Mercury Islands and their role in understanding seabird island restoration

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Abstract: The progressive removal of invasive mammals from the Mercury Islands has led to over 25 years of field study designed to test the processes of restoration and natural recovery of these seabird-driven island ecosystems. Resulting from this work, four key restoration questions can now be identified as fundamental to designing island restoration programmes. The questions are: what is the regional context of the island (biogeography); how does each island ecosystem operate (ecosystem function); how have invasive species changed the ecosystem (response effects); and how can progress towards a restoration goal be defined (outcome measures)? Examples of how these questions influenced restoration in the Mercury Islands are provided with Korapuki Island as a case study. However, unpredicted and subtle responses can eventuate. In the Mercury Islands these included a hitherto unknown honeydew parasite-bird-gecko food web and subtle effects of rats on plant regeneration. Promising outcome measures of restoration progress are now being developed, including indices of marine influence using stable isotopes of nitrogen and the use of network analysis to analyse the composition of invertebrate food webs.

Keywords: biogeography; species area; colonisation; ecosystem function; eradication; reference sites; Korapuki Island; unknown consequences; New Zealand

Introduction

Islands are not only repositories of disproportionately high numbers of endemic species (e.g. Keitt et al. 2011; Tershy et al. 2015), they have frequently become refugia against the spread of invasive species and habitat loss (Daugherty et al. 1990). For example, although New Zealand has the world's largest number of endemic species of seabirds, the country also has the largest number of threatened seabirds, with most species now confined to offshore islands following the spread of invasive species (Croxall et al. 2012). Only 20 years ago, Duffy (1994) lamented that island ecosystems were becoming so modified, most were unrecognisable. Selected invasive mammals have periodically been eradicated from islands for about 100 years (Bellingham et al. 2010a). However, the eradication of the most pervasive group, introduced rodents (Atkinson 1985; Towns et al. 2011), only became effective and widely applied at the time Duffy was despairing for the future. Today, rodent eradications have been attempted globally on at least 500 islands (Russell & Holmes 2015), with the largest number for a single country conducted in New Zealand (Howald et al. 2007; Keitt et al. 2011). The frequency of eradications in New Zealand began to rapidly increase between 1980 and 1990 (Towns et al. 2013), meaning that the potential to learn from the responses of island ecosystems to comprehensive pest removal covers only 30 years. Attempts to restore islands following eradications of rodents have an even shorter history. Here we review 28 years of restoration activity in the Mercury Islands off northeastern New Zealand. Work in the Mercury Islands developed out of two questions posed in the mid-1980s: can rats be eradicated systematically

from islands (Towns 1988), and if they can, is it possible to restore entire ecosystems previously modified by introduced mammals (e.g. Towns et al. 1990; Towns & Atkinson 1991; Towns et al. 1997)?

The developmental history of eradication technology in the context of the Mercury Islands (Towns & Broome 2003) and a summary of achievements that have stemmed from these activities have already been reviewed (Bellingham et al. 2010a; Towns et al. 2013). Instead, we focus on the question of whether entire ecosystems can be restored, since this is often the goal of invasive species eradications (Towns et al. 1990); a goal that may be particularly challenging for island ecosystems penetrated by invasive species (Norton 2009). The first of the Mercury Islands to be cleared of all invasive mammals was Korapuki (Towns & Broome 2003) and an ecological restoration plan for the island was completed 10 years ago (Towns & Atkinson 2004). Here we examine how implementing the Korapuki plan has contributed to the conceptual understanding of island restoration. We aim in particular to address a problem for seabird island ecosystems raised by Duffy (1994): "We cannot put the Humpty Dumpty of an ecosystem back together because we don't know what the original Humpty looked like, nor do we have all the pieces."

This review aims to address the technical issues raised through Duffy's "Humpty Dumpty" problem by using restoration of seabird island ecosystems in the Mercury Islands as a working example. We focus on four key subsidiary questions that are fundamental to understanding the composition and function of island ecosystems: 1) what is the regional context of the island (biogeography); 2) how does each island ecosystem operate (ecosystem function);

3) how did invasive species change the ecosystem and what effects will their eradication have (response effects); and 4) how can progress towards a restoration goal be defined (outcome measures)? The first two questions help to provide the context within which restoration targets can be set, whereas the second two address the progression of an island towards a target and are more site-based. We demonstrate the relevance of context and site-based approaches by using Korapuki Island as a case study.

Biogeography

Study area

The seven Mercury Islands (36.62S; 175.86E) form the largest of four archipelagos from which mammals have been eradicated in their namesake Mercury Islands Ecological District (MIED). The MIED is a biogeographic grouping based on shared geological and biological characteristics (McEwen 1987) and extends from Cuvier Island (36.43S; 175.77E) in the north through to the Aldermen Islands (36.97S; 176.08E) in the south. Cuvier, all Mercury Islands except Great Mercury and the Aldermen are classed as Nature Reserves under the Reserves Act 1977. These are the most highly protected reserves under New Zealand legislation, with access by permit only. Across the MIED, the range of invasive mammals present has included (Atkinson & Taylor 1992): goats (*Capra hircus*), cats (*Felis catus*), ship rats (*Rattus rattus*) and kiore (*R. exulans*) on Great Mercury; goats, cats and kiore on Cuvier; rabbits (*Oryctolagus cuniculus*), kiore and mice (*Mus musculus*) on Ohinau; rabbits and kiore on Stanley and Korapuki; and kiore alone on Double, Red Mercury, and Middle Chain (Supplementary Data). Like most offshore islands, all of the islands in MIED have at some time been modified through burning (Atkinson 2004; Bellingham et al. 2010a).

Two biogeographic concepts discussed below assist with understanding how history influences the way we view restoration of the islands in this district.

