.e. where small colonies are often extirpated and dense colonies are able to “swamp” predation effects (Jones 2000, 2003; Lyver, Robertson and Moller 2000). Thus, colonies persisting on islands with rats or recently rat-free islands likely remain in locations where per-capita predation rates were low: either in areas where productivity and density were high or where predators were less abundant. Regardless, on islands with fewer than 8 years since rat eradication, my nesting habitat models had better fit, indicating high selectivity for nest-site locations in specific areas.

When rats are removed, if populations begin to grow, persisting colonies may be initially attractive to new recruits. Although I found no significant spatial autocorrelation, islands with less time since eradication showed greater autocorrelation, suggesting a more clustered burrow distribution. Once remnant areas become crowded, new recruits may be forced into new areas, thus lowering the number of habitat covariates selected for as time increases after eradication. My data confirmed that islands with more time since
eradication had no spatial autocorrelation, fewer habitat covariates were selected for, and habitat covariates had weaker effects on nesting habitat selection. An increase in burrow density and decrease in habitat constraints after rat eradication may reflect differential recruitment and the influence of density dependence.

Nest-site selection was also related to variability in habitat measures across an island (coefficient of variation, Fig. 3.5b), with fewer habitat covariates selected for when preferred habitat was patchy and limited. In other words, if there was a lower mean and higher variation of nesting habitat (e.g. shallower soil, more gradual slopes) on an island, there were fewer habitat covariates selected for, i.e. birds were less selective.

3.4.5 Potential biases

The influence of burrow-nesting seabirds on their habitat is a potentially confounding factor in this study (Mulder et al. 2011b). Not only will the availability of preferred nesting habitat influence the distribution of seabirds, but in turn, the distribution of seabirds will influence habitat. For example, the combination of burrowing and belowground trampling can result in root damage, decreased stability of trees and shrubs, and reduced seedling survival, thus altering plant community composition in heavily burrowed areas (Smith et al. 2011). Furthermore, burrow building alters soil porosity and soil-forming processes, resulting in stronger and drier soil (Bancroft et al. 2005a). This circular feedback process between seabirds and island habitat is likely to be difficult to tease apart, especially in recovering populations.

Furthermore, I combined all species in my analysis of burrow distribution and occupancy. However, grey-faced petrels were by far the most abundant species on all islands, except for Ohinau, where flesh-footed shearwaters were most common (Buxton et al. 2013a). Both species are relatively large (mean weight: grey-faced petrel 550 g and flesh-footed shearwater 700 g) and are thought to be less severely affected by the presence of Pacific rats (Priddel et al. 2006). Less common species, such as Pycroft’s petrel (150 g) and little shearwaters (240 g), are known to have lower productivity, even to the point of total nest failure, in the presence of Pacific rats (Pierce 2002). Thus, I am unsure of how the varying abundances of each species of different sizes affected my results. Further
research should focus on the differences or similarities in recovery dynamics of various burrow-nesting seabird species.

3.4.6 Conclusions and conservation implications

Results suggest that nest-site selection, particularly the need for deeper soil, is important among recovering petrel colonies. However, results also indicate that birds can expand into new habitat, suggesting that the importance of nesting habitat quality may decrease as colonies grow. Nest site suitability may limit petrel colony expansion most heavily in small populations; highlighting the importance of habitat characteristics for petrel population recovery, both within islands and among islands.

Burrow-nesting seabird systems are complicated, including complex intra-island metapopulation dynamics and problematic nest-occupancy detection. Because of their ability to draw inference from composite systems, I propose that hierarchical Bayesian modelling may be the most capable method to address these complexities.

In New Zealand, island habitat is not homogenous, but instead includes both whole islands and within-island areas that vary in their quality as nest sites for petrels. Thus not all islands and areas within islands have the same petrel “restoration potential”. These results can be useful to delineate suitable habitat patches for petrels at restoration sites, including those with deep soil, aspect that faces prevailing winds, steeper slopes.

Historically, removing introduced mammalian predators has been used to both enhance seabird productivity and prevent the extinction of threatened populations (Rauzon 2007). Because predator eradications have become increasingly successful and common, I propose that they represent not only an effective conservation technique, but also a means to study recovery biology. In this way, strategies to restore seabird populations can be developed based on an iterative adaptive management framework (Westgate et al. 2013). Suitable nesting habitat is a fundamental requirement for burrow-nesting species, affecting fitness through reproductive success. Thus, an accurate assessment of the importance and availability of suitable nesting habitat should be an integral part of petrel restoration strategies.
Chapter 4  One method does not suit all: variable settlement responses of three procellariid species to vocalization playbacks

4.1 Introduction

For animals with high nest-site fidelity, such as long-lived colonial seabirds, deciding where to settle and breed has a disproportionately large effect on life-time reproductive output (Forbes and Kaiser 1994, Aubry et al. 2009). Nest-site selection is influenced by a number of interacting variables, including metapopulation dynamics (Schippers et al. 2009), proximity to food resources (Birkhead and Furness 1985), and nest-habitat quality (Kildaw et al. 2005). Evidence suggests that colonial animals are attracted to conspecifics when selecting habitat, because it increases the potential to find mates, dilutes the risk of predation, increases foraging efficiency, and indicates high quality nest-habitat (Schippers et al. 2011). It has been proposed that ‘social information’ provided by conspecifics is used by seabirds as an effective and reliable way of selecting optimal breeding sites (Danchin et al. 1998). Firstly, the stability of colony locations over long periods is thought to indicate favourable local conditions (Danchin et al. 1998, Doligez et al. 2003, Wagner and Danchin 2010). Secondly, patchy and unpredictable pelagic food resources spread over large distances make it more efficient to select nesting habitat on the basis of existing colony information rather than evaluate each of possibly many alternative sites (Lack 1968, Weimerskirch 2007). Thirdly, the social information necessary to evaluate potential breeding sites is readily available at colonies, due to rich visual (surface-nesting species; Kress 1983), auditory, and/or olfactory cues provided by nesting birds (Podolsky and Kress 1989).

Many studies have confirmed the attractiveness of social cues to ‘prospectors’ or sexually mature seabirds searching for a nesting site (Podolsky and Kress 1989, Major and

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Moreover, conservation practitioners have capitalized on this behaviour, using artificial social cues to lure seabirds into abandoned or unoccupied habitat, a technique known as ‘social attraction’ (Kress 1998). Where drivers of local colony extinction (e.g. predation pressure) can be overcome, social attraction can be used to facilitate seabird re-colonization and recovery (Jones and Kress 2012). Social cues are mimicked using playback of recorded vocalizations, decoys of adults, eggs, or chicks, mirrors, and odour; depending on the focal species’ nesting behaviour (Kress 1997). Social attraction is often paired with, or used as an alternative to, other more costly and labour-intensive restoration techniques, such as translocation, where chicks are transferred from an active colony (Griffith et al. 1989, Jones and Kress 2012).

Previous attempts to use social attraction as a conservation tool have had highly variable outcomes (Ahlering et al. 2010). In a global review of the world’s active seabird restoration projects, Jones and Kress (2012) found large interspecific variation in the success rate (defined locally by project managers or, generically, as the attraction and maintenance of breeding seabirds for ≥ 2 years) of acoustic and visual social attraction. For example, species in the families Sternidae and Alcidae (terns and auks) had high success rates (>75%) in response to decoys and playback, whereas species in the family Phalacrocoracidae (cormorants) had low success rates (<30%). Furthermore, studies have demonstrated intraspecific variability in response to social attraction between habitat, plots, and locations (Burger 1988, Jeffries and Brunton 2001, Parker et al. 2007).

Variability in social attraction between and among species and sites is likely to reflect differences in dispersal strategies and underlying mechanisms behind the role of social cues in habitat selection (Reed and Dobson 1993, Ahlering et al. 2010). The probability of a prospecting bird visiting other colonies will depend on the number of prospectors, the distance between sites, and connectivity between sites (Chapter 2); where more prospecting is likely to occur at a site with a dense nearby colony. To establish the source of variation in social attraction success, I propose integrating seabird dispersal and habitat selection hypotheses into the structure of social attraction experiments.

The New Zealand archipelago represents an ideal location to examine social attraction as a conservation technique for seabirds. New Zealand has one of the highest diversities of breeding seabirds in the world, dominated by the order Procellariiformes.
Evidence suggests that petrel populations once existed on the mainland of New Zealand, but with colonization by humans and subsequent habitat destruction, harvesting, and introduction of predators, most species persist now only on predator-free offshore islands (Holdaway et al. 2001, Towns 2011). With the success of introduced-predator eradication projects in New Zealand over the past few decades, a total of 100 islands are now free of non-native mammals, restoring safe breeding habitat for petrels (Towns et al. 2012b). Evidence suggests that petrel populations have yet to recover or re-colonize some sites decades after eradication (Chapter 2). The absence of remnant colonies on these islands – and the cues they would provide – suggests a lack of social information may be a major limiting factor for petrel population recovery. The large number of islands requiring active management around New Zealand and the high cost and effort required for translocation projects mean that social attraction could be a viable alternative for petrel population restoration on islands where population recovery is not occurring naturally.

In this study I selected three species of petrel of varying size: small – fluttering shearwater, *Puffinus gavia*; medium – grey-faced petrel, *Pterodroma macroptera gouldi*; and large – flesh-footed shearwater, *Puffinus carneipes*. I examined the effectiveness of social attraction by testing behavioural responses to acoustic social cues in the form of call playback. For each of the three petrel species I played calls at three sites, each with low, medium or high population densities of conspecifics within 1 km to test whether density of potential ‘source populations’ affects attraction to social cues. I tested the following hypotheses: (1) all three petrel species will be equally attracted to playback of their own species’ calls; (2) all three petrel species will be attracted to playback of other sympatric species’ calls; and (3) the level of attraction to playback will vary with local densities of conspecifics.

### 4.2 Methods

#### 4.2.1 Study species and sampling sites
I examined social attraction in three closely related procellariid species: grey-faced petrels, fluttering shearwater, and flesh-footed shearwater. All three species are colonial, nocturnal, forage at sea, and nest in burrows in often mixed-species colonies (Marchant and Higgins 1990, Warham 1990, Gaze 2000). Burrows of the three species are often found at the same sites, with different species sometimes sharing the same burrow or burrow entrance (Skegg 1963, 1964). Grey-faced petrels and fluttering shearwaters are endemic to New Zealand, while flesh-footed shearwaters also breed in Australia (Marchant and Higgins 1990). Grey-faced petrels are considered ‘not threatened’ and are a culturally significant species to northern Māori (indigenous people of New Zealand), which traditionally harvest fledglings (Lyver et al. 2008, Miskelly et al. 2008). Fluttering shearwater populations are considered ‘at risk’ and have been used in the development of seabird translocation techniques for ecological restoration programmes in New Zealand (Bell et al. 2005, Miskelly et al. 2009). Flesh-footed shearwaters are generally understudied; however, they have recently been listed as ‘declining’ because of high mortality rates resulting from interactions with long-line fisheries (Baker and Wise 2005, Miskelly et al. 2008).

I performed playback experiments at two to three plots on each of five offshore islands and one mainland peninsula on the north-east coast of New Zealand’s North Island (Fig. 4.1, Table 4.1). Sites were selected on the basis of different densities of conspecifics for each species within 1 km (low, medium, and high density ‘source population’; Table 4.1). I tested grey-faced petrel attraction on Moutohorā and Korapuki, and at Whangaruru Peninsula; fluttering shearwater attraction on Mauitaha, Korapuki, and Taranga; and flesh-footed shearwater attraction on Ohinau (Table 4.2). All sites have histories of modification by Māori and introductions of mammalian predators, but have remained relatively undisturbed since the late 19th century (Skegg 1963, 1964, McCallum et al. 1984).

At each of the six playback sites, two or three plots were placed in the coastal fringe in areas with low burrow density (<0.025 burrows/m²; Table 4.3). All playback plots were ≥ 250 m apart to ensure playback was not audible (by humans) between them. I attempted to choose plots that were similar to each other and to nesting habitat preferred by burrow-nesting seabirds identified in a previous study (Table 4.3; Whitehead et al. 2014).
Figure 4.1: Location of call-playback experiments on one peninsula and five islands off the north-east coast of New Zealand. Grey circles indicate plots where grey-faced petrel calls were broadcast; grey squares, where fluttering shearwater calls were broadcast; stars, where flesh-footed shearwater calls were broadcast
Table 4.1: Islands or mainland sites in northern New Zealand where call-playback experiments were performed from 2012-2014. Details of nearby colonies (within 1 km) which may have provided the source of prospectors attracted to playback. GFPE = grey-faced petrel, FLSH = fluttering shearwater, FFSH = flesh-footed shearwater

<table>
<thead>
<tr>
<th>Site</th>
<th>Island or mainland site</th>
<th>Introduced mammals</th>
<th>Year eradicated</th>
<th>Nearby ‘source’ seabird populations</th>
<th>Burrow density (burrows/m²)</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moutohorā</td>
<td>240</td>
<td>Goats&lt;sup&gt;a&lt;/sup&gt;, Norway rats&lt;sup&gt;b&lt;/sup&gt;, European rabbits&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1987</td>
<td>GFPE High Moutohorā</td>
<td>0.04–0.18*</td>
<td>(Imber et al. 2000, Whitehead et al. 2014)</td>
</tr>
<tr>
<td>Whangaruru</td>
<td>Scenic Reserve (Mainland) 354</td>
<td>Stoats&lt;sup&gt;d&lt;/sup&gt;, Common brushtail possums&lt;sup&gt;e&lt;/sup&gt;, Rats&lt;sup&gt;f&lt;/sup&gt;, Domestic cats&lt;sup&gt;g&lt;/sup&gt;</td>
<td>Still present</td>
<td>GFPE Low Whangaruru Scenic Reserve</td>
<td>&lt;10 breeding pairs</td>
<td>C. Stone pers. comm.</td>
</tr>
<tr>
<td>Korapuki</td>
<td>18</td>
<td>Pacific rat&lt;sup&gt;h&lt;/sup&gt;, European rabbit</td>
<td>1986</td>
<td>FLSH Medium and Green Island</td>
<td>~0.19</td>
<td>(Hicks et al. 1975)</td>
</tr>
<tr>
<td>Korapuki</td>
<td>18</td>
<td>Pacific rat, European rabbit</td>
<td>1986</td>
<td>GFPE Medium Korapuki</td>
<td>0.06–0.10</td>
<td>Chapter 3</td>
</tr>
<tr>
<td>Taranga</td>
<td>470</td>
<td>Pacific rat</td>
<td>2011</td>
<td>FLSH Low Taranga</td>
<td>&lt;10 breeding pairs</td>
<td>(Skegg 1964), RTB pers. obs.</td>
</tr>
<tr>
<td>Island</td>
<td>No.</td>
<td>Species</td>
<td>Year</td>
<td>Density</td>
<td>2005 Density</td>
<td>Location</td>
</tr>
<tr>
<td>--------</td>
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<td>--------------------------</td>
<td>------</td>
<td>---------</td>
<td>--------------</td>
<td>----------</td>
</tr>
<tr>
<td>Mauitaha</td>
<td>22</td>
<td>Pacific rat</td>
<td>Still present</td>
<td>FLSH</td>
<td>High</td>
<td>Muriwhenua</td>
</tr>
<tr>
<td>Ohinau</td>
<td>32</td>
<td>Pacific rat, European rabbit</td>
<td>2005</td>
<td>FFSH</td>
<td>High</td>
<td>Ohinau</td>
</tr>
</tbody>
</table>

Scientific names of species: \(^a\) Capra hircus; \(^b\) Rattus norvegicus; \(^c\) Oryctolagus cuniculus; \(^d\) Mustela erminea; \(^e\) Trichosurus vulpecula; \(^f\) Rattus sp.; \(^g\) Felis catus; \(^h\) Kiore Rattus exulans.

* Largest known breeding colony.
Table 4.2: Nightly call playback schedules of social attraction experiments for three species of petrel

<table>
<thead>
<tr>
<th>Island</th>
<th>Treatment</th>
<th>Playback start–finish date</th>
<th>Playback start–finish time (hours, New Zealand Standard Time)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moutohorā</td>
<td>Grey-faced petrel</td>
<td>16–24 April 2012</td>
<td>1800–2230</td>
</tr>
<tr>
<td>Whangaruru</td>
<td>Grey-faced petrel</td>
<td>30 April – 8 May 2013</td>
<td>1830–2300</td>
</tr>
<tr>
<td>Korapuki</td>
<td>Grey-faced petrel</td>
<td>22–29 April 2014</td>
<td>1800–2200</td>
</tr>
<tr>
<td>Taranga</td>
<td>Fluttering shearwater</td>
<td>21–26 September 2012</td>
<td>1900–2300</td>
</tr>
<tr>
<td>Mauitaha</td>
<td>Fluttering shearwater</td>
<td>1–6 October 2012</td>
<td>2000–0000</td>
</tr>
<tr>
<td>Korapuki</td>
<td>Fluttering shearwater</td>
<td>1–7 October 2013</td>
<td>2000–0000</td>
</tr>
</tbody>
</table>
Table 4.3: Petrel burrows and details of each call-playback site (20 m²) on five offshore islands and a mainland site (Whangaruru) on the east coast of the North Island, New Zealand. Plant species are karamū (*Coprosma macrocarpa*), flax (*Phormium* sp.), houpara (*Pseudopanax lessonii*), māhoe (*Melicytus ramiflorus*), pōhutukawa (*Metrosideros excelsa*), karaka (*Corynocarpus laevigatus*), kohekohe (*Dysoxylum spectabile*), māmāngi (*Coprosma arborea*), karo (*Pittosporum crassifolium*) and pūriri (*Vitex lucens*).

<table>
<thead>
<tr>
<th>SITE</th>
<th>Burrows</th>
<th>Whangaruru</th>
<th>Taranga</th>
<th>Mauitaha</th>
<th>Korapuki</th>
<th>Ohinau</th>
<th>Moutohorā</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8*</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>GPS coordinates</td>
<td></td>
<td>−35.36792,</td>
<td>−36.0022,</td>
<td>−36.0772,</td>
<td>−36.6592,</td>
<td>−36.8125,</td>
<td>−37.85783,</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td></td>
<td>174.37125</td>
<td>175.1081</td>
<td>174.7003</td>
<td>175.848</td>
<td>176.0378</td>
<td>176.98338</td>
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<tr>
<td>Aspect (°)</td>
<td></td>
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<td>23</td>
<td>40</td>
<td>10</td>
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<td>Slope (°)</td>
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<td>33</td>
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<td>23</td>
<td>14</td>
</tr>
<tr>
<td>Topography</td>
<td></td>
<td>Face</td>
<td>Face</td>
<td>Face</td>
<td>Terrace</td>
<td>Face</td>
<td>Face</td>
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<tr>
<td>Soil depth (cm)</td>
<td></td>
<td>44</td>
<td>19</td>
<td>36</td>
<td>48</td>
<td>67</td>
<td></td>
</tr>
<tr>
<td>Understory vegetation</td>
<td></td>
<td>Karamū/Flax</td>
<td>Karamū</td>
<td>Houpara/</td>
<td>Māhoe/</td>
<td>Māhoe/</td>
<td>Māhoe</td>
</tr>
<tr>
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<td></td>
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<td>Pōhutukawa/ Kohekohe</td>
<td>Pōhutukawa</td>
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<th>SITE 2</th>
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<th>Mauitaha</th>
<th>Korapuki</th>
<th>Ohinau</th>
<th>Moutohorā</th>
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<tr>
<td>Pōhutukawa</td>
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</tbody>
</table>

*Plot used for both fluttering shearwater and grey-faced petrel playback
†Plots used for fluttering shearwater playback only
**Plot used for grey-faced petrel playback only
However, due to habitat modification and the small amount of available habitat, this was not possible on Mauitaha and at Whangaruru Peninsula, where plots differed in topography and vegetation. At each site I used transect tapes to measure a 20-m² square plot centred on a megaphone and marked trees at the four corners and four midpoints of each boundary with reflective tape.

4.2.2 Playback recordings of petrel calls

Call recordings were obtained from the McPherson recording library (McPherson 2011). Calls from 25 individual grey-faced petrels were recorded May–July 1988 in north-east New Zealand (Motutara, Kawhitu, and Mt Maunganui); fluttering shearwater calls were recorded on Long Island, Marlborough Sounds, New Zealand in November 1983; and flesh-footed shearwater colony recordings were taken at Lord Howe Island, Australia, in February 1982.

Using the sound editing software application Audacity version 2.0.0 (Audacity Team 2012), I isolated individual calls and removed background noise. I selected calls randomly from all individuals to create 3-min call medleys. Three playback files were constructed: one with only one track of call medleys, one with two different overlaid medley tracks, and one with three. All three tapes were loaded onto an EM646 digital MP3 audio player (Dick Smith Electronics, Chullora, Australia) and broadcast repeatedly towards the ocean over a TOA 8Ω 30W megaphone (Foxpro, Lewistown, USA).

4.2.3 Playback schedule

I broadcast call playback during the pre-breeding courtship and burrow-cleaning season, in the first 3–4 hours of darkness, when the surface activity of the focal species was at its greatest (Table 4.2). On Moutohorā, due to logistical constraints, I played grey-faced petrel calls on a 2-nights-on/2-nights-off schedule, alternating between sites; while a 4-nights-on/4-nights-off schedule was employed at Whangaruru Peninsula, and on the islands of Taranga, Mauitaha, Ohinau and Korapuki. This crossover design increased
power to detect an effect of call playback, while controlling for the effects of varying habitat among plots (Diaz-Uriarte 2002, Quinn and Keough 2002).

An observer sat 10 m on the landward side of the megaphone and recorded the following information in 10 min periods: (1) number of birds (and species, if possible) seen or heard flying over; (2) number and species of calls heard within the 20-m² plot; (3) number of birds heard crashing through the canopy and landing in the plot. The quantity of these observed behaviours was used as a relative index of abundance. After each 10 min period, to maximise our chances of encountering and recording as many of the birds entering the plot as possible, the number and species of birds inside the plot were counted. Plot counts involved walking around plot boundaries by torchlight for 5 mins. At all sites, other than Moutohorā, I marked the head of each bird with liquid paper in order to determine the cumulative number of birds that were observed in the plot during the nightly sampling period. On Moutohorā, where only one observer was present, observations alternated between sites each 30 min, starting with the playback site. On Taranga, Mauitaha, Ohinau and at Whangaruru, I used an observer in each plot with nightly observer location assigned randomly between the two sites to avoid observer bias.

4.2.4 Statistical analysis

I used generalized linear mixed models (GLMM) to compare the numbers of calls, landings, and birds on the plot between control and playback treatments. Each model had a Poisson error structure, log link, and Laplace approximation. To control for the ‘switchback’ or ‘cross-over’ design repeated at multiple sites, I included plot nested within site as a random factor (Diaz-Uriarte 2002). I also included observer as a categorical random factor to remove the effects of observer bias; and time of night nested within Julian date to control for repeated counts throughout the duration of the experiment. To remove variation in colony attendance associated with the effect of moonlight (Mougeot and Bretagnolle 2000, Prugh and Golden 2014), I included four classes of moon phase, from new to full moon, as a fixed effect. A separate model was run for each species. For all species I included treatment category (playback or control) as a fixed effect, and in addition, for
Grey-faced Petrel and Fluttering shearwater, I included the effect of density of nearby conspecifics (low = 1, medium = 2, high = 3; Table 1.1).

To test for the possibility of one species responding to another species’ call-playback, I compared the numbers of calls and birds observed of one species between control and playback treatments of another species. I ran separate GLMMs for the numbers of calls and birds observed on the plot for each species, with treatment category (playback of a heterospecific – or control) as a fixed effect and plot nested within site, observer, and time of night nested within Julian date as random effects.

Finally, to examine the possibility of attraction increasing or decreasing over the duration of the experiment, I ran a third GLMM, using counts of birds on the plot during playback treatments only. In the model I included ‘number of nights of playback at a site’, species (only grey-faced petrel and fluttering shearwater), their interaction terms, Julian date, and moon phase as fixed variables and time of night, plot nested within site, and observer as a random factors.

To determine the amount of variance explained, or ‘goodness-of-fit’ of each GLMM, I estimated marginal and conditional pseudo-R$^2$ values, which are associated with fixed and fixed and random effects respectively (Nakagawa and Schielzeth 2013). I carried out all analyses in the statistical program R version 2.14.2 (R Development Core Team 2012.).

4.3 Results

4.3.1 Intraspecific reaction to playback

Of all three species, the broadcasting of playback calls elicited the strongest response in grey-faced petrel (Fig. 4.2). Grey-faced petrels were attracted to playback calls on all three sites at all treatment plots. During playback, within plot limits, mean counts of grey-faced petrel calls were six times higher ($Z_t = 2.692 P < 0.001$), mean bird counts were four times higher (Fig. 4.3; $Z_t = 1.513 P < 0.001$), and there were three times more birds observed flying over and circling plots (birds identified to species from their calls) versus nights with no playback ($Z_t = -0.327 P = 0.012$). On Korapuki, a mean of 1.83 grey-faced
petrels were identified and marked during each 15-min observation period. Moon phase significantly affected call counts only, with more calls recorded closer to the full moon ($Z_I = 0.237 \ P < 0.001$). Finally, at sites with higher density of nearby conspecifics there was a larger difference between both calls and birds on the plot during playback compared with no playback ($Z_I = 1.314 \ P = 0.013$; Fig 4.3), indicating that playback elicited a stronger response in grey-faced petrels at sites with denser nearby colonies.

Fluttering shearwater response to playback experiments differed between islands with different densities of nearby conspecifics. On Taranga, where there was a ‘low’ nearby density of conspecifics, there were no significant differences between treatment and control nights in any response metrics (all $P > 0.257$). On Korapuki, where there was a ‘medium’ density of nearby breeding conspecifics, there was a mean of 1.1 times more fluttering shearwater calls counted and 4.9 times more fluttering shearwaters observed during playback ($Z_I = 3.372, P < 0.001$) than during periods where no audio was played. Finally, on Mauitaha, where there was a ‘high’ nearby density of breeding conspecifics, there was a mean of 1.8 times more fluttering shearwater calls counted, and 19 times more fluttering shearwaters observed ($Z_I = 10.972, P < 0.001$) during playback compared with periods of no playback. Moon phase affected call counts only, with more calls recorded closer to the new moon ($Z_I = -1.288 \ P = 0.040$). The increase in observed calls and birds on the plot during playback was significantly higher with increasing density of nearby conspecifics ($Z_I = 1.937 \ P = 0.005$).

There were no significant differences between observations during flesh-footed shearwater playback and control nights (all $P > 0.089$) on Ohinau. Similarly, moon phase had no effect (all $P > 0.662$).

### 4.3.2 Interspecific responses to playback calls

Playback calls of fluttering shearwater elicited a response in grey-faced petrels. During fluttering shearwater playback treatments, there was a mean of two times more grey-faced petrel calls counted in each plot ($Z_I = 2.235 \ P = 0.025$), and three times more grey-faced petrels observed flying over ($Z_I = 2.797 \ P = 0.005$; Table 4.4). No other species responded to heterospecific calls (all $P > 0.156$).
Figure 4.2 Mean number of flesh-footed shearwater (FFSH), fluttering shearwater (FLSH), and grey-faced petrel (GFPE) observed on two 20-m$^2$ plots at two sites in north-western New Zealand ± standard error. Each plot was centred on a megaphone playing petrel calls (playback) or no sound (control)
Figure 4.3: Mean number of petrels, (a) grey-faced petrel; (b) fluttering shearwater; and (c) flesh-footed shearwater; observed on two 20-m² plots (± standard error) centred on a megaphone playing petrel calls (playback) or no sound (control) at sites with low, medium (mid), or high density potential source populations within 1 km.
Table 4.4: Behavioural response of grey-faced petrel to playback of other species calls over a megaphone. Parameter estimates ($\beta$), standard errors (SE), marginal ($R^2_m$) and conditional pseudo-$R^2$ ($R^2_c$) values are presented from generalized linear mixed models. Asterisks indicate significant results.

<table>
<thead>
<tr>
<th>Species</th>
<th>Playback treatment</th>
<th>Measurement</th>
<th>$\beta \pm SE$</th>
<th>$P$ value</th>
<th>$R^2_m$</th>
<th>$R^2_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grey-faced petrel</td>
<td>Fluttering shearwater</td>
<td>Birds on plot</td>
<td>1.74 ± 0.78</td>
<td>0.025*</td>
<td>0.081</td>
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<td>Calls on plot</td>
<td>0.06 ± 4.52</td>
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<td>0.870</td>
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<td></td>
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<td>Calls out of plot</td>
<td>−11.63 ± 4.04</td>
<td>0.004*</td>
<td>0.086</td>
<td>0.651</td>
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<tr>
<td></td>
<td></td>
<td>Fly-overs</td>
<td>2.97 ± 1.06</td>
<td>0.005*</td>
<td>0.145</td>
<td>0.850</td>
</tr>
<tr>
<td>Grey-faced petrel</td>
<td>Flesh-footed shearwater</td>
<td>Birds on plot</td>
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<td></td>
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<td></td>
<td></td>
<td>Calls out of plot</td>
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<td>Calls on plot</td>
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<td>Fly-overs</td>
<td>−2.27 ± 1.27</td>
<td>0.074</td>
<td>0.145</td>
<td>0.850</td>
</tr>
</tbody>
</table>
4.3.3 Duration of playback

Overall, I found weak evidence that nightly plot counts of fluttering shearwaters and grey-faced petrel decreased with increasing nights of playback ($Z_f = -0.200 \ P = 0.061$). I found no effect of the interaction between species and number of nights of playback. I found no significant effect of Julian date or moon phase on the number of birds observed on a plot ($P > 0.386$).

4.4 Discussion

I found marked differences in the responsiveness of three petrel species to playback calls at each of the various sites. Grey-faced petrels were attracted to calls of their own species across all study islands. This level of responsiveness suggests that grey-faced petrels are likely to be a strong candidate species for the use of auditory attraction methods to facilitate recovery or re-colonization. Although there was no explicit control, in a restoration initiative at Young Nick’s Head, New Zealand, grey-faced petrels re-colonized a call-playback site within 3 years of the installation of both a permanent playback system and artificial burrows (Sawyer and Fogle 2010). In contrast to grey-faced petrels however, I found varying levels of responsiveness by fluttering shearwaters on different islands (Fig. 4.3). Other studies have experienced similarly variable results to social attraction in this species. For example, on Matiu/Somes Island, a small (25 ha) newly predator-free island in New Zealand, fluttering shearwater calls were broadcast for 4 years, with little response. The broadcasting equipment was moved ~500 m, to a site with different habitat features, and within the year, fluttering shearwaters were observed using artificial nest boxes adjacent to the playback site (S. Cotter Matiu/Somes Charitable Trust pers. comm. 2012). Finally, I did not observe any behavioural response to playback by flesh-footed shearwaters on the single study island for this species. Due to logistical constraints, I was unable to replicate this component on other islands, thus I was unable to assess whether this lack of response is characteristic of the species in general, or of my particular study.
I observed a weak decrease in the number of birds observed on plots after more nights of call playback. The relationship was likely not related to nightly conditions or moon light, as there was no significant effect of Julian date or moon phase. I am unsure of the behavioural underpinnings of this result, but speculate that it may be related to stimulus habituation or perhaps the short duration of the stimulus was insufficient to induce individual birds to linger, settle, and attract more birds. I highlight the importance of this finding as a potential source of variation and caution that response may weaken in prolonged attraction experiments.

I found that grey-faced petrels responded to fluttering shearwater call playback, suggesting that grey-faced petrels may be attracted to heterospecific vocalizations. Considering the overlap in nesting habitat between the two species, social cues provided by either species could be useful indicators of breeding habitat quality (Mönkkönen et al. 1999, Buxton and Jones 2012a). However, evidence suggests that grey-faced petrels are also attracted to human-produced noises (Tennyson and Taylor 1990). Future research should investigate the responsiveness of petrels to random noise versus call playback as a biologically relevant social cue.

4.4.1 Reasons for the differences in responses to auditory cues

It is possible that variation in attraction to call playback observed among species in this experiment may reveal differences in species-specific dispersal dynamics. Procellariid seabirds are generally considered to be philopatric, showing a preference to return to their natal site with low levels of both natal and breeding dispersal (Greenwood and Harvey 1982, Warham 1990, Ovenden et al. 1991). It is possible that interspecific differences in the rates of philopatry may drive the different responses to playback calls, especially if juvenile birds of some species have a much higher probability of returning to their natal site than others.

Alternatively, evidence suggests that for procellariiform species immigration rates are variable, but can be high in some circumstances, with consequences for metapopulation structure (Inchausti and Weimerskirch 2002, Milot et al. 2008, Pascoe et al. 2011). Immigration rate is likely to be influenced by density-dependent processes, both at the
natal colony, affecting the size of the pool of birds available to explore a new colony; and at new colonies, by the number of birds already breeding at that colony (Oro et al. 2006). The probability that individuals will prospect at a ‘new’ colony not only depends on the size of the pool of pre-breeding birds available to prospect, but also the connectivity and distance between prospective colonies and the natal colony (maximum distance ~ 25 km; Chapter 2). It is also likely that these prospectors will decide to settle and breed at a ‘new’ colony based on local nest-habitat quality (Chapter 3), which can be assessed on direct quality of environmental factors (e.g. food availability, vegetation type; Buckley and Buckley 1980, Pampush and Anthony 1993, Jones 2001) and indirect information from established breeders (e.g. presence or breeding success of conspecifics; Boulinier and Danchin 1997, Danchin et al. 1998). Thus, variability in response to playback may be further influenced by the size of the available pool of prospectors (i.e. density of a source population), connectivity between populations, and local nest-habitat quality. My results suggest that both grey-faced petrels and fluttering shearwaters show a greater response to call playback with nearby (within 1 km) mid- or high-density colonies. I hypothesize that increasing response may be associated with a larger local ‘pool of prospectors’ and thus a higher probability of prospectors finding the playback site and responding to the playback signal.

4.4.2 Social attraction as a restoration tool

Over the past few decades as the number of restoration initiatives has increased, interest in social attraction as a method to lure birds to sites has increased (Jones and Kress 2012). Social attraction offers a potential alternative or supporting mechanism to the translocation of chicks (Kress 1998, Ewen et al. 2012). Translocations require a high financial investment, large amounts of field effort, and there is a lag time (2-10 years) between transfer of petrel chicks and age at first breeding (Miskelly et al. 2009). Thus, social attraction represents a less labour intensive cost-effective petrel restoration technique because it has the potential to attract breeding-age adults to a site. Social attraction may be an especially valuable tool in New Zealand, where citizen science is widespread, with increasing numbers of restoration initiatives established by local community groups (e.g.

However, my results, and those of other experiments, demonstrate that attraction to social cues in seabirds is likely to be highly variable and affected by a potentially complex suite of factors. To increase the effectiveness of social attraction, notably the attraction of petrels to auditory cues, research should be aimed at quantifying the sources of variability associated with the technique. These including factors associated with petrel ecology, such as interspecific differences in dispersal rates, density dependence, habitat preferences, and size and distance of restoration sites from source populations; and factors associated with experimental design, such as spacing of cues, time of year, and cue type (Ahlering et al. 2010). Vocal repertoires in seabirds have received little research attention in New Zealand, especially those in the Procellariid family. Studies elsewhere indicate that some species of petrel (e.g. Leach’s storm-petrel, *Oceanodroma leucorhoa*; Podolsky and Kress 1989) are differentially attracted to various call types, highlighting the need for further study of the context of different call types and replication of different call types in social attraction experiments.

### 4.4.3 Conclusion

The scale and success of human-introduced predator eradication projects have increased on islands around the world (Keitt et al. 2010). Consequently, the importance of developing effective and affordable restoration techniques for populations affected by predators has also increased. Social attraction using call playback represents a potentially cost-effective tool for encouraging re-colonization and recovery of petrels. However, caution is advised, as responses to social cues can vary between sites and species. I recommend longer term social experiments and higher replication at the species, site, and island level before restoration efforts proceed.
Chapter 5  Applying assembly rules to seabird restoration: patterns of burrow-nesting seabird species co-occurrence after rat eradication

5.1  Introduction

Rodents (*Rattus sp.*) have been introduced to 90% of island archipelagos around the world and have altered island communities by extirpating or severely reducing population sizes of native species (Atkinson 1985, Towns et al. 2006). However, in the past three decades, efforts to restore islands by eradicating rodents have increased, with over 300 islands successfully cleared of rats (Keitt et al. 2011, DIISE 2014). Not only has this prevented the extinction and facilitated the recovery of many species; it has also provided the opportunity to investigate how altered animal communities recover and reassemble.

Although the re-colonization and re-distribution of affected species after rodent eradication is complex, with multiple ecological and anthropogenic drivers (Chapter 2), the outcome will be limited by underlying assembly rules (Lockwood 1997, Palmer et al. 1997, Temperton et al. 2004). Assembly rules are ecological mechanisms governing colonization, and eventual community structure; including inter-specific competition or facilitation, and environmental constraints (Diamond 1975, Gotelli 1999, Temperton and Hobbs 2004). At the foundation of restoration ecology is the assumption that interactions between different species, and between species and habitat, will influence how a community of plants or animals “reassembles” after disturbance (Hobbs and Norton 2004). However, little is known about how inter-specific interactions affect post-eradication wildlife recovery outcomes (Oro et al. 2009).

Burrow-nesting petrels (order Procellariiformes) are particularly vulnerable to rodents, due to their easily accessed nests and lack of appropriate behavioural adaptations to ground-based predators (Moors and Atkinson 1984, Jones et al. 2008, Towns et al. 2011b). New Zealand supports the greatest diversity of burrow-nesting petrels in the world, with over 34 petrel, shearwater, and diving petrel species breeding within the

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archipelago (Taylor 2000). Here, petrels often nest in large, sympatric, multi-species colonies on offshore islands free of the effects of mammalian predators. Rodents have invaded ~40% of islands around the New Zealand archipelago since human arrival 800 years ago (Towns et al. 2011b), and over the past 50 years at least one rodent species has been removed from over 80 islands (Clout and Russell 2006). Evidence suggests that rodent eradication has facilitated the recovery and re-colonization of some species of burrow-nesting seabirds (Chapter 2; Towns et al. 2006). However, some species have not yet re-colonized or populations have not responded and only now are the drivers responsible for these patterns being investigated (Chapter 2).

As a petrel community reassembles after predator eradication, the earliest species to prospect will likely reflect the distance to source populations and meta-population dynamics (i.e. dispersal limitation; Oro and Ruxton 2001, Young et al. 2001), while recruitment is density dependent (Crespin et al. 2006). However, the establishment and persistence of species in the resulting community will ultimately be restricted by the effects of inter-specific interactions and habitat suitability during reassembly (Weiher and Keddy 2001). Suitable nesting habitat may be limited, resulting in competition and avoidance between species (Wallace et al. 1992). Conversely, social facilitation is an important resource among colonial seabirds, whereby the presence of others signals safe nesting habitat for young prospecting birds, resulting in co-occurrence and aggregation between species (Schippers et al. 2011).

Seabird conservation management has tended to focus on one species at a time and ignore the interactions among seabird species; however, species interactions are a fundamental element of seabird ecology and have significant implications for restoration success (Lewison et al. 2012). For example, interference competition between broad-billed prions (*Pachyptila vittata*) and endangered Chatham petrels (*Pterodroma axillaris*) on South-east Island, NZ, poses the most serious threat to the latter (Was et al. 2000). This example illustrates the possibility of a “priority effect” during seabird community reassembly, where the establishment of one or more petrel species resists the colonization and persistence of another (Young et al. 2001, Fukami et al. 2005). Alternatively, the presence of one species, or a combination of species, may enhance the recovery of others (Bruno et al. 2003, Greipsson 2011). The compatibility of different species could be
invaluable for improving active seabird management efforts. Namely, predicting which species combinations would be most successful in reintroduction projects and identifying “priority species” which, when actively enhanced, may hinder or facilitate the recovery of others (Fischer and Lindenmayer 2000, Seddon et al. 2007).

In this study I examine the role of assembly rules in the recovery of burrow-nesting seabird populations by comparing different species’ nesting habitat use and co-occurrence on NZ islands that vary according to the presence, absence, or time since eradication of Pacific rats (*Rattus exulans*). I measured species occupancy and habitat characteristics in plots to address four questions: (1) is the distribution of petrel species affected by nesting habitat; (2) does the occurrence of petrel species reflect a random distribution or do species co-occur more or less than expected by chance; (3) do co-occurrence patterns differ on islands with different times since rat eradication; (4) do some species pairs co-occur more frequently than others, and if so, can a “priority species” be identified? I predict that reassembly in petrel communities will be governed by facilitation, resulting in species co-occurring more than expected by chance. However, rodents may have altered community structure in such a way that new species combinations on rat eradicated islands result in exclusion, and thus less co-occurrence than expected by chance.

### 5.2 Methods

I addressed the research questions outlined above using a hierarchical approach:

(i) To investigate the relationship between the occurrence of petrel species and habitat, I assessed nesting habitat use by ranking and averaging a series of generalized linear mixed models (GLMM) using the presence or absence of a species in a plot as a binomial response variable and a suite of relevant habitat covariates as predictors.

(ii) To examine whether petrel species were more likely to aggregate or to avoid each other in burrow-nesting petrel communities, I compared observed species distributions with randomly generated species distributions.

(iii) Using similar methods to (ii), I investigated: (a) petrel species distributions over time after rat eradication by comparing co-occurrence of petrel species on six islands.
representing a chronosequence of time since Pacific rat eradication; and (b) potential interactions between species pairs by examining pair-wise co-occurrence among islands.

(iv) To consider how petrel species turnover between years and individual species’ detectability might affect my results, I compared species occupancy within plots between years and days.

5.2.1 Study Area and species

I assessed community structure on five islands representing 0-24 years of recovery time after Pacific rat, and in some cases European rabbit, eradication: Mauitaha, Taranga, Ohinau, Kawhitu, and Korapuki; and one island, Ruamaahuanui, which never had predators introduced (Table 5.1). All islands are within 7-13 km of the North Island within or adjacent to the Hauraki Gulf Marine Park and have similar general vegetation structure and climatologic and geological features (Fig. 5.1A-C). All islands have similar disturbance histories, having been subjected to extensive burning and terracing by Māori; however, all islands have been protected as nature reserves and have remained relatively undisturbed since the mid-19th Century (Sladden and Falla 1928, Edgar 1962). Island vegetation is dominated by early successional species such as pōhutukawa (*Metrosideros excelsa*), kanuka (*Kunzea ericoides*), and bird-dispersed secondary species such as māhoe (*Melicytus ramiflorus*) and māpou (*Myrsine australis*) (Atkinson 2004).

All study islands have similar nearby populations or ‘pools’ of sympatric burrow-nesting petrel species (Table 5.2). Limited available information suggests that burrows of all species tend to be mixed, with no hetero-specific separation of physical habitat characteristics, and different species sometimes occupying burrows of others (Hicks et al. 1975, Pierce 2002). Petrel burrows are more often located in deep soil on steep, rocky westerly slopes with karamū (*Coprosma macrocarpa*) understory (Chapter3). Species range in size from 130-800 g and forage from near-shore to open-ocean (Table 5.2)

5.2.2 Survey design
I surveyed for seabird breeding burrows, burrow occupancy, and habitat characteristics in plots across study islands by first establishing transects running from coast to coast perpendicular to the long axis of each island (Table 5.1). Along each transect I randomly placed one to six 3 m-radius circular plots (Fig. 5.1D), resulting in a total of 68-132 plots on each island (Table 5.1). Within each plot, I assessed the following habitat variables: aspect, slope, elevation, topography, soil depth, soil strength, soil texture, percent cover of boulders, stem count for each species between 2.5–10 cm in diameter at chest height (dbh), and canopy species and percent cover. For each seabird burrow whose entrance fell more than half-way inside plot limits, I assessed occupancy using an infrared burrow camera (henceforth “burrow-scope”; Sextant Technology Ltd., Wellington, New Zealand). Because of the steep terrain on Taranga, transects were constrained by proximity to existing tracks. Because of logistical constraints, habitat survey data was not available from Ruamaahuanui, instead I assessed species occupancy in 21 randomly placed 10 by 10 m permanent plots. All surveys were conducted at some stage of the breeding cycle (courtship to chick rearing) of all study species (Table 5.1). For more details of habitat survey methods, see Chapter 3.

Burrow-scope surveys may overlook a proportion of individuals down burrows (e.g. ~34% of Sooty Shearwater, *Puffinus griseus*, nests missed in the Snares Islands; Hamilton 2000). Thus, observed measures of species occupancy are likely to be associated with an unknown detection error. Furthermore, although burrow-nesting petrels are thought to have high nest-site fidelity, intermittent breeding and failed breeding attempts may cause community structure within plots to vary between years (Warham 1996, Erikstad et al. 1998). To examine inter-annual changes in community structure and burrow-scope detection error for different species, I established 5-m-radius circular plots on five islands (Table 5.1). I placed plots randomly within burrowed areas; centre points were marked with an aluminium pole; and each burrow entrance within the 78.5 m² plot limits was marked with a numbered cattle tag. To assess changes in community structure between years, I inspected each burrow for occupancy in two consecutive years (Table 5.1). To estimate detection error for each species, I inspected each burrow twice within two to three days in 2013 on Ohinau, Kwhitu, and Korapuki.
Table 5.1: Six islands off the northeastern coast of New Zealand’s North Island surveyed for burrow-nesting seabird occupancy. Each island differs in the presence (“still present”), absence (“n/a”), or time since Pacific rat and European rabbit eradication.

<table>
<thead>
<tr>
<th>Island</th>
<th>Island size (ha)</th>
<th>Yr rats eradicated</th>
<th>Yr rabbits eradicated</th>
<th>Yrs surveyed</th>
<th>Month surveyed</th>
<th>Transects</th>
<th>3-m-radius habitat plots</th>
<th>5-m-radius plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mauitaha</td>
<td>22</td>
<td>still present</td>
<td>n/a</td>
<td>2011/2012</td>
<td>December/October</td>
<td>31</td>
<td>68</td>
<td>13</td>
</tr>
<tr>
<td>Taranga</td>
<td>470</td>
<td>2011</td>
<td>n/a</td>
<td>2011/2012</td>
<td>November/October</td>
<td>61</td>
<td>120</td>
<td>27</td>
</tr>
<tr>
<td>Ohinau</td>
<td>32</td>
<td>2005</td>
<td>2005</td>
<td>2012/2013</td>
<td>October</td>
<td>33</td>
<td>100</td>
<td>31</td>
</tr>
<tr>
<td>Kawhitu</td>
<td>100</td>
<td>1991</td>
<td>1991</td>
<td>2012/2013</td>
<td>November</td>
<td>35</td>
<td>121</td>
<td>36</td>
</tr>
<tr>
<td>Korapuki</td>
<td>18</td>
<td>1986</td>
<td>1986</td>
<td>2012/2013</td>
<td>December</td>
<td>41</td>
<td>101</td>
<td>19</td>
</tr>
<tr>
<td>Ruamaahuanui</td>
<td>21</td>
<td>n/a</td>
<td>n/a</td>
<td>2010</td>
<td>November</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
</tbody>
</table>
Figure 5.1: Location of study islands off the north-eastern coast of the North Island, New Zealand, including those in the Hen and Chicks group (A), the Alderman group (B), and the Mercury group (C). Inset (D) represents an example of the survey design performed on each island shown on Korapuki, where lines indicate transects and circles indicate plots.
Table 5.2: Common name, species name, and relevant attributes of the seven burrow-nesting petrel species found on six islands off the north-eastern coast of New Zealand’s North Island

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Mean mass (g)</th>
<th>Egg laying</th>
<th>Age at first breeding</th>
<th>Foraging</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sooty shearwater</td>
<td>Puffinus griseus</td>
<td>800</td>
<td>December</td>
<td>5 to 7</td>
<td>Pelagic</td>
<td>New Zealand</td>
</tr>
<tr>
<td>Flesh-footed shearwater</td>
<td>Puffinus carneipes</td>
<td>700</td>
<td>December</td>
<td>~5</td>
<td>Occassionally inshore, mostly shelf/pelagic</td>
<td>15 nearshore islands North Island, NZ; Lord Howe Island, AU; Ile St Paul, FR</td>
</tr>
<tr>
<td>Grey-faced petrel</td>
<td>Pterodroma macroptera gouldi</td>
<td>550</td>
<td>June-July</td>
<td>~4</td>
<td>Shelf/pelagic</td>
<td>Mainly on nearshore islands on the east coast of North Island, NZ</td>
</tr>
<tr>
<td>Fluttering shearwater</td>
<td>Puffinus gavia</td>
<td>365</td>
<td>October</td>
<td>unknown</td>
<td>(not well known)</td>
<td>Nearshore islands north of Marlborough Sounds, NZ</td>
</tr>
<tr>
<td>Little shearwater</td>
<td>Puffinus assimilis</td>
<td>240</td>
<td>July</td>
<td>unknown</td>
<td>unknown</td>
<td>Near- and offshore islands from the Kermadec Islands to Wellington, NZ</td>
</tr>
<tr>
<td>Pycroft's petrel</td>
<td>Pterodroma pycrofti</td>
<td>150</td>
<td>December</td>
<td>~3</td>
<td>unknown</td>
<td>Nearshore islands in north-eastern New Zealand</td>
</tr>
<tr>
<td>Common diving petrel</td>
<td>Pelecanoides urinatrix</td>
<td>August-September</td>
<td>2 to 3</td>
<td>Nearshore Island off New Zealand, south-east AU, and subantarctic islands</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*All information collected from (Marchant and Higgins 1990) and http://www.nzbirdsonline.org.nz/*.
5.2.3 Statistical analyses

All statistical analyses were performed in R version 2.14.2 (R Development Core Team 2012.). Data are presented as mean ± standard error (SE) and statistical significance was evaluated at $\alpha = 0.05$, unless otherwise specified.

5.2.3.1 Modelling nesting habitat use

Prior to modelling, I simplified habitat covariates by, first, omitting one of each pair of correlated variables (where $r_s \geq 0.5$), determined by calculating a Spearman’s correlation matrix. Second, I used a two-way indicator species analysis (TWINSPAN; Hill 1979) to reduce the full set of canopy and stem species into a smaller set of uncorrelated vegetation classes. Finally, I transformed categorical covariates (aspect, topography, canopy and stem vegetation classes from TWINSPAN analysis) into dummy variables by setting one class as a reference class with a coefficient of zero (Hardy 1993) and removed dummy variables with low frequency among plots ($\leq 5\%$).

To determine nesting habitat use of each species, I ranked and averaged a series of binomial GLMMs (Manly et al. 2002). Separate global models were fitted for each species using the package lme4 (Bates et al. 2012), with the presence or absence of a bird in $\geq 1$ burrow in a plot as the binary response variable, simplified habitat covariates as explanatory variables, and island as a random factor. To ensure resulting parameter estimates would be comparable, I scaled habitat covariates by subtracting the mean and dividing by one standard deviation (Schielzeth 2010). Interaction terms were not included, because mixed models would be overparameterized and thus would not converge (Ginzburg and Jensen 2004). I generated 25 candidate models using a combination of the dredge function in MuMIn package (Bartoń 2013) and biologically plausible models constructed based on field observations (Table 5.3).

I used an information-theoretic approach to rank candidate models using Akaike’s information criterion for small sample sizes (AICc), and AICc weights ($w_i$) to evaluate model likelihood (Burnham and Anderson 2002). I used model averaging to generate
parameter estimates and unconditional standard errors, which were used with parameter likelihoods to draw inferences for each habitat covariate (Johnson and Omland 2004).

Positive spatial autocorrelation is a general property among ecological variables across geographic space, whereby pairs of locations at a closer distance are more similar than expected for randomly associated pairs (Legendre 1993). To test for this phenomenon, I constructed variograms from residuals of top habitat use models. Distance classes were calculated from the eastings and northings of plot centres (geoR package; Ribeiro and Diggle 2001). Spatial autocorrelation was assessed using the “range”, or distance class on the x-axis of the variogram, at which a “sill”, or asymptote, was reached (Chapter 3). If a sill in the semivariance was not reached within a range of 30 m (suggesting spatial autocorrelation up to 30 m, the minimum distance between 95% of plots), an autocovariate term would be incorporated into the global model (Smith 1994).

5.2.3.2 Species co-occurrence

To acquire a basic visual description of species-environmental affinities, I performed a Principal Component analysis (PCA) so that each species could be compared in reduced ordination space. Arrows on PCA graphs represent correlations between environmental variables and principal components. Only nesting habitat variables from the highest ranked habitat use models were used.

To examine the structure of species co-occurrence I used “null model testing”. This compares patterns in an observed species presence-absence matrix with those predicted for null matrices – simulated communities that have been assembled randomly (Gilpin and Diamond 1982, Gotelli and Graves 1996b, Gotelli 2000, Webb et al. 2010). I created two sets of simulated null communities: (i) unconstrained, and: (ii) constrained by the effects of local habitat suitability. During the generation of the latter set of null communities I used relative site-specific probabilities of occurrence (from habitat use models above) as likelihoods of a species occupying a site (Peres-Neto et al. 2001).

I constructed seven community matrices (one summarizing species presence-absence data from all plots on all islands, and six separate matrices for plots on each island) and 15 pair-wise species co-occurrence matrices (six species total). For each matrix, observed checkerboard scores (C-scores) were calculated (Stone and Roberts 1992).
Table 5.3: Global generalized linear mixed models and their respective degrees of freedom (df) used to generate model sets to determine nesting habitat use of six species of burrow-nesting petrel on five islands off the north-east coast of New Zealand’s North Island. S indicates stem counts of plant species, while C indicates canopy cover of plant species. Island was included as a random factor in each model.

<table>
<thead>
<tr>
<th>Species</th>
<th>df</th>
<th>Global model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flesh-footed shearwater</td>
<td>17</td>
<td>N + W + Elevation + Slope + Soil depth + Soil strength + Rock + Total small stem count + Total canopy cover + PohutukawaC + MahoeC + KanukaC + MahoeS + KaramuS + MapouS</td>
</tr>
<tr>
<td>Grey-faced petrel</td>
<td>18</td>
<td>S + W + Elevation + Slope + Soil depth + Soil strength + Rock + Total canopy cover + Total small stem count + Total MahoeC + KanukaC + MahoeS + KaramuS + MapouS + KaroS</td>
</tr>
<tr>
<td>Fluttering shearwater</td>
<td>14</td>
<td>N + S + W + Elevation + Slope + Soil depth + Soil strength + Rock + Total canopy cover + Total small stem count + Total canopy cover + PohutukawaC + MahoeC + MahoeS</td>
</tr>
<tr>
<td>Little shearwater</td>
<td>17</td>
<td>N + S + W + Elevation + Slope + Soil depth + Soil strength + Rock + Total canopy cover + Total small stem count + PohutukawaC + MahoeC + MahoeS + KaramuS + MapouS</td>
</tr>
<tr>
<td>Pycroft’s petrel</td>
<td>17</td>
<td>N + S + W + Elevation + Slope + Soil depth + Soil strength + Rock + Total canopy cover + Total small stem count + PohutukawaC + MahoeC + MahoeS + KaramuS + MapouS</td>
</tr>
<tr>
<td>Common diving petrel</td>
<td>13</td>
<td>S + W + Elevation + Slope + Soil depth + Soil strength + Rock + Total small stem count + Total canopy cover + MahoeC + KaroS</td>
</tr>
</tbody>
</table>
The C-score statistic quantifies the number of sites for which one species is present and another is absent for all species pair combinations, where larger C-scores indicate an increasing degree of avoidance between species (Stone and Roberts 1990). I used C-scores to assess co-occurrence because it has good Type I error properties; thus, it has greater power to detect patterns in non-random data sets despite background noise in co-occurrence patterns (Gotelli 2000, Webb et al. 2010). C-scores are sensitive to the number of sites occupied and number of species pairs. Because this would confound comparisons between islands with different petrel densities and species richness, I standardized C-scores, accounting for the number of species pairs and site combinations (Ulrich and Gotelli 2013).

I developed null communities using the `permat` function in the package ‘vegan’ (Oksanen et al. 2013). To constrain null communities based on habitat suitability, I constructed a species-specific relative probability matrix using predicted probabilities from my habitat use models (Peres-Neto et al. 2001). To estimate site-specific probabilities of species occurrence, I calculated predicted probabilities of occurrence from top habitat models with the best performance. ‘Best performance’ was evaluated based on accuracy of GLMM predictions, quantified using the area under a receiver-operating characteristic curve (AUC) in the ‘PresenceAbsence’ package (Freeman and Moison 2008). AUC values below 0.6 indicate a performance no better than random, values between 0.7-0.9 are considered useful, while values >0.9 have excellent predictive power (DeLong et al. 1988). Relative probability matrices corresponded to observed community matrices; therefore, I generated each constrained null community by weighting the occurrence of a species in a given plot based on relative probabilities from habitat use models. I used Monte Carlo simulations of 1,000 iterations. I averaged C-scores among simulated null communities, generating mean and standard deviation values for unconstrained and constrained models.

In a community that exhibits isolated species, or competitive exclusion, the C-score simulated using null communities should be significantly less than observed C-scores. To test whether observed co-occurrence patterns differed from simulated co-occurrence patterns, I calculated the probability of obtaining simulated C-scores different from observed C-scores.

5.2.3.3  **Burrow occupancy estimates**
To examine potential changes in community structure between years, I first compared the rate of turnover between species. I fit a binomial GLMM in the package lme4, with change or no change of a species’ presence within a plot as a binary response variable, species as an explanatory variable, and plot number nested within island as a random variable. Second, I compared the proportion of plots with a change in species composition between years between islands. In this case, the response variable was a binary change/no change in community composition between years (e.g. grey-faced petrel and flesh-footed shea in 2011, grey-faced petrel in 2012 = 1; grey-faced petrel in 2011, grey-faced petrel in 2012 = 0), the explanatory variable was island, and plot number a random variable.

To assess the effects of detection error on observed community structure, I estimated the proportion of plots with a change in observed species composition between burrow occupancy checks (2-3 days apart). Similar to above, two binomial GLMM were fitted: one examining species turnover and one examining changes in community composition between occupancy checks. In the former model, species was the explanatory variable; in the latter model, island was the explanatory variable; and in both cases plot number was a random variable.

### 5.3 Results

Across all six islands, I surveyed 540 plots, 340 of which had at least one burrow. The most frequently detected species among islands was the grey-faced petrel (*n* = 253), with the exception of Ohinau, which was dominated by flesh-footed shearwaters (Fig. 5.2). The second most numerous species, present on all islands, was the little shearwater (*n* = 23). I detected very few sooty shearwaters (2 individuals on Korapuki only) so I removed this species from further analyses.
Figure 5.2: Mean burrow occupancy*burrow entrance density per plot for each petrel species (common diving petrel (DIPE), flesh-footed shearwater (FFSH), fluttering shearwater (FLSH), grey-faced petrel (GFPE), little shearwater (LISH), and Pycroft’s petrel (PYPE) on five islands off the north-east coast of the North Island of New Zealand with different time since Pacific rat eradication. Mauitaha is still inhabited by Pacific rats; Ruamaahuanui (Nui) never had mammals introduced and all other islands ordered from left to right by increasing time since eradication.

5.3.1 Habitat use between species

After simplifying habitat covariates (see methods and Chapter 3), I used between 11 and 16 to construct global models for each species (Table 5.3). I found no evidence of spatial autocorrelation (sill reached in ≤30 m; Appendix C1), thus no autocovariate term was included.

The occurrence of all petrel species in plots was affected by soil depth (Table 5.3). In general, larger species (flesh-footed shearwater, grey-faced petrel, fluttering shearwater) used deeper soil, while smaller species (Pycroft’s petrel, little shearwater, and common diving petrel) used shallower soil (Fig. 5.3A). For all species except Pycroft’s petrel,
occurrence was affected by elevation. Larger species (flesh-footed shearwater, grey-faced petrel) were more likely to use higher elevations, while smaller species (fluttering shearwater, little shearwater, and common diving petrel) used lower elevations (Fig. 5.3B). Similarly, larger species used steeper slopes (grey-faced petrel) and plots with westerly aspects (flesh-footed shearwater and fluttering shearwater), while smaller species used shallower slopes (fluttering shearwater and Pycroft’s petrel). Grey-faced petrel, little shearwater, and Pycroft’s petrel were more likely to be observed in plots with stronger soil (Fig. 5.3D).

95% confidence intervals for most weighted parameter estimates overlapped zero, other than the effect of soil depth and the presence of māhoe stems on grey-faced petrels – the most common species – indicating strong effects of these habitat variables.

5.3.2 Species co-occurrence

Principal Components analysis suggested no separation between species distribution along environmental variables (all species circles overlapping; Fig. 5.4).

Because no habitat information was available for plots on Ruamaahuanui, I was unable to constrain null models on this island and models among all islands. Among islands I found a significant difference between species distribution in unconstrained null communities and observed communities (Table 5.5). The observed C-value was less than the mean C-value generated by null communities, suggesting aggregation among species. When co-occurrence matrices were separated by island, Korapuki and Kawhitu (rats removed > 20 years ago) had the largest observed C-scores, which were significantly larger than constrained null model C-scores, indicating species avoidance on these islands, or in other words, mutually exclusive distributions. Ohinau, Taranga (rats removed < 8 years ago), and Mauitaha (rats present) had smaller observed C-scores than on Korapuki and Kawhitu, indicating less exclusive distributions on these islands. C-scores were significantly larger than constrained null model C-scores on Ohinau (rats removed 8 years ago), which indicated species avoidance, while observed C-scores did not differ from constrained null model C-scores on Taranga and Mauitaha, indicating no relationship among different species distributions. Ruamaahuanui (never invaded by predators) had the
largest observed C-score, which was significantly smaller than unconstrained null model C-scores, indicating positive association among species.

Table 5.4: Summed averaged Akaike’s weights ($w_i$), weighted parameter estimates ($wPE$), and unconditional standard errors ($SE_\mu$) calculated from all candidate models describing nesting habitat use for burrow-nesting petrels on five islands off the north-eastern coast of New Zealand’s North Island

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat covariate</th>
<th>$w_i$</th>
<th>$PE \pm SE$</th>
<th>lower 95%</th>
<th>upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Flesh-footed shearwater</strong></td>
<td>Mahoe canopy</td>
<td>1.00</td>
<td>$5.69 \pm 4.44^a$</td>
<td>-3.01</td>
<td>14.39</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>1.00</td>
<td>$-0.03 \pm 1.16$</td>
<td>-2.30</td>
<td>2.24</td>
</tr>
<tr>
<td></td>
<td>Rock cover</td>
<td>0.96</td>
<td>$-8.09 \pm 6.00^a$</td>
<td>-19.85</td>
<td>3.67</td>
</tr>
<tr>
<td></td>
<td>Soil strength</td>
<td>0.79</td>
<td>$0.57 \pm 1.08$</td>
<td>-1.55</td>
<td>2.69</td>
</tr>
<tr>
<td></td>
<td>Northerly aspect</td>
<td>0.78</td>
<td>$1.05 \pm 0.57^a$</td>
<td>-0.07</td>
<td>2.17</td>
</tr>
<tr>
<td></td>
<td>Westerly aspect</td>
<td>0.78</td>
<td>$6.27 \pm 3.40^a$</td>
<td>-0.39</td>
<td>12.93</td>
</tr>
<tr>
<td></td>
<td>Soil depth</td>
<td>0.78</td>
<td>$-0.72 \pm 0.68^a$</td>
<td>-2.05</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>Total stem count</td>
<td>0.78</td>
<td>$0.11 \pm 0.95$</td>
<td>-1.75</td>
<td>1.97</td>
</tr>
<tr>
<td></td>
<td>Elevation</td>
<td>0.70</td>
<td>$4.62 \pm 3.61^a$</td>
<td>-2.46</td>
<td>11.70</td>
</tr>
<tr>
<td></td>
<td>Pohutukawa canopy</td>
<td>0.70</td>
<td>$11.29^a$</td>
<td>-35.25</td>
<td>9.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$-3.116 \pm$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mahoe stems</td>
<td>0.70</td>
<td>$2.918^a$</td>
<td>-8.84</td>
<td>2.60</td>
</tr>
<tr>
<td><strong>Grey-faced petrel</strong></td>
<td>Mahoe canopy</td>
<td>1.00</td>
<td>$-0.29 \pm 0.17^a$</td>
<td>-0.62</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Soil depth</td>
<td>1.00</td>
<td>$0.59 \pm 0.16^a$</td>
<td>0.28</td>
<td>0.90</td>
</tr>
<tr>
<td></td>
<td>Mahoe stems</td>
<td>1.00</td>
<td>$0.48 \pm 0.18^a$</td>
<td>0.13</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>0.96</td>
<td>$0.26 \pm 0.15^a$</td>
<td>-0.03</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>Soil strength</td>
<td>0.89</td>
<td>$0.29 \pm 0.17^a$</td>
<td>-0.04</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Weighted estimates with strong effects (i.e., SEs that did not bound zero).</td>
<td></td>
<td></td>
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<tr>
<td>--------------------------</td>
<td>-----------------------------------------------------------------------------</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Westerly aspect 0.72 0.20 ± 0.14a -0.47 0.07</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total stem count 0.54 0.30 ± 0.16a -0.61 0.01</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Elevation 0.25 0.30 ± 0.19a -0.07 0.67</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Tactful shearwater Elevation 0.98 -3.82 ± 3.64a -10.95 3.31</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Soil depth 0.98 1.83 ± 1.26a -0.64 4.30</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Slope 0.87 -1.42 ± 1.31a -3.99 1.15</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Westerly aspect 0.30 5.64 ± 1.26a 3.17 8.11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Little shearwater Elevation 0.81 0.78 ± 0.50a -1.76 0.20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soil strength 0.56 0.48 ± 0.35a -0.21 1.17</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Rock cover 0.29 0.34 ± 0.29a -0.23 0.91</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soil depth 0.22 -0.37 ± 0.36a -1.08 0.34</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total stem count 0.22 0.26 ± 0.24a -0.21 0.73</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pycroft’s petrel Slope 0.51 -0.40 ± 0.33a -1.05 0.25</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Soil depth 0.50 -0.51 ± 0.41a -1.31 0.29</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Soil strength 0.49 0.45 ± 0.35a -0.24 1.14</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Common diving petrel Elevation 0.98 -3.52 ± 2.35a -8.13 1.09</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total stem count 0.62 -1.10 ± 0.87a -2.81 0.61</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mahoe canopy 0.49 0.75 ± 0.67a -0.56 2.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Karo stems 0.27 0.73 ± 0.39a -0.03 1.49</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Westerly aspect 0.23 0.63 ± 0.56a -0.47 1.73</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soil depth 0.10 -0.70 ± 0.70a -2.07 0.67</td>
<td></td>
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<td></td>
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</tr>
</tbody>
</table>
Figure 5.3: Mean values of habitat covariates affecting the probability of plot occupancy of six burrow-nesting petrels on five islands off the north-east coast of the North Island of New Zealand. Species are ordered from largest, to smallest (flesh-footed shearwater: FFSH, grey-faced petrel: GFPE, fluttering shearwater: FLSH, little shearwater: LISH, Pycroft’s petrel: PYPE, and common diving petrel; DIPE). Error bars indicate standard error.
Figure 5.4: Principal component plot of the distribution of burrow-nesting petrel species on islands off north-eastern New Zealand: common diving petrel (DIPE), flesh-footed shearwater (FFSH), fluttering shearwater (FLSH), grey-faced petrel (GFPE), little shearwater (LISH), and Pycroft’s petrel (PYPE). Arrows represent the correlation between environmental variables and principal components (PC). S indicates stem counts of plant species, while C indicates canopy cover of plant species.
Table 5.5: Observed and unconstrained (un) and constrained (cn) simulated co-occurrence indices (C-scores) of six burrow-nesting petrel species on six islands off the north-east coast of New Zealand’s North Island. Mauitaha is still inhabited by Pacific rats; Ruamaahuanui (Nui) never had mammals introduced and all other islands are ordered top to bottom by increasing time since eradication. Asterisks indicate statistical difference between observed and simulated C-scores.

<table>
<thead>
<tr>
<th>Island</th>
<th>Observed C-score</th>
<th>un C-score ± SD</th>
<th>P</th>
<th>cn C-score ± SD</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ruamaahuanui</td>
<td>0.032</td>
<td>0.073 ± 0.109</td>
<td>0.04*</td>
<td>0.019 ± 0.185</td>
<td>0.02*</td>
</tr>
<tr>
<td>Korapuki</td>
<td>0.025</td>
<td>0.018 ± 0.172</td>
<td>0.01*</td>
<td>0.004 ± 0.038</td>
<td>0.03*</td>
</tr>
<tr>
<td>Kawhitu</td>
<td>0.025</td>
<td>0.009 ± 0.106</td>
<td>0.24</td>
<td>0.004 ± 0.038</td>
<td>0.03*</td>
</tr>
<tr>
<td>Ohinau</td>
<td>0.011</td>
<td>0.009 ± 0.154</td>
<td>&lt;0.01*</td>
<td>0.009 ± 0.157</td>
<td>&lt;0.01*</td>
</tr>
<tr>
<td>Taranga</td>
<td>0.005</td>
<td>0.006 ± 0.066</td>
<td>0.29</td>
<td>0.005 ± 0.049</td>
<td>0.45</td>
</tr>
<tr>
<td>Mauitaha</td>
<td>0.017</td>
<td>0.012 ± 0.162</td>
<td>0.07</td>
<td>0.013 ± 0.169</td>
<td>0.08</td>
</tr>
<tr>
<td>All islands</td>
<td>0.019</td>
<td>0.022 ± 0.105</td>
<td>0.04*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

When co-occurrence matrices were separated into species pairs, most observed C-scores were smaller or not significantly different than unconstrained null model C-scores, indicating association between species pairs or independent species co-occurrence respectively (Table 5.6). The exceptions were: grey-faced petrel and little shearwater and grey-faced petrel and flesh-footed shearwater, where observed C-scores were significantly larger. This suggests a negative association between these pairs.

Although I was only able to draw limited inference (due to low species occurrence on some islands and different species pairs per island), I separated and analyzed species pairs by island (Appendix C2). On Ruamaahuanui (never invaded by predators), most species were co-occurring more than expected by chance, with the exception of little shearwater and grey-faced petrel, where large observed C-scores suggested negative association.
Table 5.6: Associations between each pair of six burrow-nesting petrel species on six islands off the north-east coast of New Zealand’s North Island, where +, -, and 0 indicate positive, negative, and no association respectively. Species co-occurrence was determined by comparing co-occurrence indices from observed communities and simulated null communities.

<table>
<thead>
<tr>
<th></th>
<th>FFSH</th>
<th>GFPE</th>
<th>FLSH</th>
<th>LISH</th>
<th>PYPE</th>
<th>DIPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>FFSH&lt;sup&gt;a&lt;/sup&gt;</td>
<td>n/a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GFPE&lt;sup&gt;b&lt;/sup&gt;</td>
<td>+</td>
<td>n/a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FLSH&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-</td>
<td>+</td>
<td>n/a</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LISH&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>n/a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PYPE&lt;sup&gt;e&lt;/sup&gt;</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>DIPE&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0</td>
<td>+</td>
<td>0</td>
<td>+</td>
<td>0</td>
<td>n/a</td>
</tr>
</tbody>
</table>

<sup>a</sup>Flesh-footed shearwater
<sup>b</sup>Grey-faced petrel
<sup>c</sup>Fluttering shearwater
<sup>d</sup>Little shearwater
<sup>e</sup>Pycroft’s petrel
<sup>f</sup>Common diving petrel

5.3.3 Burrow occupancy estimates

I found no evidence of a difference between islands in the proportion of plots with an inter-annual change in community composition (all $P > 0.06$). Among islands, the mean proportion of plots with a change in community composition between years was 0.18 ± 0.04 (± SE). There was a significantly lower proportion of inter-annual change in presence or absence in common diving petrels versus flesh-footed shearwater and grey-faced petrel ($Z_4 = 2.75$, $P = 0.01$, $Z_4 = 3.44$, $P < 0.001$).
I found no evidence of a difference between islands in the proportion of plots with a
different community composition between occupancy checks (all $P > 0.16$). I also found
no evidence of a difference between species in the proportion of change in observed
presence or absence between occupancy checks (all $P > 0.11$). The mean proportion of
plots with a change in community composition between occupancy checks was 0.05 ±
0.03.

5.4 Discussion

My results provide evidence that, among islands, all petrel species use nesting habitat
with specific characteristics, nesting habitat preference overlaps among petrel species, and
that different species co-occur more often than expected by chance. Thus, both biotic and
abiotic factors may affect community reassembly. Furthermore, petrel species were
randomly distributed on islands with <1 year since rat eradication, more mutually exclusive
on islands with >20 years since eradication, and more aggregated on predator unininvaded
islands. Here I discuss how community assembly rules can provide a conceptual
foundation for understanding the processes that determine the distribution and co-
occurrence of different species after restoration.

5.4.1 Nesting habitat use

For burrow-nesting petrels, suitable burrows are essential for reproductive success
and the availability of appropriate burrow-nesting habitat may limit population size
(Rosenzweig 1981). I found that nesting habitat use of all species was affected by soil
depth and, for some species, soil strength. Soil properties are an important nesting habitat
feature for burrow-nesting animals, as they can affect the excavation, stability, and thermal
of most species was also affected by elevation, slope, and western aspect, which are
thought to be linked to wind exposure, and thus affect the ease of take-off and landing
(Bourgeois and Vidal 2007, Rayner et al. 2007b). Petrels have high wing-loading and
updrafts on high slopes facing prevailing winds are thought to increase lift (Schulz et al. 2005, Scott et al. 2009).

The use of nesting habitat covariates differed between larger and smaller species (Fig. 5.3). For example, larger birds used deeper soil, while smaller birds used shallower soil. Similarly, larger birds used steeper slopes, higher elevations, and westerly aspects facing prevailing winds (Table 5.4). Differences in nesting habitat use may reflect niche partitioning and competitive exclusion. Evidence suggests that competitive exclusion may be governed by body size in some seabirds; with larger, dominant species excluding smaller species (Ramos et al. 1997, Oro et al. 2009). However, I found little evidence, among islands, for inter-specific exclusion among habitat types (all circles overlap; Fig. 5.4). Thus, differences in habitat use may simply reflect habitat requirements (Martin et al. 2004), where larger birds will require deeper soil and more lift (Fischer and Griffin 2000, Sato et al. 2009).

5.4.2 Species co-occurrence between islands

Among islands, species co-occurred more than expected by chance, indicating that overall, species are positively associated. However, I was unable to constrain this model for the effects of nesting habitat; thus, it is unclear if positive association between species was due to habitat association or inter-specific interactions. Considering there was extensive overlap and flexibility in habitat use between species (Fig. 5.3, Table 5.4), the latter situation is more likely. If the results reflect dynamic ecological interactions, the positive association between species could result from hetero-specific social facilitation (Whittam and Siegel-Causey 1981, Danchin and Wagner 1997). Colonial burrow-nesting petrels are thought to settle more often among pre-existing colonies, due to the increased potential to find mates, diluted risk of predation, increased foraging efficiency, and indication of high quality nest-habitat (Forbes and Kaiser 1994, Danchin et al. 1998). Considering the similar ecological needs of sympatric petrel species, pre-existing colonies of hetero-specifics likely reflects high quality nesting habitat in a similar way (Warham 1990, Mönkkönen et al. 1999).
On Kawhitu, Korapuki, and Ohinau, significantly larger observed versus simulated C-scores suggested negative association between species. Negative associations between species typically result from either competitive exclusion or species associations with different habitats (Gotelli and Graves 1996a). If co-occurrence patterns differ from unconstrained simulated communities, but not from simulated communities constrained by environmental covariates, it supports the hypothesis that nesting habitat has shaped community structure (Peres-Neto et al. 2001). On the other hand, if co-occurrence differs significantly from a constrained simulated community, similar to results on all three islands (Table 5.5), it supports the hypothesis that inter-specific interactions, such as competition or facilitation, shaped community structure (Bradley and Bradley 1985).

Although caution must be taken when assuming a causal effect of Pacific rats, evidence suggests that the density of burrows, and thus the relative abundance of birds, increases with time since rat eradication (Chapter 3). Thus, the relationship between species associations and time since eradication may reveal inter-specific dynamics in reassembling petrel communities. On Mauitaha and Taranga, in the presence of rats or soon after rat eradication, species were randomly distributed, rather than positively associated. This suggests that predation pressure may have altered petrel species distribution. On Korapuki and Kawhitu, where rats were removed over 20 years ago, allowing more time for petrel communities to recover and reassemble, negative associations were more prominent. Negative associations between species on Korapuki and Kawhitu could represent a transitional community structure on a pathway leading back to a positively associated species distribution similar to the rat-uninvaded Ruamaahuanui, where re-colonization and recovery is resulting in competition and exclusion (Martorell and Freckleton 2014). Conversely, negative associations could represent an alternative community structure, different from that on Ruamaahuanui caused by differences in reassembly history (Chase 2003, Lockwood and Samuels 2004, Temperton and Hobbs 2004, Temperton et al. 2004). Assembly is a non-linear process, and historical disturbance can force a community along a variety of alternative successional pathways (Lockwood and Samuels 2004). Evidence suggests that species which had facilitative associations as part of a larger combination, can form competitive associations by themselves (Diamond 1975). In these altered communities, some species may remain rare because they cannot
withstand inter-specific competition, especially if the population of dominant species continues to increase (Oro et al. 2009). Further research should aim to investigate the nature of inter-specific interactions during recovery of petrel communities. If indeed there is a threshold dividing communities where competitive exclusion is predominant from those where species co-occurrence is predominant, then active restoration interventions may be required to overcome this threshold (Greipsson 2011).

5.4.3 Co-occurrence between species pairs

Results suggested that Ruamaahuanui, which has never been invaded by predators, had positive associations between most species pairs (Appendix C2). Conversely, on rat eradicated islands, associations between species pairs were mostly negative. Rats are known to have stronger detrimental effects on smaller seabirds, which often decimate entire colonies (Jones et al. 2008). It is likely that Pacific rats reduced populations of small burrow-nesting seabirds but had little effect on larger seabirds. Thus, negative associations in communities after rat eradication may be due the relatively fast recovery of large species, which were less affected by predation, precluding the recovery of smaller species (Durant et al. 2012).

Pacific rats are thought to have relatively little effect on populations of grey-faced petrel, the most abundant species on the islands used in this study (P. Lyver pers. comm.). Among all islands, there were negative associations between grey-faced petrel and little shearwaters and grey-faced petrel and flesh-footed shearwater. In this way, grey-faced petrel may be acting as a “priority species”, where their occurrence may result in a lower chance of little shearwater and flesh-footed shearwater recovery (Young et al. 2001). Negative interactions may be especially important in informing active restoration, where the transfer or attraction of negatively associated pairs should be avoided (Jones and Kress 2012).

5.4.4 Error in burrow occupancy estimates
Two potential sources of error in this study include: the possibility that seabird species distributions are dynamic and change annually, or that detection error in species occupancy observations biased results (MacKenzie et al. 2004, Maron et al. 2005). Factors responsible for possible changes in the distribution of petrel species between years include variation in at-sea resources, density fluctuations of predators, and changes in at-sea threats (Ballance 2007, Cubaynes et al. 2011). Due to subtle differences in foraging requirements, changes in the abundance of at-sea resources affect different species in different ways (Table 5.2). Years with poor oceanic conditions often result in some species skipping breeding or having high reproductive failure, thus altering community composition (Erikstad et al. 1998). Although I found that a small proportion of plots had inter-annual changes in community composition (~18%), there was no difference in this change between islands. Thus, changes in community composition may affect results between years, but likely wouldn’t affect the ability to compare species associations between islands.

Assessment of burrow occupancy using a burrow-scoped is associated with a probability of ‘false absence’, or the failure to detect birds that are actually present (Hamilton 2000, Whitehead et al. 2014). Some species may be more conspicuous than others and will always be detected when present at a location, while others will more often go undetected when present, skewing the analysis of community composition (MacKenzie et al. 2004). I found that detection error was similar for all species and the proportion of plots where community composition changed between occupancy checks was less than 5%, suggesting that detection error may not have been a substantial issue in my data.

The issue of appropriate inferential methods in species co-occurrence analysis has led to heated debate and continued methodological development (Connor and Simberloff 1979, Diamond and Gilpin 1982, Gilpin and Diamond 1982, Peres-Neto et al. 2001, MacKenzie et al. 2004). Currently, analytical methods that incorporate inter-annual change and imperfect detection require extremely large data sets (MacKenzie et al. 2004). Large sample sizes can be impractical for some species of burrow-nesting seabirds, due to low burrow occupancy rates and fragile, easily disturbed unstable habitat caused by burrowing (Warham 1990, Bertram et al. 1999). Thus, future research should focus on
developing both statistical and survey methods to decrease uncertainty in community composition caused by inter-annual variation and detection probability.

5.4.5 Conclusions and conservation implications

Much of our understanding of seabird population recovery after predator eradication comes from studies of one species (Chapter 2; Lavers et al. 2010). Although this information is extremely valuable, in many cases seabirds nest in multispecies colonies, where inter-specific interactions may ultimately influence community level recovery. Burrow-nesting seabird communities disturbed by the introduction of rats may have skewed species associations, resulting in negative associations preventing the recovery of certain species.

Here, I show that co-occurrence analysis can generate insight into burrow-nesting seabird community assembly. I found that among islands, seabird associations tend to be positive, meaning that some species could facilitate the presence, and perhaps the recovery of others. Conversely, seabird associations were more negative on islands with more time since eradication, suggesting that in the process of recovery, species interactions either become more competitive or that some species combinations vary in competitiveness over time. More research is needed to disentangle the effects of these inter-specific interactions on the ultimate outcome of community reassembly after restoration.
Chapter 6  Evidence for positive and negative density dependence mediating colony growth of burrow nesting seabirds

6.1  Introduction

Across the globe, the introduction of predators by humans has been implicated in the extinction, extirpation, or severe population reduction of numerous island species (Chapter 2; Atkinson 1989, Towns et al. 2006). The most widespread of invading predators are rodents, which have invaded 90% of island groups (Jones et al. 2008). Colonial, burrow-nesting petrels were particularly vulnerable to rodent introduction because of their easily-accessed nests and lack of appropriate anti-predator behavioural adaptations (Moors and Atkinson 1984). Because petrels act as ecosystem engineers, providing islands with indispensable sources of nutrients and physical disturbance, the reduction of their populations has had dramatic cascading effects on entire island ecosystems (Croll et al. 2005, Fukami et al. 2006, Smith et al. 2011). Over the past three decades, efforts to eradicate introduced rodents and restore islands have accelerated, with over 800 islands cleared of rats and all other types of non-native mammal (Keitt et al. 2010, Keitt et al. 2011). Although petrel population response will likely play a disproportionately large role in the recovery of island ecosystem functioning, only now are factors driving colony recovery being studied (Chapter 2; Jones 2010a).

After predator eradication, the re-colonization, re-distribution, and growth of an affected colony of seabirds is a complex process, with multiple ecological and anthropogenic drivers (Chapter 2). The structure of a remnant colony will depend on the type of predator, the vulnerability of different species to predation, and the spatio-temporal nature of interactions between predators and seabird prey (Jones et al. 2008, Lavers et al. 2010). As recruitment increases, the selection of a nesting site will be both positively and negatively density-dependent (Crespin et al. 2006). Positive density dependence will initially be important, where colonial animals are more likely to settle amongst conspecifics due to increased potential of finding mates, diluted predation risk, and indication of high-quality nesting habitat (Wittenberger and Hunt 1985, Danchin and
Wagner 1997, Schippers et al. 2011). However, as more birds settle, and inter- and intra-specific competition occurs, new recruits will eventually be forced into new, unoccupied habitat (Forbes and Kaiser 1994). This model of seabird colony growth is known as the “ideal despotic Allee model”: a hybridization of the “ideal Allee” model, where the benefits of group living result in inverse density-dependence in small groups, and the “ideal despotic” model, where dominant individuals secure good quality territories and force others into less favorable habitat (Fretwell and Lucas 1969, Fretwell 1972, Kildaw et al. 2005). The “ideal despotic Allee model” is thought to typify seabird colony formation and growth and could readily be applied to colony recovery after predator removal.

The wide-reaching effects of predator introduction are well exemplified in New Zealand, where, since the arrival of humans and rats in the 13th Century AD (Wilmshurst et al. 2008), rodents have invaded over 40% of islands in the archipelago (Holdaway 1999, Towns 2011). Evidence suggests that the combined effects of disturbance, habitat alteration, and, notably, predation by introduced mammals such as rodents, have restricted burrow-nesting seabird populations to predator-free offshore islands (Jones 2000, Taylor 2000). The reduction in seabird numbers has resulted in reduced soil fertility and altered above- and below- ground ecosystem dynamics (Fukami et al. 2006). In response, New Zealand has performed more successful rodent eradications than any other country, resulting in over 30,000 hectares of newly predator-free breeding space and enormous opportunity for investigating how petrels respond to rodent eradication.

Although efforts to eradicate rodents have become extremely successful, evaluating the ecological response to island restoration, especially for petrels, remains uncommon, and robust post-eradication monitoring programmes have yet to be designed. Developing a model of population growth in order to develop a priori predictions about recovery is one of the fundamental elements of effective monitoring (Lindenmayer and Likens 2010). Thus, here I test the “ideal despotic Allee model” of petrel colony growth after rat removal on islands off the north-eastern coast of New Zealand’s North Island, to develop predictions about burrow-nesting seabird response to eradication.

Since no pre-eradication data were available, I use a chronosequence approach, where a series of islands representing a chronological sequence of increasing time since eradication were used (Perrow and Davy 2002). I compare the density and spatial
distribution of petrel burrows among eight islands that varied in the presence, absence, or times since eradication of Pacific rats (*Rattus exulans*). I hypothesize that colony growth after eradication will follow an “ideal despotic Allee model”, with increasing burrow density, and eventually, increasing colony area and decreasing burrow clustering on islands with more time since eradication. I counted burrow entrances along transects, measured burrow density and a suite of habitat variables in plots, and re-measured burrow density in a time series after rat eradication to address four questions. First, does burrow density or burrow clustering increase on islands with more time elapsed since rat eradication? Second, does the spatial extent of a colony increase on islands with more time since rat eradication? Third, does the relationship between burrow density, the spatial extent of burrows, and time since rat eradication change after controlling for nesting habitat availability? Fourth, are changes in burrow density between islands with different times since eradication reflected in changes over time after eradication within an island?

6.2 Methods

6.2.1 Study area and species

I assessed burrow abundance on eight islands off the northeastern coast of New Zealand’s North Island (Fig. 6.1). Five islands represented 7–26 years of recovery after Pacific rat eradication (Table 6.1): Pacific rats and European rabbits (*Oryctolagus cuniculus*) were eradicated from Korapuki, Kawhitu, and Ohinau in 1986, 1991, and 2005 respectively; and Pacific rats were eradicated from Whakau (Red Mercury) and Taranga in 1992 and 2011 respectively. Mauitaha (22 ha) is still inhabited by Pacific rats whereas two islands, Ruamaahuanui (21 ha) and Middle (13 ha) never had mammalian predators introduced.

All islands are within 7–13 km of New Zealand’s mainland, and have similar climate, geology, and vegetation structure. Climate is warm-temperate, soils are volcanic in origin and thus considerably friable, and vegetation is characteristic of post-fire succession, dominated by pōhutukawa (*Metrosideros excelsa*), kanuka/manuka (*Kunzea ericoides/Leptospermum scoparium*), and māhoe (*Melicytus ramiflorus*) (Sladden and Falla...
1928, Edgar 1962, Wright 1978, McCallum et al. 1984, Taylor and Lovegrove 1997, Atkinson 2004, NIWA 2012). Furthermore, all islands were extensively burned and terraced by Māori, but have remained relatively undisturbed since the mid-19th Century. (Sladden and Falla 1928, Edgar 1962, McCallum et al. 1984). All islands are currently protected as nature reserves.

Seven species of burrow-nesting seabirds in the order Procellariiformes were present on our study islands: grey-faced petrel (*Pterodroma macroptera gouldi*), fluttering shearwater (*Puffinus gavia*), flesh-footed shearwater (*Puffinus carneipes*), little shearwater (*Puffinus assimilis*), common diving petrel (*Pelecanoides urinatrix*), sooty shearwater (*Puffinus griseus*), and Pycroft’s petrel (*Pterodroma pycrofti*). Limited available information suggests that burrows of all species tend to be sympatric, with more association between species than expected by chance (Chapter 5). Although some species have different physical nesting habitat preferences, general habitat use overlaps (Chapter 5; Hicks et al. 1975, Pierce 2002). I surveyed islands when all petrel species were at some stage of the breeding cycle (Table 6.1).

### 6.2.2 Field surveys

I used a systematic sampling approach to estimate burrow density and area, involving transects and plots on five islands: Mauitaha, Taranga, Ohinau, Kawhitu, and Korapuki (Table 6.1).

To estimate burrow area, I ran transects from coast to coast at even intervals perpendicular to the long axis of each island. The resulting distance between transects was between 10–40 m, depending on island size. Transect direction was determined by compass bearing. I searched 1 m either side of the transect centre line for seabird burrows. A burrow was defined as a cavity in the soil or below a rock or log >20 cm in length, with an entrance >12 cm² (measured using a soil probe marked at 6 and 20 cm). Each burrow was marked using a handheld Global Positioning System (GPS 60CSx Garmin, Kansas, USA). I searched between 31 and 61 transects on Mauitaha, Taranga, Ohinau, Kawhitu, and Korapuki (Table 6.1). Because of the steep terrain on Taranga, transects were shorter and constrained by proximity to existing tracks. To estimate burrow density,
Figure 6.1: Location of study islands off the north-eastern coast of the North Island, New Zealand, including those in the Hen and Chicken group (A), the Mercury group (B), and the Aldermen group (C). Scale bars indicate 1 km. Distance between islands has been reduced.
Table 6.1: Eight islands off the northeastern coast of New Zealand’s North Island surveyed for burrow-nesting seabirds using plots, transects, cluster analysis (Cluster), and plots assessed in a time series (Time series). Each island differs in the presence (“still present”), absence (“n/a”), or time since rat eradication.

<table>
<thead>
<tr>
<th>Island</th>
<th>Area of island (ha)</th>
<th>Year rats eradicated</th>
<th>Year surveyed</th>
<th>Month surveyed</th>
<th>Transects</th>
<th>Plots</th>
<th>Cluster</th>
<th>Time series</th>
<th>Years monitored</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mauitaha</td>
<td>22</td>
<td>still present</td>
<td>2011/2012</td>
<td>December/October</td>
<td>31</td>
<td>68</td>
<td>Y</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Taranga</td>
<td>470</td>
<td>2011</td>
<td>2011/2012</td>
<td>November/October</td>
<td>61</td>
<td>120</td>
<td>Y</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Ohinau</td>
<td>32</td>
<td>2005</td>
<td>2012</td>
<td>October</td>
<td>33</td>
<td>100</td>
<td>Y</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Ruamaahuanui</td>
<td>21</td>
<td>n/a</td>
<td>2010</td>
<td>November</td>
<td>n/a</td>
<td>76</td>
<td>N</td>
<td>Y</td>
<td>2006-2008, 2010,</td>
</tr>
<tr>
<td>Middle</td>
<td>13</td>
<td>n/a</td>
<td>2003</td>
<td>November</td>
<td>n/a</td>
<td>13</td>
<td>N</td>
<td>N</td>
<td>2012</td>
</tr>
</tbody>
</table>
I surveyed between one and six 3-m-radius circular plots along each transect at randomly-assigned distances. This resulted in a total of 68-132 plots on each island (Table 6.1). Within each plot I counted all seabird burrows where the midline of the entrance fell within plot limits. To assess the degree of burrow clustering I measured and compared the distance between the plot centre (a random point) to the nearest burrow and the distance from that burrow to the nearest neighbouring burrow. Burrow clustering was assessed on five islands only (Mauitaha, Taranga, Ohinau, Kawhitu, Korapuki).

Finally, to account for nesting habitat availability on each island, I recorded key nesting habitat variables in each plot including: aspect, slope, elevation, topography, soil depth, soil strength, soil texture, percentage cover of boulders, stem count for each species between 2.5-10 cm in diameter at chest height (dbh), and canopy species and percent cover. Habitat survey methods are described in detail in Chapter 3.

It was not possible to search transects on Ruamaahuanui because of high burrow density and thus high risk of burrow collapse. Instead, I used similar 3-m-radius circular plots surveys whose locations were allocated randomly as part of a previous study (Whitehead et al. 2014). Burrow density estimates on Whakau and Middle were based on opportunistic surveys from previous studies, involving 4-m-radius circular plots and 40 m² search transects respectively (G. Taylor unpub. data; Table 6.1).

### 6.2.3 Historical time-series data

To compare results from the chronosequence of islands with actual measures of change in burrow density over time, I examined permanent plots with time series of burrow counts. Plots with annual counts of burrow density after eradication were available on two islands: Kawhitu and Korapuki, and one island (Ruamaahuanui) which never had rats (Table 6.1).

On Kawhitu, petrel burrow density was assessed in 1993, 1998, and 2003 using 2 methods: 5 m radius circular plots every 10-20 m along a transect and 3 groups of small adjacent square plots. Circular plots were placed at every marker along the main north-western track from sea-level, while square plots consisted of one 400 m² plot, assessed in 16 increments of 25 m².
On Korapuki and Ruamaahuanui, 20 permanent “occupancy” plots of 100 m² were placed randomly over the surface of each island. The four corners of each plot were marked with aluminium poles and each burrow was marked with a cattle tag. In 2003 and 2012 on Korapuki, burrow abundance was also assessed within 21 transects of 40 m² (20 m long, searching 1 m either side of the centre line) deviating from the main ridgeline track.

6.2.4 Data analysis

To examine the relationships between burrow density and clustering with time since eradication I used a Bayesian hierarchical modelling approach. All models were fitted using OpenBUGS (Lunn et al. 2000), called from R version 3.0.1 using BRugs and R2WinbBUGS (Sturtz et al. 2005, Thomas et al. 2006, R Development Core Team 2013). To ensure convergence and minimize autocorrelation between chains, I ran 30000 iterations with a burn-in of 10000 and a thinning rate of 10 (Gelman et al. 2004). In all models, the ‘number of years since predator eradication’ on predator free Ruamaahuanui was set to 100, representing the approximate amount of time since this island was burned by Māori.

To determine the spatial extent of burrowed areas (hereafter “colonies”) all calculations were performed in ArcGIS for Desktop (10.1, ESRI Inc., USA).

6.2.4.1 Burrow density and clustering.

To examine the relationship between time since eradication and burrow density, I used a varying intercept Bayesian hierarchical regression model. I modelled burrow density ($X_{jk}$) as:

$$X_{jk} \sim \text{Normal}(\psi_{jk}, \sigma_{jk})$$

where $\psi_{jk}$ was the mean predicted density of burrows in plot $j$ on island $k$, with precision $\sigma_{jk}$, and was estimated in a linear regression of the form:

$$\psi_j \sim \alpha_j + \beta_{tse}TSE + \sum_{t=1}^{L} \beta_{tk} x_{tk}$$

where $\beta_{tse}$ was the rate at which burrow density increased with the number of years after eradication and $\beta_{tk}$ was the effect of nesting habitat variation among islands $k$. 
(environmental covariates $x_t$ – soil depth; southern and western aspect; slope; rock cover; karamū ($Coprosma macrocarpa$) stem count, māhoe ($Melicytus ramiflorus$) stem count; and total stem count – were selected based on habitat selection models; Chapter 3). The intercept ($\alpha_{jk}$) and $\beta_{tk}$ came from a prior distribution of hyper-parameters $M_\alpha$ and $\sigma^2_\alpha$ (and $M_\beta$ and $\sigma^2_\beta$):

$$
\alpha_{jk} \sim \text{Normal}(M_\alpha, \sigma^2_\alpha),
$$

$$
M_\alpha \sim \text{Normal}(0,1000),
$$

$$
\sigma^2_\alpha \sim \text{InverseGamma}(0.1, 0.1)
$$

while $\beta_{tse}$ had a non-informative prior distribution (Gelman and Hill 2007).

I ran two separate models: one excluding environmental covariates ($\sum_{l=1}^t \beta_{lk} x_{lk}$ Eq. 2), including density data from all eight islands; and another including environmental covariates and only six islands with habitat data, to determine the effect of nesting habitat availability on change in burrow density after eradication. Posterior distributions were interpreted by generating mean $\beta_{tse}$ values with 95% credible intervals. To quantify model fit I compared model predictions with observed burrow density using area under Receiver Operating Characteristic curves (AUC) in the PresenceAbsence package (Freeman and Moison 2008). AUC values vary between 0 and 1, with values $\leq 0.6$ indicating a model performance no better than random, and values $\geq 0.7$ considered useful (Fielding and Bell 1997).

To examine the degree of burrow clustering, I compared the distances between random points and burrows and between neighbouring burrows with time since eradication. I used two models with similar structure to Eq. 1 and 2, one where $\psi_{jk}$ was the mean predicted distance between random points and burrows and one where $\psi_{jk}$ was the mean predicted distance between neighbouring burrows. If neither distances changed with relation to time since eradication I assumed no difference in clustering. If distances between random points and burrows decreased (relative to distances between neighbouring burrows) with time since eradication, I interpreted this as a decrease in the amount of clustering.

### 6.2.4.2 Burrowed area.
To determine the extent of areas with burrows (hereafter “colony area”) I first calculated point density functions of burrows marked during transect (or, in the case of Ruamaahuanui, plot) searches. In ArcMap, ‘point density’ calculates the density of point features, in this case burrows, around a neighbourhood defined around each output raster cell (Silverman 1986). I used a neighbourhood radius size of 10 m, because most burrows still considered to be within a cluster were found at this distance (RTB pers. obs.), and a raster size of 15 by 15 m, which matched the reference frame of digital elevation models (DEM) used below. I then reclassified point densities into three classes – low (1-15 burrows), medium (16-30 burrows), and high (31+ burrows) – and converted them to polygons. The total area of each polygon, representing a colony of particular density class, was then calculated using the ‘calculate areas’ tool in ArcMap spatial statistics. The total area of colonies of each density class was divided by the total island area to correct for island size. Finally, I created a raster layer of surveyed areas (along transects) with and without burrows present.

To estimate the effects of varying nesting habitat availability on colony area, I compared observed presence of a burrow (above) with burrow presence predicted from models of habitat use. If burrows were present in a large proportion of habitat where predicted probability of use was high (>50%), this suggested that birds were nesting in, and potentially filling, suitable habitat. Whereas, if burrows were absent from a large proportion of habitat where predicted probability of use was high, this suggested that birds were not occupying potentially suitable habitat (i.e. habitat availability was not necessarily a limiting factor).

To build predictive habitat models I used a Bayesian hierarchical logistic regression, where the probability of a burrow being present ($\phi_{jk}$) in plot $j$ on island $k$ was modelled as:

$$\text{logit}(\phi_j) \sim \alpha_{jk} + \sum_{l=1}^{L} \beta_{lk} x_{lj}$$

where $x_{lj}$ were the environmental covariates $l$ and $\beta_{lk}$ were the associated parameters. I included only environmental covariates that were available as GIS layers from DEMs: slope, elevation, and categorical aspect. Aspect was transformed into a dummy variable by setting one class as a reference class with a coefficient of zero (Hardy 1993). The intercept $\alpha_{jk}$ and parameters $\beta_{lk}$ were given similar prior distribution as shown in Eq. 3-6. To determine which combination of environmental covariates
resulted in the best predictive power I examined the deviance information criterion (DIC) and AUC. DIC values represent model fit and are penalized by the number of effective parameters; however, the number of parameters is not clearly defined for multilevel models and is unstable, even from simulations that have converged (Zhu and Carlin 2000, Gelman and Hill 2007). Thus I assessed model fit using a combination of the lowest DIC and highest AUC value.

To estimate where burrows would be present, I predicted the probability of presence within rasters based on DEMs from Land Information New Zealand (LINZ; Columbus et al. 2011). I calculated slope, elevation, and aspect within rasters using the spatial analysis extension in ArcMap. Aspect rasters were reclassified into north, south, east, and west categories. I limited predictions to rasters with point density data (i.e. along transects).

**6.2.4.3 Time-series.**

To examine the relationship between years and burrow density in permanent plots measured at a time series (Table 6.1), I used a separate Bayesian linear regression model for each island. On Kawhitu and Korapuki, where different plot types were used, the effects of year and plot type were tested.

**6.3 Results**

**6.3.1 Burrow density and clustering among islands**

I estimated the relationship between burrow density and time since eradication by counting burrow entrances in 707 plots among eight islands (Table 6.1). I found that burrow density was positively related to time since eradication (mean effect size 0.1; 95% credible intervals 0.01 – 0.05, Fig. 6.2A). However, this model had low predictive power (AUC = 0.62 ± 0.02). To remove the effects of variation in habitat availability between islands, I used burrow entrance data and environmental covariates from 597 plots on six islands. In this model, burrow density was still positively related to time since eradication, although the relationship was weaker (0.05; 0.01 – 0.11, AUC = 0.71 ± 0.02, Fig. 6.2B). Burrow density was also positively related to soil depth, slope, rock cover, southerly aspect, and the presence of māhoe and karamū stems (Appendix D1).
Figure 6.2: Predicted burrow density (per m\(^2\)) at different time periods after rat eradication. Lines represent the mean posterior effect size from Bayesian hierarchical models of burrow density versus time since rat eradication (A), with the effects of nesting habitat removed (B). Grey shading represents loess slope smoothing based on the variation in predicted densities.

I found no evidence of change in distance between neighbouring burrows with time since eradication 95% credible intervals overlapped zero: -1.0 – 0.1). Distance between random points and burrows decreased on islands with more time since eradication (-2.6; -5.7 – -0.1, 95% CIs). On Korapuki, an island with more than 25 years since eradication, the ratio between distances of random points to burrows and between neighbouring burrows was close to one (Fig. 6.3). This indicated that burrows
were less clustered (more randomly distributed) on islands with more time since eradication.

![Figure 6.3: The ratio ("clustering ratio") between the distances of random points and burrows and between neighbouring burrows (± standard error) on islands off the northeast coast of New Zealand with different times since Pacific rat eradication (number of years since eradication on the x-axis). A clustering ratio of one (dashed line) indicates no spatial structuring amongst burrows.]

### 6.3.2 Burrow area among islands

I searched a total of 214 transects on five islands (and 76 plots on Ruamaahuanui). Using point density functions I found a total of 5 colonies on Mauitaha (Pacific rats present), 91 on Taranga (rats removed 2011), 117 on Ohinau (rats removed 2005), 451 on Kawhitu (rats removed 1991), 179 on Korapuki (rats removed 1986), and 84 on Ruamaahuanui (rats never introduced). The maximum density of colonies increased with time since eradication from 1.78 (burrows/225 m² raster) on Mauitaha to 247.22 (burrows/225 m² raster) on Ruamaahuanui. Total burrowed area, in proportion to island area, was larger on islands with more time since eradication, from 0.01 on Mauitaha, 0.01 on Taranga, 0.08 on Ohinau, 0.11 on Kawhitu, and 0.27 on Korapuki (Fig. 6.4 and 6.5). Finally, the proportion of area
searched with at least one burrow increased with time since eradication from 0.31 on Mauitaha, 0.37 on Taranga, 0.39 on Ohinau, 0.50 on Kawhitu, 0.71 on Korapuki, and 0.93 on Ruamaahuanui.

Predictive habitat models with the highest predictive power (AUC = 0.76 ± 0.02) included slope, elevation, aspect, and the interaction between slope and aspect (Appendix D2). Burrows were more likely to be found in areas with steeper slopes (Appendix D3). Islands with less time since eradication (and smaller colony area, Fig. 6.5) had a higher proportion of rasters with large predicted probability of use but no burrows present (Table 6.2). This indicated that although the predicted probability of burrow presence was high, suggesting that habitat was suitable, burrows were absent, suggesting that habitat was not limiting burrow distribution. Conversely, on islands with more time since eradication (with larger colony area), there was a low proportion of rasters with burrows absent where predicted probability of burrow presence was high. This suggests that birds are filling suitable habitat. Furthermore, on some islands (e.g. Kawhitu – 21 years since rat eradication) burrows were present in rasters with low predicted probability of presence, suggesting that birds are also occupying less suitable habitat.

### 6.3.1 Burrow density time series

Although I had a low sample size, intra-island burrow density time series model results confirmed chronosequence results. On Korapuki and Kawhitu, islands with rats removed 21 and 26 years ago respectively, I found a small rate of burrow density increase within permanent plots over time (mean effect sizes 0.054 and 0.014 respectively; Table 6.3). On Ruamaahuanui, a predator-free island, I found a small rate of burrow density increase (mean effect size 0.029); however, 95% credible intervals overlapped zero (-0.021 – 0.080), indicating that there was no evidence of a relationship between burrow density and year.
Figure 6.4: Point density functions calculated from burrows marked along search transects (black lines) or within plots (dots) from islands off the northeast coast of New Zealand’s North Island. Islands are arranged with increasing time since Pacific rat eradication from left to right, top to bottom, where rats are still present on Mauitaha and were never introduced to Ruamaahuanui. Darker shades of grayscale indicate higher density burrow clusters. Scale bars indicate m.
*Ruamaahuanui

Figure 6.5: Proportion of island area with ≥0.001 burrows/m$^2$ calculated from point density functions on six islands off the northeastern coast of New Zealand’s North Island, each with a different amount of time since rat eradication (indicated on the x-axis). Burrow densities per 225 m$^2$ raster were low (1-15 burrows), mid (16-30), and high (≥ 31 burrows)
Table 6.2: The total proportion of rasters with burrows present (Burr pres) or absent (Burr abs) on eight islands off the northeastern coast of New Zealand’s North Island, where the predicted presence (P(pres) – from predictive habitat models) of a burrow was greater or less than 0.5. Islands are in ascending order from least to most time since Pacific rat (Rattus exulans) removal, where Mauitaha still has rats present and Ruamahuanui never had rats introduced.

<table>
<thead>
<tr>
<th>Island</th>
<th>Burr pres, P(pres)&gt;0.5 or Burr abs, P(pres)&lt;0.5</th>
<th>Burr abs, P(pres)&gt;0.5</th>
<th>Burr pres, P(pres)&lt;0.5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mauitaha</td>
<td>0.33</td>
<td>0.67</td>
<td>0.00</td>
</tr>
<tr>
<td>Taranga</td>
<td>0.43</td>
<td>0.55</td>
<td>0.02</td>
</tr>
<tr>
<td>Ohinau</td>
<td>0.46</td>
<td>0.51</td>
<td>0.02</td>
</tr>
<tr>
<td>Stanley</td>
<td>0.50</td>
<td>0.47</td>
<td>0.03</td>
</tr>
<tr>
<td>Korapuki</td>
<td>0.71</td>
<td>0.28</td>
<td>0.01</td>
</tr>
<tr>
<td>Ruamaahuanui</td>
<td>0.88</td>
<td>0.11</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Table 6.3: Median effect sizes and 95% credibility intervals from Bayesian logistic regression models predicting the relationship between years (since Pacific rat – Rattus exulans – eradication on Kawhitu and Korapuki) and petrel burrow density in permanent plots on three islands in northeastern New Zealand.

<table>
<thead>
<tr>
<th>Year rats eradicated</th>
<th>Mean Parameter Estimates</th>
<th>Credible Intervals 5%</th>
<th>95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kawhitu</td>
<td>1991</td>
<td>0.014†</td>
<td>0.002</td>
</tr>
<tr>
<td>Korapuki</td>
<td>1986</td>
<td>0.054†</td>
<td>0.017</td>
</tr>
<tr>
<td>Ruamaahuanui</td>
<td>Never present</td>
<td>0.029</td>
<td>-0.021</td>
</tr>
</tbody>
</table>

† Credible intervals do not overlap 0, indicating a strong effect.
6.4 Discussion

Results indicated that, on islands where more time has elapsed since rat eradication, mean burrow density was higher and colony area greater. Although burrows were clustered in distribution on all islands, clustering decreased on islands with more time since eradication. These results suggest a rapid rate of increase of overall burrow density and burrowed area on islands after rat eradication, and that both positive and negative density dependence may be mediating colony growth.

6.4.1 Potential caveats

Although I found a strong relationship between burrow density and colony area with time since rat eradication, caution must be taken when inferring a causal relationship with Pacific rat removal (Craig 1983, Jones 2001). Current distribution of burrow-nesting petrels on restored islands is likely to be shaped by a set of interacting variables including: other introduced species (e.g. European rabbits), habitat modification, history of human harvesting, and historical distribution. I emphasize that, in this study, I use patterns of burrow distribution along the chronosequence of islands as a proxy for potential colony expansion after restoration, not as a direct indication of population recovery after rat removal.

In this study I use burrow density as a proxy for petrel abundance, as it is has been shown to provide a temporally and spatially stable index of bird numbers (Rayner et al. 2007a). Other indices, for example burrow occupancy assessed with infrared burrow cameras (Lyver et al. 1998), vary widely with season, at-sea conditions, and are associated with detection error (Sutherland and Dann 2012). However, burrow density alone may not be appropriate as comprehensive index of population size, and more research is needed to examine the relationship between abundance and burrow density.

Similarly to Chapter 3, I did not distinguish between species in the analyses, despite the fact that grey-faced petrels and flesh-footed shearwaters were the most abundant species on islands (Buxton et al. 2013a). Again, I was unsure how the varying abundances of each species of different sizes affected results.

6.4.2 Increase in burrow density and colony area
A common assumption in petrel ecology is that predator removal may be insufficient to achieve population recovery, due to high levels of philopatry, low incidence of new colony formation, long generation times, low reproductive output, and extrinsic factors impeding passive recovery (Warham 1996, Jones and Kress 2012). However, increasing evidence suggests that seabird island ecosystem restoration, and thus burrow-nesting seabird population recovery, may occur in mere decades after eradication (Jones 2010b, Jones 2010a), although patterns and rates of recovery of the birds themselves were unknown (Chapter 2).

My data demonstrate that petrel burrow density increased among islands with more time since rat eradication at a rate as great as 0.1 burrows/m² per year (Fig. 6.2). This relatively fast rate of increase is similar to those found in other burrow-nesting seabird populations after predator eradication: for example, a colony of ancient murrelets (Synthliboramphus antiquus) doubled in size five years after the removal of black (Rattus rattus) and Norway rats (Rattus norvegicus), while two species of tropicbirds re-colonized and grew in population size by 2% per year after the removal of feral cats (Felis catus; Regehr et al. 2007, Ratcliffe et al. 2010). I found that the highest level of burrow clustering was on islands with rats still present, while clustering decreased on islands with more time since eradication (Fig. 6.3). I infer that the presence of Pacific rats may have restricted petrels to nest in patches where they could escape predation, either where petrel density was high before rat invasion and predation was swamped (Lyver et al. 2000, Regehr et al. 2007), or in areas infrequently used by predators. Because rodents generally use all areas of an island (Moller and Craig 1987), the former explanation is the most likely. Finally, I found that the extent of burrowed areas increased with time: burrows were found in 50% of areas searched on islands with 20 years since rat eradication and in over 70% of areas searched on islands with over 25 years since eradication.

I postulate that the pattern of burrow density and distribution found on study islands provide support for the “ideal despotic Allee” model of petrel colony growth after rat eradication (Kildaw et al. 2005). An increase in burrow density and maintenance of burrow clustering on islands with more time since eradication suggests that persisting colonies may be initially attractive. The attractiveness of established colonies to new recruits is thought to be pervasive among gregarious animals, such as burrow-nesting seabirds (Danchin and Wagner 1997). However, as time passes after eradication, and the number of recruits into remnant areas increases, established
colonies may become crowded, making it more advantageous for recruitment into new habitat (Fretwell 1972, Forbes and Kaiser 1994). This was also observed in my data, where burrows were found in almost all suitable habitat (Table 6.3), colony area was greater (Fig. 6.4 and 6.5), and clustering decreased on islands with more time since rat eradication.

6.4.3 Effect of nesting habitat abundance

Environmental covariates are known to affect the density and distribution of burrow-nesting seabirds (Chapter 3). Abiotic and biotic factors determining nesting habitat quality often include soil type, which must be soft enough to excavate, but strong enough to avoid collapse; canopy and understory vegetation, which adults must penetrate safely to reach their burrow; ground cover, which must be avoided or burrowed under; slope, which affects soil drainage; and aspect, elevation, and topography, which affect the ease of take-off and landing (Burger and Gochfeld 1991, Thompson and Furness 1991, Rodway et al. 1998, Bancroft et al. 2005b).

The data suggest that environmental factors affected both burrow density and colony area. For example, among islands, higher burrow density was associated with deeper soil, the presence of large boulders, southern aspect, and the presence of māhoe and karamū stems (Appendix D1). Furthermore, burrows were more likely to be found in areas with steeper slopes (Appendix D3). However, there were large amounts of variation in burrow density and colony area that could not be explained by environmental factors alone (Table 6.2). For example, there was a large proportion of suitable habitat on Mauitaha, Taranga and Ohinau (Pacific rats still present, removed in 2011, and removed in 2005 respectively) that was not occupied with burrows. When habitat covariates were included in a model comparing burrow density with time since eradication, model fit increased, while the relationship between burrow density and time since eradication was still strong. I infer that, although nesting habitat is important in determining the distribution and density of petrel burrows, time since rat eradication still contributed to the final pattern of observed burrow distribution. I therefore conclude that although there may be interactive effects between colony recovery and nesting habitat quality, and that habitat should not be ignored, the effects of habitat are
not necessarily enough to restrict increases in colony growth after eradication (Chapter 3; Major et al. 2011).

### 6.4.4 Conservation implications

Increase in burrow density and increase in burrowed area have several significant restoration and management implications. Because of their role as ecosystem engineers, the growth of burrow-nesting petrel colonies can provide important insights into island ecosystem recovery (Mulder et al. 2009, Mulder et al. 2011b). Burrow building alone alters the physical and chemical properties of soil, increasing porosity and soil-forming processes, and resulting in stronger and drier soil (Bancroft et al. 2005a). Thus, a relatively rapid increase in burrow density and distribution after rat eradication may reflect a rapid change in soil dynamics. It has been postulated that a burrow density of 0.3-1 burrows/m² is needed to promote ecosystem recovery to never-invaded control levels (Towns et al. 2009, Jones 2010a). I found that areas with these extreme levels of density covered over 2.5% of the total island surface on islands with > 20 years since rat eradication, which was about half of the total island surface with high burrow densities observed on Ruamaahuanui (∼0.50%; Fig. 6.5), the control island that never has had rats present. Furthermore, mean burrow density on restored islands was less than half (<0.1 burrows/m²) that on the never-invaded Ruamaahuanui (>0.2 burrows/m²). Thus, although increases in the number of burrows after rat eradication may seem relatively rapid, burrow densities on restored islands have probably not yet reached a level where introduced-predator-free seabird-dominated ecosystem functioning is possible (Jones 2010b).

However, the relatively rapid increase in burrow density observed in this study, without active intervention, raises the question in which cases and to what extent should managers actively work to facilitate seabird recovery (Holl and Aide 2011, Jones and Kress 2012)? My data contradict the idea of slow or non-existent petrel recovery and instead suggest that island managers should carefully consider when the benefits of active restoration outweigh the cost. In order to actively speed petrel recovery on islands with remnant colonies, the most effective strategy may be to lure birds into new habitat, which they would only otherwise inhabit passively after filling remaining patches. Several techniques have been developed to actively anchor seabirds into new
Despite the potential caveats, my data confirm that much valuable information can be ascertained from monitoring the passive recovery of seabirds after predator removal to guide ecological understanding and restoration. Generally, invasive-predator eradication projects have been undertaken without adequate consideration of the gathering of pre-eradication data or the setting of feasible goals, and thus, lack the capacity to reliably assess project success and the impact of predator removal on seabirds (Phillips 2010). A lack of monitoring of burrow-nesting seabirds in particular is likely due to their nocturnal and burrowing behaviour, making surveying costly, logistically challenging, and often not feasible (Buxton and Jones 2012b, Schumann et al. 2013). My results can be used to guide potentially effective monitoring strategies. For example, the data show that an increase in colony density and extent are expected after eradication, which suggests that post-eradication monitoring should target areas which are burrowed at the time of eradication, but also non-burrowed areas where colonies may spread in the future.
Chapter 7  Designing an effective monitoring strategy for burrow-nesting seabirds in New Zealand

7.1  Introduction

Population monitoring is of increasing practical importance to conservation managers for detecting trends in threatened species populations, informing adaptive management by measuring the outcome of restoration, and providing estimates for population trajectory models under predicted future conditions (Block et al. 2003, Bart et al. 2004, Field et al. 2007). Burrow-nesting seabirds are important animals, acting as apex predators in their marine environment and ecosystem engineers at their island breeding grounds (Sydeman et al. 1997, Veit et al. 1997, Smith et al. 2011). Yet, these birds are among the most threatened group of marine animals (Dulvy et al. 2003, Croxall et al. 2012). One of the most acute threats to burrow-nesting seabird populations has been the introduction of non-native predators to breeding islands (Donlan and Wilcox 2008, Bellingham et al. 2010). However, over the past 6 decades, island restoration efforts targeting non-native predators have accelerated and, to date, predators have been removed from over 800 islands around the world (Keitt et al. 2010, Keitt et al. 2011). Thus, monitoring population decline and potential recovery of these birds is important, but acquiring reliable abundance estimates is challenging, and thus has rarely been done.

There is mounting interest in establishing effective methods to monitor fluctuations in burrow-nesting seabird populations (Lewison et al. 2012). Firstly, because breeding success and adult survival directly reflect changes in marine resources, seabirds can act as indicators of marine health (Parsons et al. 2008, Durant et al. 2009, Cury et al. 2011). Second, on land burrow-nesting petrels act as ecosystem engineers, providing islands with marine-derived nutrients and physical disturbance (Smith et al. 2011). Thus, monitoring petrels after the eradication of non-native predators from islands could provide a prognosis of island ecosystem recovery after restoration actions (Chapter 2; Jones 2010a). Finally, seabirds are an important source of food and cultural identity for many people around the world, many of whom are committed to ensuring harvest is sustainable (Montevecchi et al. 2007, Lyver et al. 2008, Moller 2009).
Despite their importance, reliable population estimates for petrels are scarce, due to associated challenges: petrels have cryptic nesting behaviour (below-ground nesting and nocturnal colony attendance; Warham 1990); heavily burrowed friable soils make surveying difficult without collapsing burrows (Kennedy and Pachlatko 2012); and accessing island breeding grounds is expensive and logistically challenging (Schumann et al. 2013). Additionally, there are complex sources of variation associated with measuring seabird colonies which must be incorporated into a sampling design (MacKenzie et al. 2002). This includes large inter and intra-island spatial variation, where colonial petrels nest in clusters within an island and colony size can vary from a few hundred to over half a million (Jones 2000, Rayner et al. 2007a, Newman et al. 2009). Furthermore, because petrels nest in burrows, counts of breeding birds or chicks must be estimated, either using relative indices of abundance such as surface counts before birds enter nests (Renner et al. 2011), nocturnal call counts (Buxton and Jones 2012b, Borker et al. in press), or burrow densities (McKechnie et al. 2009); or by examining burrow contents using infrared cameras (Lyver et al. 1998) or observation lids over excavated nesting chambers (Rayner et al. 2007a). Indices of population status will have wide confidence intervals and considerable assumptions, while burrow occupancy estimates will be associated with detection error (MacKenzie et al. 2002, Mackenzie 2005, Renner et al. 2011). The limited availability of reliable population size estimates for burrow-nesting petrels highlights the need to address and guide the collection of robust metrics of change.

New Zealand holds the greatest diversity of procellariiform seabirds (Taylor 2000) and the largest area of newly predator-eradicated space in the world (Towns 2011, Towns et al. 2012b). Nevertheless, in New Zealand, monitoring programmes are rarely implemented for petrels, and when they are, they often suffer from poor design and lack of statistical rigor. However, impetus for designing a nationally consistent monitoring strategy is evolving. Monitoring the response of wildlife to invasive species removal on offshore islands has recently been recognized as a key national issue (Lee et al. 2005, Department of Conservation 2010, Towns et al. 2012a). Furthermore, a rigorous terrestrial sampling programme began in 2011 to assess gains and losses of biodiversity within plots at terrestrial mainland sites (initiated by the Department of Conservation, DOC, and Landcare Research; MacLeod et al. 2012). Both DOC and Māori (indigenous peoples of New Zealand) are interested in expanding this monitoring
scheme to offshore islands, using petrels as biological indicators (B. Greene, DOC, pers. comm., Moller 2009).

Characteristics of a robust ecological monitoring programme include: use of appropriate environmental indicators, carefully posed questions and objectives, and a statistically robust design (Carignan and Villard 2002, Field et al. 2007). To assess the latter, power analyses are often employed to ensure that sample size will be great enough to detect biologically relevant changes (Hatch 2003). Without these analyses, a conservation programme risks misallocating limited financial resources thereby reducing the ability to respond to real population declines (Field et al. 2005). Power calculations estimate the precision of inference one expects to achieve given a sample size, an estimate of variability between samples, an effect size, and a significance criterion (Hatch 2003, Gelman and Hill 2007, Seavy and Reynolds 2007). Generally, power analyses use pre-existing data to parameterize models as a function of a range of samples to be collected (Gerrodette 1987). The resulting level of statistical power represents the probability of rejecting the null hypothesis when it is false (i.e. detecting a population trend when one actually occurs; Cohen 1988).

Here, I develop a monitoring programme prototype for procellariiform seabirds in New Zealand, using burrow density as a proxy for relative abundance. I propose that examining population changes of burrow-nesting petrels after the removal of non-native predators from offshore islands may represent a useful preliminary monitoring objective in New Zealand, and could form the framework for a more general programme. I perform a power analysis using burrow-nesting petrel survey data from islands off the north-eastern coast of New Zealand’s North Island to address the following questions:

(i) How does the statistical power of detecting a change in burrow density after predator eradication in New Zealand differ with varying levels of survey intensity (number of plots and islands) and frequency?

(ii) How would survey intensity and frequency need to be adjusted to achieve the same power if seabirds were actively managed after eradication (e.g. translocation or social attraction), or conversely, if birds were declining at a rate considered by the IUCN as vulnerable, endangered, or critically endangered?

(iii) Can surveys be stratified by habitat characteristics to increase power?

Finally, I examine whether burrow density can reliably predict the abundance of petrels. I discuss whether the model sampling design represents an adequate method to
detect long-term trends in burrow-nesting petrel abundance and consider adaptive design recommendations that could be applied as conditions change in the future.

7.2 Methods

7.2.1 Potential monitoring design

To determine the power of detecting different levels of change in burrow density with varying survey intensity I performed a power analysis using data simulations. Power calculations proceed by defining relationships among four parameters of statistical inference: number of samples, variability of samples not attributable to the effect of interest, effect size of the response variable of interest (in most cases, time), and significance criterion (generally $\alpha = 0.05$; Hatch 2003).

7.2.1.1 Sampling intensity

To constrain sample sizes used in the power analysis within realistic fieldwork agendas, I performed a literature review of island monitoring programmes around New Zealand. I collated information on the range of offshore island monitoring intensities in New Zealand by examining published and unpublished reports of monitoring projects after predator eradication. Using an updated list of successful eradication projects on New Zealand islands (final search, July 2012; Chapter 2), I searched Google Scholar and Web of Science with each island’s name and *monitor* as keywords. If no information was available, I contacted local biodiversity rangers (DOC) or other relevant research personnel and asked: how many islands are visited for monitoring, how often are islands visited, how much time is spent monitoring each island, and if there are any existing monitoring goals or benchmarks for wildlife monitoring, namely for seabirds. I used responses to compile a series of monitoring strategies that varied in the number of islands, plots, and inter-annual measurements after eradication.

7.2.1.2 Estimating variance

Power analyses require survey data from which the underlying variability in the metric of interest can be estimated. I used survey data from seven islands within 7–20 km of New Zealand’s North Island (Fig. 7.1).
All study islands had similar climate, geology, and vegetation structure (Chapter 6). Five islands represented 0–26 years of recovery after Pacific rat eradication (Table 7.1). Norway rats (*Rattus norvegicus*), domestic sheep (*Ovis aries*), cattle (*Bos primigenius*), goats (*Capra hircus*), and European rabbits were eradicated between 1970-1987 from Moutohorā. One island, Ruamaahuanui, never had predators introduced. All islands have similar disturbance and habitat modification histories, with extensive burning and terracing by Māori (Sladden and Falla 1928, Edgar 1962, McCallum et al. 1984). Disturbance was more intense on Moutohorā, which was mined for sulphur and rock and grazed by cattle, sheep, and goats from 1868–1984 (Imber et al. 2000, Imber et al. 2003).

On each island, except for Moutohorā and Ruamaahuanui, I counted burrow entrances in 3-m-radius circular plots placed randomly along search transects. Additionally, I recorded a suite of habitat variables including: aspect, slope, elevation, topography, soil properties, and counts of canopy and stem plant species. Survey methods are described in detail in Chapter 3. On Moutohorā and Ruamaahuanui plot locations were randomly assigned across accessible parts of the islands (Whitehead et al. 2014).

Seven species of burrow-nesting seabirds in the order Procellariiformes were present on study islands: grey-faced petrel (*Pterodroma macroptera gouldi*), Pycroft’s petrel (*P. pycrofti*), fluttering shearwater (*Puffinus gavia*), flesh-footed shearwater (*P. carneipes*), little shearwater (*P. assimilis*), sooty shearwater (*P. griseus*), and common diving petrel (*Pelecanoides urinatrix*). The most common petrel species observed was grey-faced petrel (Chapter 5). Because burrows of all species tend to be sympatric, with more association between species than expected by chance, I assumed that power analyses applied to communities of all species (Chapter 5, Hicks et al. 1975, Pierce 2002).

### 7.2.1.1 Effect sizes

I tested the power of detecting five hypothetical population trends (effect sizes, or “β”; Cohen 1988):
Figure 7.1: Location of eight study islands off the north-eastern coast of the North Island, New Zealand.
Table 7.1: Comparison of survey plot type, number of each plot type, and survey timing on eight islands off the northeastern coast of New Zealand’s North Island. Surveys were undertaken to measure the abundance and occupancy of petrel burrows. Each island differs in the presence (“still present”), absence (“n/a”), or years since rat (*Rattus* sp.) eradication

<table>
<thead>
<tr>
<th>Survey plot type</th>
<th>Mauitaha</th>
<th>Taranga</th>
<th>Ohinau</th>
<th>Kawhitu</th>
<th>Moutohora</th>
<th>Korapuki</th>
<th>Ruamaahuanui</th>
<th>Ruamaahuaiti</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island size (ha)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>22</td>
<td>470</td>
<td>32</td>
<td>100</td>
<td>148</td>
<td>18</td>
<td>21</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Year rats eradicated</td>
<td>still present</td>
<td>2011</td>
<td>2005</td>
<td>1991</td>
<td>1987</td>
<td>1986</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Number of plots</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>27</td>
<td>14</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>10 by 10 m plots</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year surveyed</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>2010</td>
<td>2010/2012</td>
<td>2008/2010</td>
<td>2008</td>
</tr>
<tr>
<td>Month surveyed</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>November</td>
<td>November</td>
<td>November</td>
<td>November</td>
</tr>
<tr>
<td>Number of plots</td>
<td>68</td>
<td>120</td>
<td>100</td>
<td>132</td>
<td>n/a</td>
<td>101</td>
<td>76</td>
<td>n/a</td>
</tr>
<tr>
<td>3-m-radius plots</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Year surveyed</td>
<td>2011/2012</td>
<td>2011/2012</td>
<td>2013</td>
<td>2013</td>
<td>n/a</td>
<td>2013</td>
<td>2011</td>
<td>n/a</td>
</tr>
<tr>
<td>Month surveyed</td>
<td>December</td>
<td>November</td>
<td>October</td>
<td>November</td>
<td>n/a</td>
<td>December</td>
<td>March</td>
<td>n/a</td>
</tr>
<tr>
<td>Number of plots</td>
<td>13</td>
<td>27</td>
<td>31</td>
<td>36</td>
<td>n/a</td>
<td>19</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>5-m-radius plots</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Year surveyed</td>
<td>2011/2012</td>
<td>2011/2012</td>
<td>2012/2013</td>
<td>2012/2013</td>
<td>n/a</td>
<td>2012/2013</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Month surveyed</td>
<td>October</td>
<td>October</td>
<td>December</td>
<td>December</td>
<td>n/a</td>
<td>December</td>
<td>n/a</td>
<td>n/a</td>
</tr>
</tbody>
</table>
1) a “passively managed” increase in burrow density after rodent eradication (i.e. where seabirds are left to recover after eradication with no other management interventions) of 1.8% per year. This value was based on differences in burrow density among the chronosequence of islands after Pacific rat eradication from this study (Table 7.1; Chapter 6);

2) an “actively managed” increase in burrow density after rodent eradication of 2.96% per year. Active management involves enhancing or re-introducing populations using techniques such as social attraction and translocation (Jones et al. 2011). Although I was interested in the possible doubling of the rate of population increase with active versus passive management (1.8*2 = 3.6%); I constrained this value based on rates of recovery in a recent review of active seabird management (Jones and Kress 2012);

3) a decline of 50% over 3 generations, meeting the IUCN criterion for listing a species as vulnerable. I used a generation time of 17.6 years, calculated by taking a mean of generation times available in the literature for petrels in the same size range as species present on study islands (130-950 g; Saether et al. 2005, Garnett et al. 2011, IUCN 2012, Miskelly 2013). This resulted in a mean decline of 0.95% per year (50% / 17.6*3);

4) a decline of 70% over 3 generations, meeting the IUCN criterion for listing a species as endangered (resulting in a mean decline of 1.33% per year); and

5) a decline 95% over 3 generations, meeting the IUCN criterion for listing a species as critically endangered (1.71% per year).

As a basis for power analyses, I considered the objective of achieving >80% probability of detecting trends ("power"; Cohen 1988, Freilich et al. 2005). This value is slightly lower than the minimum monitoring standards proposed for large-scale breeding bird surveys across North America, but includes the variation in power to detect trends in seabird populations over time (Hatch 2003, Seavy and Reynolds 2007).

### 7.2.1.2 Power calculations

Power calculations were performed by repeatedly simulating data constrained by population variance inferred from 3-m-radius circular plot data (see above), and subsequently fitting a multi-level model to each data set (Gelman and Hill 2007). By performing these calculations for a number of different monitoring scenarios, I determined the extent to which survey intensity (number of plots and islands), survey frequency
(number of surveys per decade), and the extent of decline or increase influence the power
to detect trends in burrow density (relative petrel abundance).

To construct a hypothetical distribution from which data could be simulated, I used
burrow density data from 3-m-radius plots (Table 7.1). I determined inter-island and inter-
plot variance and residual standard deviation by fitting the following varying intercept
linear mixed effects model (GLMM):

\[ y_i \sim N(\alpha_{jk} + \beta_t t_i, \sigma_y^2) \]  

where $\beta_t$ is rate at which burrow density ($y_i$) changes with years (effects size) and $\alpha_{jk}$ is
the intercept, which varies between islands $j$ and plots $k$. Initially, I used a $\beta_t$ examining
the change in burrow density with years since Pacific rat eradication (“passive recovery”
Table 7.2). For each sampling intensity, I simulated 1000 sets of ‘fake data’.
I then fitted each simulated data set to a nested hierarchical multi-level model of the form:

\[ y_i \sim N(\alpha_{j[k[i]]} + \beta_{j[k[i]]} t_i, \sigma_y^2) \]  

where $\beta_{j[k[i]]}$ is rate at which burrow density ($y_i$) increases (effects size) each decade in
each plot $k$, on each island $j$, where measurements are taken at $i$ intervals per decade.
From each fitted model I obtained 95% confidence intervals for the parameter $\beta_{j[k[i]]}$ (i.e.
the confidence intervals around the effect of decade). Power was calculated as the
proportion of the 1000 simulations where the lower bound of the 95% interval exceeded
zero (i.e. burrow density changed significantly with decade; Gelman and Hill 2007).
Models were fitted using the package lme4 in R version 2.14.2 (Bates et al. 2012, R
Development Core Team 2012.). Models had Gaussian error structures and Laplace
approximations.

7.2.1.3 Stratification
As a means of minimizing unexplained variance and increasing power, other seabird monitoring approaches stratify sampling effort (Thompson 2002, Pearson et al. 2013). Strata are defined based on geomorphic features that are known to be associated with varying levels of burrow density, which can be defined prior to sampling using mapping layers. To examine the possibility of stratifying sampling, I determined the effect of features that are readily available as layers in ArcGIS (ESRI Inc., USA) for offshore islands in New Zealand. These included island size, slope, elevation, and slope aspect (Columbus et al. 2011). Island size was separated into small (<100 ha) and large (>100 ha), based on the mean size of offshore islands (Clout and Russell 2006). Slope and elevation were each separated into two categories based on the median value from each island, while slope aspect was separated into four categories (north, south, east, and west).

To determine the effect of categorical features on burrow density I used an information theoretic, model averaging approach. I fitted a GLMM with habitat features, time since eradication and the interaction between slope and elevation as fixed effects; and island as a random effect. To ensure that resulting parameter estimates would be comparable, data were standardized by subtracting the mean and dividing by two standard deviations (Schielzeth 2010). To generate a set of models with different combinations of covariates I used the ‘dredge’ function implemented in the MuMIn package. Models were ranked based on Akaike’s Information Criterion values corrected for small sample sizes (AICc) and top models were selected based on ΔAICc values of less than 10 (Grueber et al. 2011). I averaged the resulting top models to generate parameter estimates and unconditional standard errors, which were used to estimate the effect size for each habitat feature (Johnson and Omland 2004). To determine how each feature with strong effects on burrow density affected power, I incorporated parameter estimates of features whose standard errors did not overlap with zero into the simulation of data (Eq. 1). I simulated 1000 separate data sets for each feature. I then fitted the model in Eq. 2 and calculated the mean resulting power. If a feature decreased the resulting power, I assumed more plots should be placed in areas with those characteristics.

7.2.2 Burrow density vs. bird density
To assess the ability of burrow density to predict the density of petrels in a plot, I used a Bayesian hierarchical framework. I used burrow density and occupancy data from 10 by 10 m permanent plots on four islands and 5-m-radius circular plots on five islands (Table 7.1).

Locations of 10 by 10 m plots were selected randomly using ArcGIS for Desktop (10.1, ESRI Inc., USA) and were established as part of a long-term monitoring project (Table 7.1; Whitehead et al. 2014). I placed 5-m-radius circular plots randomly within burrowed areas found along search transects (Table 7.1; Chapter 5). Plot corners or centres were marked with aluminium poles, and each burrow entrance was marked with a numbered cattle tag. Plot surveys were undertaken annually or biannually for 2-5 years from 2006-2013 (Table 7.1). Burrow occupancy was assessed using infrared cameras or ‘burrow-scopes’ (Sandpiper Technologies, Manteca, California, USA and Sextant Technology Ltd., Wellington, New Zealand). Occupied burrows were defined as those with petrel adults, adults on eggs, or chicks. Plot surveys were undertaken when all petrel species were at some stage of the breeding cycle (courtship, laying, incubation, or chick rearing; Table 7.1). For further detail of standardized burrow occupancy protocol, see Whitehead et al. (2014) and Chapter 5.

To maximize inference between years, sites, and islands, I used a Bayesian hierarchical modelling approach. I calculated the number birds \( X_{jkl} \) in plot \( j \) on island \( k \) in year \( l \) by taking the product of the number of burrows \( Y_{jkl} \) and burrow occupancy probability \( P(occ)_{jkl} \):

\[
X_{jkl} = Y_{jkl} \times P(occ)_{jkl}
\]

Burrow occupancy probability is likely associated with a detection error (Mackenzie 2005). However, because detection probabilities were found to be high and relatively constant for grey-faced petrel (probability of detecting an egg – 0.714 and chick – 0.955 with a burrow-scope; Whitehead et al. 2014) and I did not have sufficient data to address this issue, I assumed detection probability to be constant.
I modelled the number of birds \((X_{jkl})\) as:

\[
X_{jkl} \sim \text{Binomial}\left(P(\text{occ}_{jkl}), Y_{jkl}\right)
\]

where \(P(\text{occ})_{jkl}\) was the occupancy probability of each burrow \((Y_{jkl})\) in plot \(j\) on island \(k\) in year \(l\), and was modelled as:

\[
\psi_{jkl} \sim \alpha_{kl} + \beta_{lk} x_{lk}
\]

where \(\beta_{lk}\) was the effect of the observed density of birds among islands \(k\) and years \(l\). The intercept \((\alpha_{kl})\) and \(\beta_{lk}\) came from a (non-informative) prior distribution of hyper-parameters \(M_\alpha\) and \(\sigma^2_\alpha\) and \(M_\beta\) and \(\sigma^2_\beta\) (Gelman et al. 2004):

\[
\alpha_{kl} \sim \text{Normal}(M_\alpha, \sigma^2_\alpha), \hspace{1cm} M_\alpha \sim \text{Normal}(0,1000), \hspace{1cm} \sigma^2_\alpha \sim \text{InverseGamma}(0.1,0.1)
\]

Models were fitted using OpenBUGS (Lunn et al. 2000), called from R version 3.0.1 using BRugs and R2OpenBUGS (Sturtz et al. 2005, Thomas et al. 2006, R Development Core Team 2013). To ensure convergence and minimize autocorrelation between chains, I ran 10000 iterations with a burn-in of 1000 and a thinning rate of 10 (Gelman et al. 2004).

To compare the amount of inter and intra-annual variation in burrow density versus burrow occupancy, I used a similar GLMM structure as in Eq. 1. I used data from islands with \(\geq 3\) years of burrow density and occupancy data (Moutohorā, Ruamaahuanui, and Ruamaahuaiti; Table 7.1). First, I fitted burrow density data, where \(\beta_t\) was the rate at which burrow density \((y_t)\) changed between years, and months nested within years.
Finally, I fitted burrow occupancy data, where $\beta_t$ was the rate of change between years, and months nested within years, and $y_t$ was burrow occupancy.

### 7.3 Results

I identified a total of 88 islands around New Zealand with predators removed between 1936 and 2011. Of these, 66 have had monitoring activities occurring at some point between eradication and 2014 (Appendix E). Generally, research personnel visited islands annually, for a mean of five days for seven years (Appendix E). A review of grey-faced petrel surveys revealed that, of 29 islands where petrels were repeatedly monitored, most were opportunistic and descriptive rather than quantitative (Greene and Earl in review). Overall, DOC indicated that a national monitoring scheme for burrow-nesting petrels on offshore islands would likely involve 15 islands (three groups of five islands with small, medium, and large populations of petrels), visited for 3-5 days (depending on island size) every five years (B. Greene pers. comm.). Thus, I tested the power of three separate monitoring programmes with 9, 12, or 15 islands (allowing for three groups of three, four, or five islands), each with 10-200 circular plots of 3-m-radius, measured 1-10 times within a decade (Fig. 7.2 and 7.3).

From circular plots on seven study islands, I found plots nested within islands had a variance of 0.037, islands had a standard deviation (sd) of 0.104, and plots within islands had a sd of 0.210. Based on the chronosequence of time since rat eradication on these islands, I found an increase in burrow density of 18 % ($T_1 = 0.121, P < 0.001, R^2 = 0.2$) per decade.

To detect this rate of change in burrow density after rat eradication with 80% power, I found that monitoring programmes with nine islands must monitor a minimum of 110 plots seven times in a decade (Fig. 7.2A); monitoring programmes with 12 islands must monitor a minimum of 80 plots seven times in a decade (Fig 7.2B) and monitoring programmes with 15 islands must monitor a minimum of 100 plots six times a decade (Fig. 7.2C).

Using the same variance and sd, and a total of 15 islands with varying numbers of plots and inter-annual monitoring frequencies, I then tested how different levels of increase
or decrease in burrow density would affect power (Fig. 7.3; Table 7.2). If burrow density increased at a rate slightly less than double the trend observed after rat eradication (29.6%, a potential increase if birds are actively managed; Jones and Kress 2012), a monitoring program with 15 islands must monitor a minimum of 70 plots five times in a decade to achieve 80% power. To detect a decline in burrow density meeting IUCN criteria of vulnerable, endangered, and critically endangered with 80% power, 80, 50, and 30 plots respectively on 15 islands must be monitored annually (Fig. 7.3; Table 7.2).

I tested how burrow density varied with categories of island size, slope, elevation, aspect, and the interaction between slope and elevation. I found no evidence of a difference in burrow density between small and large islands; low and high elevation; north, west, and east aspect (Fig. 7.4, Table 7.3). I found a strong effect of slope, the interaction between slope and elevation, and a moderate effect of southern aspect, with higher burrow density in steeper slopes and southerly aspects, but fewer birds on steep slopes at low elevation (Table 7.3). When power analyses were run incorporating each of these three parameters, I found that monitoring plots on steep slopes increased power (mean power ± SE; steep slope: 0.66 ± 0.03, shallow slope 0.50 ± 0.03), monitoring plots on shallow slopes and low elevation decreased power (shallow slope and low elevation: 0.51 ± 0.03, steep slope and high elevation: 0.59 ± 0.03), while monitoring plots with southerly aspects had no effect (south: 0.52 ± 0.03, north, east, or west: 0.51 ± 0.03).

Among islands, burrow density was positively related to the density of birds observed within a plot; however, for a given burrow density, there was a wide range of petrel densities (Fig. 7.5). Models predicted a positive relationship between burrow density and petrel numbers on some islands (Moutohorā, Ruamaahuaiti), no relationship on some (Ohinau, Kawhitu, and Mauitaha), and conversely, a negative relationship on others (Korapuki and Nui; Table 7.4). The reason for the lack of a reliable relationship between burrow density and petrel density is likely due to the large amount of variation in burrow occupancy among plots (Fig. 7.6).
Figure 7.2: Power to detect a decadal increase of 18% in burrow density after rat eradication on islands off the northeast coast of New Zealand with increasing numbers of 3-m-radius plots on 9 (A), 12 (B), or 15 (C) islands. Greyscale indicates increasing numbers of island visits per decade, where 10 indicates annual visits. Purple dashed line indicates 80% power.
Figure 7.3: Power to detect different levels of increase or decrease in burrow density if increasing numbers of 3-m-radius plots are monitored on 15 islands (A) every year or (B) every 2 years. Dashed line indicates 80% power
Table 7.2: The mean percent change in burrow density under each management type (inferred from the literature – see text) and the number of 3-m-radius circular plots on 15 islands required to detect this change with 80% power when plots are surveyed once a year (annually) or once every two years (biennially)

<table>
<thead>
<tr>
<th>Management type</th>
<th>Annual change in burrow density</th>
<th>Annual plot measurements</th>
<th>Biennial plot measurements</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active recovery after predator eradication</td>
<td>3.0%</td>
<td>10</td>
<td>70</td>
</tr>
<tr>
<td>Passive recovery after predator eradication</td>
<td>1.8%</td>
<td>30</td>
<td>160</td>
</tr>
<tr>
<td>Listing as vulnerable</td>
<td>-0.9%</td>
<td>80</td>
<td>&gt;200</td>
</tr>
<tr>
<td>Listing as endangered</td>
<td>-1.3%</td>
<td>50</td>
<td>&gt;200</td>
</tr>
<tr>
<td>Listing as critically endangered</td>
<td>-1.7%</td>
<td>30</td>
<td>190</td>
</tr>
</tbody>
</table>
Figure 7.4: Mean burrow density (± standard error) in each habitat feature available as a GIS layer on offshore islands in north-eastern New Zealand. In other words, it would require fewer plots to detect changes in burrow density on steeper slopes at higher elevations.
Table 7.3: Summed Akaike weights (\( w \)), weighted parameter estimates (\( w\text{PE} \)), and unconditional standard errors (SE\( \mu \)) calculated from candidate models describing the effect of categorical habitat features (Feature) on petrel burrow density on seven islands off the northeast coast of New Zealand

<table>
<thead>
<tr>
<th>Feature</th>
<th>Category</th>
<th>( w )</th>
<th>( w\text{ParE} \pm \text{SE}( \mu )</th>
<th>upper 95% CI</th>
<th>lower 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td></td>
<td></td>
<td>0.082 ± 0.004</td>
<td>0.074</td>
<td>0.090</td>
</tr>
<tr>
<td>Slope</td>
<td>Shallow(^a)</td>
<td></td>
<td>0.88 0.03 ± 0.009</td>
<td>0.015</td>
<td>0.048</td>
</tr>
<tr>
<td></td>
<td>Steep</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time since eradication</td>
<td>1.00</td>
<td></td>
<td>1.00 0.119 ± 0.009</td>
<td>0.102</td>
<td>0.136</td>
</tr>
<tr>
<td>Aspect</td>
<td>None(^a)</td>
<td></td>
<td>0.03 0.016 ± 0.010</td>
<td>-0.003</td>
<td>0.035</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td></td>
<td>0.01 -0.012 ± 0.012</td>
<td>-0.036</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td></td>
<td>0.01 0.003 ± 0.010</td>
<td>-0.018</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td></td>
<td>0.01 0.002 ± 0.010</td>
<td>-0.017</td>
<td>0.021</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td></td>
<td>0.01 0.001 ± 0.009</td>
<td>-0.018</td>
<td>0.018</td>
</tr>
<tr>
<td>Elevation</td>
<td>High(^a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td></td>
<td>0.02 -0.001 ± 0.009</td>
<td>-0.018</td>
<td>0.018</td>
</tr>
<tr>
<td>Slope*Elevation</td>
<td>Shallow*high(^a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Steep*low</td>
<td></td>
<td>0.01 -0.054 ± 0.018</td>
<td>-0.089</td>
<td>-0.018</td>
</tr>
<tr>
<td>Island size</td>
<td>Large(^a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Small</td>
<td></td>
<td>0.01 0.001 ± 0.011</td>
<td>-0.020</td>
<td>0.022</td>
</tr>
</tbody>
</table>

\(^a\) Category set as reference
Figure 7.5: Relationship between burrow density (burrows/m$^2$) and petrel density (number of birds observed in burrows/m$^2$) among eight islands in north-eastern New Zealand. Grey shading represents linear smoothing based on the variation in bird density.
Table 7.4: Mean effect sizes and 97.5% credibility intervals (CI) from Bayesian models predicting the relationship between petrel density and burrow entrance density in permanent plots on islands in north-eastern New Zealand. Italicized values have CI which do not overlap with zero

<table>
<thead>
<tr>
<th>Island</th>
<th>Mean</th>
<th>SD</th>
<th>2.50% CI</th>
<th>97.50% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kawhitu</td>
<td>0.776</td>
<td>1.189</td>
<td>-1.557</td>
<td>3.157</td>
</tr>
<tr>
<td>Korapuki</td>
<td>-0.674</td>
<td>0.331</td>
<td>-1.316</td>
<td>-0.049</td>
</tr>
<tr>
<td>Mauitaha</td>
<td>0.760</td>
<td>1.960</td>
<td>-3.128</td>
<td>5.039</td>
</tr>
<tr>
<td>Moutohorrā</td>
<td>1.675</td>
<td>0.314</td>
<td>1.060</td>
<td>2.292</td>
</tr>
<tr>
<td>Ohinau</td>
<td>-0.375</td>
<td>1.125</td>
<td>-2.743</td>
<td>1.637</td>
</tr>
<tr>
<td>Ruamaahuaiti</td>
<td>1.526</td>
<td>0.258</td>
<td>1.018</td>
<td>2.026</td>
</tr>
<tr>
<td>Ruamaahuanui</td>
<td>-0.537</td>
<td>0.162</td>
<td>-0.844</td>
<td>-0.210</td>
</tr>
<tr>
<td>Taranga</td>
<td>1.855</td>
<td>1.534</td>
<td>-0.779</td>
<td>5.205</td>
</tr>
</tbody>
</table>
Figure 7.6: Relationship between burrow density and predicted probability of burrow occupancy from hierarchical Bayesian models using data from eight islands in north-eastern New Zealand. Dashed lines represent credible intervals. RIti indicates Ruamaahuaiti and RNui indicates Ruamaahuanui.
I found no evidence of change in mean burrow density among months or years sampled (all $P > 0.117$; Fig. 7.7). I found significant differences in burrow occupancy among years on Ruamaahuanui, where burrow occupancy decreased over time ($T_1 = -2.593, P = 0.010$). Years and months explained little of the variation in burrow density ($R^2 = 0.109$) and burrow occupancy ($R^2 = 0.009$).

Figure 7.7: Mean burrow density, burrow occupancy, and petrel density measured in 10 by 10 m plots over from 2006-2008 and in 2010 on Moutohorā (Mouto), Ruamaahuaiti (Riti), and Ruamaahuanui (Rnui) in north-eastern New Zealand
7.4 Discussion

Robust ecological monitoring is essential for detecting changes in wildlife abundance. Counts, indices, or estimates of populations serve as guides for documenting the effects of management activities or signalling incipient population decline (Gibbs et al. 1998). Despite the central role that burrow-nesting seabirds play in both marine and terrestrial ecosystems and the large proportion of species vulnerable to extinction, especially in New Zealand, national monitoring strategies have yet to be devised. New Zealand represents an ideal location to monitor burrow-nesting seabirds, as one of these birds’ main threats, non-native predators, have been removed from most islands around the archipelago (Towns et al. 2012b). Here I outline a monitoring programme with enough power to detect potential increases in petrel burrow density after predator eradication or declines large enough to qualify for IUCN red-listing. I discuss extensions and refinements needed to generate a consistent, but flexible, petrel monitoring strategy.

7.4.1 Current monitoring programmes

I found considerable variation in current monitoring strategies for offshore islands in New Zealand (Appendix E). Of the 88 offshore islands with predators removed, few had long-term programmes in place to measure wildlife response after eradication. In most cases, especially for seabirds, population estimates are anecdotal, observational, “best-guesses”, or inventory surveys, rather than replicated monitoring (blank rows in Appendix E; Taylor 2000, Greene 2012). In other cases, where colonies were small, each burrow was monitored (e.g. black petrel Procellaria parkinsoni and Westland petrel Procellaria westlandica; Bell et al. 2013, Wood and Otley 2013). If these small populations grow, colony-wide monitoring will no longer be realistic and subsamples will need to be taken, which will no longer be comparable to initial surveys (Witmer 2005). Other studies used search transects spanning the colony area (e.g. flesh-footed shearwater Puffinus carneipes; Baker et al. 2010, Waugh and Taylor 2012). Although this method is feasible for small to mid-sized colonies, it is not practical in dense colonies, where walking longer distances increases chances of burrow collapse (Bancroft 2009). Furthermore, colony transects are
incapable of detecting expansion outside the current burrowed area (Chapter 6). Finally, I observed that monitoring around New Zealand is a highly de-centralized activity, with studies carried by DOC, Landcare Research, the Ornithological Society of New Zealand, Te Papa Tongarewa Museum, universities and private consultancies (Appendix E; Marsh and Trenham 2008). These inconsistencies make data incomparable and highlight the need to develop a coherent sub-sampling strategy, despite the current size of a population or institution performing the research.

7.4.2 Developing a monitoring strategy

I constrained the sample size of the proposed monitoring programme using DOC’s prospective target of three groups of islands measured every five years for three to five days (B. Greene, DOC, pers. comm.).

To detect increases in burrow density after predator eradication or decreases in density resulting in IUCN red-listing, I recommend monitoring 80 circular plots of 3-m-radius on 15 islands (three groups of five islands) every year. To reduce the number of visits to once every five years, the upper limit of survey time proposed by DOC, an unrealistic number of plots (>300) must be monitored. Instead, I recommend increasing the number of years monitored to biennially or annually (Table 7.2).

I did not test the effect of increasing plot size, which may reduce variation between plots (Hatch 2003). However, I do not recommend the use of transects, distance sampling, or large plots within dense colonies, due to high risk of burrow collapse and the ease of placing stabilizing wooden boards on paths to and around marked plots (West and Nilsson 1994).

I examined how sampling could be stratified, based on habitat features which affect burrow density and were available as ArcGIS layers. I found no evidence of difference in burrow density between small (≤ 100 ha) or large (> 100 ha) islands. Other studies found similarly insignificant effects of island size on numbers of burrow-nesting seabirds (Byrd et al. 2005, de León et al. 2006, Pearson et al. 2013). Regardless, the same number of plots on a smaller island will proportionally sample more area than a large island and thus be more likely to detect burrows. Furthermore, managers must consider island size due to the
logistical difficulties associated with covering larger island areas. Thus, I suggest that either more time be allocated to monitor large islands, or large islands can be structured into ‘sections’ or ‘sectors’ where monitoring is temporally staggered (Morisson et al. 2001). I found higher burrow density and greater power to detect changes in burrow density in areas with steeper slopes and at high elevations with steeper slopes (Table 7.2). Thus, I recommend stratifying plot placement, with more plots placed on shallow slopes at low elevations. Evidence suggests that burrow density is influenced by several other habitat features, including soil depth, rock cover, and the presence of māhoe (Melicytus ramiflorus) and karamū (Coprosma macrocarpa) (Chapter 3, Whitehead et al. 2014). When fine-scale GIS data become available on offshore islands in New Zealand, these habitat strata could be considered as well. However, evidence also indicates that habitat use is less specific at higher burrow densities, so as colonies expand this stratification may be less relevant (Chapter 3).

Evidence suggests that seabird colony recovery may be mediated by density, where remnant clusters or colonies initially increase in density before birds expand into new habitat (Chapter 6; Kildaw et al. 2005). Thus, practitioners may want to consider: preliminary surveys to find remnant colonies; cluster sampling, where sampling is stratified according to density; and/or adaptive sampling, where sampling can be modified in a way that is still comparable as colonies expand (Morisson et al. 2001, Thompson 2002). I suggest sampling be stratified by density, and that plots placed in remnant colonies be monitored more often, especially ≤ 20 years after predator eradication (Pearson et al. 2013).

7.4.3 Using burrow density as indices of petrel abundance

Petrel burrows provide temporally and spatially stable indices of abundance (Rayner et al. 2007a, McKechnie et al. 2009). The most common technique to estimate numbers of breeding petrels has been to assume that each burrow represents a breeding pair, estimate burrow density in representative samples, and apply these estimates to measured areas of occupancy (Priddel et al. 2006, Scott et al. 2009). However, the implicit assumption that burrow abundance reflects bird abundance is often untested and could
generate variable estimates of population size between years (Sutherland and Dann 2012). Furthermore, burrow attrition rate is highly variable, where the rate of burrow persistence is related to substrate and vegetation and not necessarily abandonment or occupancy (Bancroft et al. 2005b). Results demonstrate that burrow density and bird abundance are positively related among islands (Fig. 7.5). However, there was considerable intra-island variation in bird abundance; suggesting that burrow density is more reliable for reflecting larger changes in abundance and may be of limited utility to detect small changes in petrel abundance over small time scales (Fig. 7.7).

The high spatial and temporal variation in burrow occupancy raises doubts of the ability of occupancy rate estimates to predict changes in population size (Fig. 7.6). Previous studies confirm high temporal variation of occupant density at individual monitoring sites and spatial variation among sites and islands (Ratcliffe et al. 2008, McKechnie et al. 2009). For petrels, breeding can be intermittent (Cubaynes et al. 2011) and highly asynchronous (Simons 1981, Warham 1990, Tavecchia et al. 2008) and breeding success is heterogeneous (Barbraud and Weimerskirch 2005), leading to considerable differences in population size estimates from raw occupancy data (Sutherland and Dann 2012). Long-term trends in population estimates, of primary interest in monitoring programmes, may thus be masked by the inter-annual variability of burrow occupancy.

Until the relationship between burrow occupancy, burrow density, and the abundance of birds is better understood for petrels in New Zealand, I do not recommend relying on either measure alone. Furthermore, I combined all species when comparing burrow density and occupancy. However, the abundance of each petrel species may have a different relationship with burrow density and population trends of less abundant species may be masked by changes in burrow density caused by more prevalent species (e.g. Pycroft’s petrels - small vulnerable populations versus grey-faced petrels - large stable populations; Birdlife International 2014). To resolve this relationship, I recommend that monitoring plots not only be stratified by habitat and density (see above), but also that a proportion of plots be set aside as references, to be monitored more frequently and thoroughly, especially in the early stages of a monitoring programme (Sutherland and Dann 2012).
7.4.4 Other considerations

I acknowledge that estimating a statistically sound sample size is only the first step in devising a successful monitoring programme. Indeed, the most significant limiting factor will be securing long-term funding, and subsequently optimising the monitoring strategy to the budget (Caughlan and Oakley 2001, Field et al. 2005). The most important aspect of a monitoring programme is an explicit and well-reasoned objective (Nichols and Williams 2006, Field et al. 2007). The initial objective was to examine changes in petrel abundance after predator removal; however, when other management objectives, such as declines resulting in IUCN red-listing were considered, sampling intensities changed. Monitoring objectives will naturally evolve as conditions change. Altering objectives without breaching the integrity of a monitoring plan can be facilitated by outlining potential changes before the initiation of the programme (Ringold et al. 1996). Furthermore, a well-developed partnership amongst seabird scientists, Māori kaitiaki (natural resource guardians), statisticians, resource managers, and community groups will be key to an enduring national monitoring strategy (Moller et al. 2004, Lindenmayer and Likens 2010). Finally, as technology continues to develop, lower cost indices of seabird abundances may arise and could eventually be incorporated into monitoring strategies. Already, new tools and concepts are being tested and applied, such as automated acoustic sensors (Buxton and Jones 2012b, Borker et al. in press), radar (Gauthreaux and Belser 2003, Zaugg et al. 2008), and complex modelling (Tavecchia et al. 2009, Gimenez et al. 2012); offering great promise for the future of burrow-nesting seabird monitoring.
Chapter 8  Synthesis and General Discussion

8.1 Testing a model of seabird recovery

Throughout this thesis, I build on an initial conceptual model of seabird colony growth, constructed by combining generic population models and metapopulation models (Chapter 2). I identified important predictor variables and used them to test which factors were driving seabird recovery and re-colonization on islands around New Zealand. Because seabirds are generally assumed to be philopatric, it is thought that dispersal is limited, and thus, that intrinsic factors drive population dynamics (Warham 1990, Milot et al. 2008). However, I found little evidence that intrinsic variables, such as age at first reproduction and time since eradication, were influencing recovery. Conversely, the most influential factors were extrinsic, including distance to a source population (i.e. metapopulation connectivity) and metapopulation status. Furthermore, I found a lack of colony recovery on islands with extremely small (<25 individuals) or extremely large (>1000 individuals) remnant colonies, suggesting that density-dependence is operating during colony expansion.

From there, I narrowed my focus to examine recovery of burrow-nesting petrel colonies at an island scale. I examined the effects of nesting habitat selection (Chapter 3), attraction to social cues (Chapter 4), and inter-specific interactions (Chapter 5) on colony recovery after Pacific rat (Rattus exulans) eradication, and further considered the role of density (Chapter 6). I found that selectivity of particular nesting habitat, social attraction, inter-specific facilitation, and colony expansion after rat eradication were mediated by positive and negative density-dependence (Fig. 8.1). Generally, the pattern of burrow density and distribution found on study islands provided support for the “ideal despotic Allee” model of petrel colony growth (Kildaw et al. 2005). This model proposes that growth is initially positively density-dependent; thus, after introduced predator eradication, persisting seabird colonies will be attractive (Danchin and Wagner 1997). However, as time passes and the number of recruits into remnant areas increases, established colonies may become crowded, and negative density dependence results in recruitment into
unoccupied and less favoured habitat (Fretwell 1972, Forbes and Kaiser 1994).

2 – Conceptual model of seabird population recovery
- Low probability of recovery on island with > 25 km to a source population, no other species of seabird breeding, very large or small remnant seabird colonies; and species with declining metapopulations

ACTIVELY ENHANCED RECOVERY
- Attraction to playback decreases with smaller nearby source populations
- Grey-faced petrel make ideal candidates for enhancement using vocalization playback

FACTORS AFFECTING PASSIVE RECOVERY
3 – Nest-habitat selection
- Petrels prefer deeper soil
- Nesting habitat may be less important with more time after eradication

5 – Inter-specific interactions
- Petrel species co-occur more than expected by chance, suggesting inter-specific facilitation
- Exclusion between species may increase with time after eradication

6 – Density dependence
- Colony expansion is both positively and negatively density dependent

7 – Effective monitoring of burrow-nesting seabirds
- 80 plots of 3 m radius measured annually on 15 islands will pick up changes in burrow density of interest to conservation managers
- Burrow abundance is positively related to bird abundance

Burrow-nesting seabird recovery after Pacific rat eradication from islands in northeastern New Zealand

Figure 8.1: Thesis flow chart, with the main findings from each chapter. Chapters within the grey box focus on burrow-nesting seabirds on islands off the north-eastern coast of New Zealand’s North Island. Chapters within the green box examine factors affecting passive colony recovery, while the orange box examines a potential method of actively enhancing colony recovery. Thesis results can feed back to improve the initial conceptual model of seabird recovery. The effects of nest-habitat selection, inter-specific interactions, and social attraction were mediated by density.
In Chapter 5, I explored how inter-specific interactions may affect the reassembly and ultimate structure of petrel communities after Pacific rat eradication. I found that, among islands, petrel species were more positively associated than expected by chance, suggesting that the presence of pre-existing colonies of one species could facilitate the recovery of other species (Mönkkönen et al. 1999). However, species became more negatively associated with increasing time since rat eradication. This highlights the intricacies of petrel community reassembly, in which disturbance can result in altered species combinations being exclusive rather than facilitative (Diamond 1975, Temperton et al. 2004). In these altered communities, some species may remain rare because they cannot withstand inter-specific competition, especially if the population of a dominant species continues to increase (Oro et al. 2009).

Due to the complexities of life history, ecology, and behaviour in burrow-nesting seabirds, many questions about recovery are still left unanswered. However, my hope is that this thesis represents a first attempt at modelling seabird recovery dynamics, can be improved upon as research progresses. As data from robust and consistent long-term monitoring projects (following suggestions in Chapter 7) become available, they can feed back into improving our understanding of population growth (Fig. 8.1).

### 8.2 Adaptive management of seabird recovery

Adaptive management (AM) is a structured, iterative process of management decision-making, which can guide the achievement of restoration goals in the face of uncertainty (Walters 1986). Because of the complexities of seabird population dynamics, even after outlining and testing a model of recovery, many questions still remain. In this sense, AM is an ideal framework for island restoration, in which predator eradications can be undertaken not only to protect vulnerable species, but also to learn about processes governing recovery (Holling 1978, Shea et al. 1998). Further understanding of recovery and re-assembly of a seabird community and island systems could then be used to inform future management decisions. Thus, this thesis can be considered as supplying the first steps of an AM process (Murray and Marmorek 2003, Williams 2011). The conceptual model in Chapter 2 synthesized existing knowledge about seabird population growth and
made predictions about recovery after predator eradication. Chapters 3-6 determined whether post-eradication outcomes matched those predicted. Finally, this chapter outlines how results can be used to adapt future island restoration plans. Furthermore, AM places explicit value on monitoring as a means of learning about management outcomes (Gibbs et al. 1999). Chapter 7 provides a monitoring strategy to evaluate changes in populations of burrow-nesting seabirds with enough power to track the response after predator eradication and thus feedback into the iterative AM loop (Fig. 8.1; Ringold et al. 1996, Lindenmayer and Likens 2010).

### 8.3 Management implications and recommendations

#### 8.3.1 Prioritizing seabird restoration techniques

Restoration following predator eradication can be passive, where populations are left to recover or re-colonize naturally (Scott et al. 2001) or active, where immigration is deliberately enhanced through techniques such as translocation or social attraction (Griffith et al. 1989, Kress 1998). Although active management techniques have been tested for many different species of seabird (Jones and Kress 2012), no scheme existed for prioritizing sites or species that would benefit most from active management after eradication. Considering the high costs and complex logistics associated with active seabird management, the allocation of financial resources to situations where the most benefit will accrue is of the utmost importance (Borker et al. in press, Spatz et al. in press).

This thesis indicated that the most important factor influencing recovery on New Zealand islands was distance to a source population, with little passive re-colonization or recovery on islands with no source population within 25 km. Recovery is further limited by low richness of sympatric species, highly altered habitat, very large or very small remnant colonies, and in species with declining metapopulations. On islands meeting the majority of these characteristics, active enhancement of seabird populations could be prioritized (Fig. 8.2).
I examined one method of active restoration: social attraction, using vocalization playbacks. For many seabird species, social cues provided by colonies are known to be highly attractive to individuals seeking a nest site (Kildaw et al. 2005). Conservation practitioners have used this affinity to establish colonies at unoccupied sites using artificial visual and auditory social cues, a technique termed ‘social attraction’ (Kress 1997, 1998, Ahlering et al. 2010). However, social attraction success rates have varied between sites and species (Jones and Kress 2012). I tested the most important factor affecting recovery – a nearby source population – (Chapter 2) as a possible source of variation in response to
vocalization playbacks. I found variation in response to playbacks among sites and species tested, where attraction to playback declined with decreasing density of nearby source populations. Thus, social attraction can represent a cost-effective alternative to other restoration approaches for some species (Fig. 8.2). However, to maximize its effectiveness, variation in response should be assessed before embarking on restoration initiatives.

8.3.2 Factors affecting burrow-nesting seabird colony expansion

By examining nest-site selection on islands at different stages of recovery after Pacific rat eradication, I found that birds showed less preference for specific nesting habitat with increasing time since rat eradication. This suggests that the strength of nest-habitat selection in burrow-nesting petrels may be influenced by density, with higher-quality nesting habitat being relatively more important in small recovering populations. Generally, a higher abundance of burrows and occupied burrows were observed in areas with deeper soil. More burrows were also found on steeper slopes facing prevailing winds, with māhoe *(Melicytus ramiflorus)* plants present, characteristics found to be important for other species of petrel on other islands (Schulz et al. 2005, Rayner et al. 2007b, Whitehead et al. 2014). Thus, when attempting to restore burrow-nesting seabird populations, these particular nesting habitat characteristics should be available, as colony expansion may be restricted by their presence or absence (Fig. 8.2).

Co-occurrence analyses of petrel communities among islands indicated that, on islands with more time since rat eradication, species were more negatively associated than by chance. Particular species pairs (e.g. grey-faced petrel *Pterodroma macroptera gouldi* and little shearwater *Puffinus assimilis* and grey-faced petrel and flesh-footed shearwater *Puffinus carneipes*; Chapter 5) had mutually exclusive distributions. This suggests that some species may exclude the recovery of others, especially if the population of a dominant species recovers more rapidly after predator eradication. Therefore, compatibility between remnant species must be established (Fig. 8.2) in order to ascertain whether certain species will passively recover and to understand the repercussions of actively encouraging the recovery of multiple species.
8.3.3 Monitoring burrow-nesting seabird populations

Throughout my thesis, when reviewing the seabird literature from around New Zealand, there was a conspicuous lack of post-eradication monitoring studies. Generally, any monitoring of seabirds around the archipelago lacked statistical rigour and repeatability. In spite of this, monitoring seabird population trends is essential for detecting changes in conservation status, initiating management interventions, or assessing the efficacy of restoration actions (Field et al. 2007, Sutherland and Dann 2014). For burrow-nesting seabirds, because these species are inconspicuous when nesting and often nocturnal at their remote breeding grounds, obtaining accurate population estimates are especially laborious and expensive. Thus, populations cannot be counted directly but must be estimated from derived parameters (Rodway and Lemon 2011).

Repeated counts of burrows or individuals within permanently-established monitoring plots have been used as a practical alternative to full-scale population surveys, providing an indication of population trends (Anker-Nilssen et al. 1996, Schumann et al. 2013). Using a power analysis, I found that monitoring 80 circular plots of 3-m-radius on 15 islands annually is sufficient to detect most changes in burrow-nesting seabird relative abundance relevant to conservation managers with 80% power. To detect changes in burrow density after predator eradication with 80% power, 70 (active management) or 150 (passive management) circular plots on 15 islands must be monitored every two years (Fig. 8.2). Because colony expansion seems to follow an ideal despotic Allee model (Chapter 6), plot placement should be stratified based on the location of remnant colonies. However, as global anthropogenic threats continue to alter seabird populations, conservation priorities and management objectives may change. Thus, I recommend that this sampling protocol act as a guide, to be set in an adaptive monitoring framework allowing for shifting future conditions (Lindenmayer et al. 2011).

8.3.4 Global context

Although this thesis was largely specific to seabirds in northern New Zealand, at its foundation is a comprehensive conceptual model of seabird recovery. Thus, while aspects
of the prioritization scheme and monitoring protocol presented in Fig. 8.2 are New Zealand species-specific, both can be used as a general framework for seabird management after eradication. For example, although sites with shallow soil and a lack of māhoe are less likely to promote recovery of procellariids in north-eastern New Zealand specifically, soil and vegetation properties are likely to influence colony expansion of a variety of burrow nesting species. Future directions

### 8.4 Future directions

#### 8.4.1 Metapopulation management

Behavioural characteristics such as site fidelity, natal philopatry, and conspecific attraction are thought to limit dispersal, and thus recovery and re-colonization, of colonial seabirds (Kildaw et al. 2005, Matthiopoulos et al. 2005, Oro et al. 2011). However, I found evidence that recovery of seabirds after introduced predator eradication in New Zealand is at least partly influenced by immigration. Although procellariiforms are commonly assumed to be philopatric, the ecological and evolutionary mechanisms underlying dispersal decisions are not well understood (Warham 1990, 1996). However, teasing apart the relative importance of metapopulation connectivity as opposed to intrinsic growth is crucial if we are to understand how colonies are formed and how they grow (Oro and Ruxton 2001, Oro 2003). Understanding the ecological processes controlling dispersal among seabird colonies can inform metapopulation-, rather than island-scale management.

#### 8.4.2 Seabird recovery and island restoration

Because of the importance of seabird population expansion for the recovery of island ecosystem functioning (Jones 2010b, Jones 2010a), a question that naturally follows from my thesis is: how do increases in burrow density translate into increases in nutrients and subsequent ecosystem reassembly? Seabirds affect entire island food webs and it remains to be seen how these complex networks of interacting species will reassemble as seabird abundance increases (Polis and Hurd 1995, Polis et al. 1997). Degraded systems
often do not respond predictably to restoration and can be resilient to restoration actions (Suding et al. 2004). Thus, applying successional recovery pathway models to the processes of seabird colony expansion and island ecosystem reassembly can help identify thresholds or tipping points separating degraded islands from ‘seabird islands’ (Hobbs and Norton 2004). In this way, management interventions required to return an island to a less degraded state may be identified (Hobbs and Norton 1996).

8.4.3 Seabird restoration and monitoring in a changing climate

Introduced predators are only one of the many threats facing seabird populations (Croxall et al. 2012). Currently, one of the most pervasive sources of mortality of procellariiform seabirds is incidental bycatch during fishing activities (Anderson et al. 2011). Because procellariiformes are k-selected, the removal of juvenile and adult birds as bycatch has profound impacts on population dynamics (Hunter et al. 2000, Furness et al. 2012). Insidious compounding threats, such as anthropogenic climate change, plastic pollution, oil spills, heavy metals, and radioactive material cause further concern for the status of the world’s seabirds (Elliott et al. 1992, Burger 1993, Laist 1997, Votier et al. 2008, Bond and Lavers in press). As anthropogenic threats continue to increase, restoration techniques will be vital for mitigating sizeable seabird population declines (Pascoe et al. 2011). Given the likelihood that populations will continue to decline, and that human-induced population crashes may become more frequent, monitoring recovery and understanding the factors that affect recovery is of the utmost importance (Gårdmark et al. 2003, Jenouvrier et al. 2009).

8.5 Conclusions

Since its inception as a discipline in conservation biology 60 years ago, island restoration has reached a turning point. It has gone from a field that was dominated by refining methods of removing non-native predators, to one where the recovery of island ecosystems and wildlife can be observed or encouraged. With over 800 islands around the
world free of introduced predators, we can begin to examine community reassembly, and potentially manage this process to accelerate and maximize recovery.

Here I used introduced predator eradications as a natural experiment to examine the recovery dynamics of a pivotal faunal group, burrow-nesting seabirds. I showed that, despite the tenet that seabirds are strictly philopatric, population recovery is influenced heavily by dispersal. Furthermore, colony expansion was affected by positive density-dependence at small population sizes, and negative density-dependence as populations grew. This suggests that remnant colonies of a certain size should recover passively after eradication, but competition will ultimately slow recovery or force colonies to expand into unoccupied habitat. Thus, nesting burrows can expand naturally in both density and spatial extent after predator eradication. Because burrowing activity enhances soil aeration and soil formation, this pattern of recovery could initiate the recovery of ecosystem functioning. At sites where recovery is not occurring naturally, I demonstrated that recruitment could be encouraged using vocalization playbacks.

Understanding the relationship between petrel colony recovery and the recovery of island food webs could better resolve the process of island ecosystem reassembly. By studying this further, it may be possible to enhance the recovery of certain seabird species as a means of stimulating the recovery of entire island ecosystem structure and function.
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