Vicariance

The biotic composition of islands in the MIED is largely a function of island origin (e.g. Towns 1994, 2002b; Towns et al. 1997), notably isolation due to sea level rise following the last glaciations (e.g. Hayward 1986). Oceanic islands far from the main islands of New Zealand, such as the Kermadecs (30.37S; 178.48W), were never connected to larger land masses and are colonised by chance, resulting in genetic drift and high levels of endemism of those species that survive (e.g. Carlquist 1965).

In contrast, islands such as those in MIED are within 20 km of the coast (i.e. on the continental shelf) of New Zealand and were part of the mainland during the last glaciation. As sea levels rose, the newly formed islands contained gradually constrained subsets of mainland terrestrial communities. Populations in these subsets were derived from genetically diverse gene pools, so drift was much less likely and thus endemism is relatively uncommon. Furthermore, these islands support many terrestrial species unable to disperse over water, including a great diversity of flightless invertebrates as well as terrestrial reptiles (Daugherty et al. 1990). Bathymetric analyses within MIED indicate that by about 8 000 years ago, Cuvier and the Aldermen had already been separated from the mainland for at least 4 000 years, but the Mercury and Ohinau Islands had only recently lost their dry land connection to the peninsula (Figure 1). At that point, the Mercury archipelago had not formed, but was an extended "Great Mercury super-island". The concept of vicariance applies here: present disjunctive distributions reflecting the fragmentation of contiguous populations by rising sea levels as a geographic barrier (Wiley 1988). Thus, species today confined to individual islands likely once inhabited the whole Great Mercury super-island.
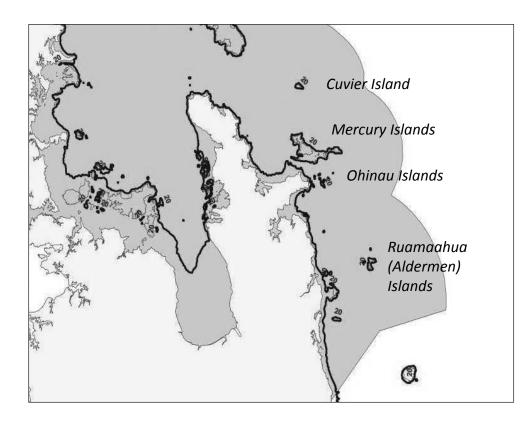

Figure 1. Coastlines around the Coromandel Peninsula at about 8 000 years ago based on the 20 m isobaths (shaded areas are sites within Hauraki Gulf Marine Park) showing four main archipelagos in Mercury Islands Ecological District.

Past connections to the mainland and inclusion within the same ecological district might imply wide application of a variance model. However, the relationship between biota of the Mercury archipelago and others in MIED is not particularly clear. For example, two species of skinks, *Oligosoma whitakeri* and *O. alani,* are present on mammal-free islands in the Mercury Islands but absent from mammal-free islands in the Aldermen. However, a related species, *O. oliveri* is present in both archipelagos (Pickard & Towns 1988). Likewise, the tusked wētā (*Motuweta isolata*), although present in the Mercury Islands, is absent from mammal-free islands in the Aldermen. Subtle differences such as these may reflect differences in isolation history. These differences suggest that for poorly dispersed groups such as flightless invertebrates and reptiles, there has been less unity of distribution than is implied by the vicariance model. Consequently, if high ecological integrity is the restoration goal (see below), the most defensible approach may be to focus within archipelagos; acknowledging that the greatest risk of errors for assumptions about community composition would likely arise from extrapolations between them.

Species-area relationships

A fundamental principle of island biogeography is that, aside from some exceptions, the number of species usually increases in proportion to area (McArthur & Wilson 1967). For example, Whitaker (1978) used this relationship to predict the expected species diversity of reptiles on islands with and without introduced rodents. Although the species-area relationship holds for islands without invasive mammals (e.g. Borrelle et al. 2015), the reverse can develop on islands with invasive vertebrates. As a result, the smallest Mercury Islands, which have not been invaded by mammals, now have more reptile species than larger ones invaded by kiore and rabbits. A similar relationship in response to predation pressure is likely to hold for the large flightless invertebrates.

Species-area relationships are useful because they provide an empirical measure of the proportional reduction of assemblages in the presence of introduced mammals, as well as a basis for predicting the composition of restored assemblages. For example, islands with invasive mammals in the MIED had a 50% reduction in reptile fauna and 75% reduction in wētā fauna (e.g. Towns et al. 1997), which thereby suggests the level of species restoration required for each group.

Ecosystem function

Without detailed understanding of how island ecosystems function when invasive species are absent, it may be difficult to determine how restoration efforts should proceed on islands where invasive species have been present. This understanding can be greatly assisted through the use of reference sites (White & Walker 1997), which are model sites or islands used in order to predict the trajectory or endpoint of an impaired ecosystem after restoration interventions (e.g. Balaguer et al. 2014). Although such sites help with understanding ecosystem function, they do not necessarily indicate the capacity for natural dispersal into previously modified sites. As we discuss below, dispersal ability of some species (particularly plants) often relies on a vertebrate dispersal agent.

Reference sites

Within the MIED, six small islands (3-30 ha) that have never been invaded by introduced mammals can be used as reference sites for restoration of the eight islands (18-1872 ha) from which invasive species have been or are being removed. Five of these reference islands have high seabird abundance and extreme surface fragility due to burrowing by birds. On the larger reference islands (>2 ha), in addition to seabirds, there are dense and diverse reptile populations and numerous species of flightless invertebrates, including wētā, gastropods and spiders (Towns et al. 2009; Bellingham et al. 2010a). These sites indicate the structure and function of seabird driven island ecosystems of different sizes before mammalian predator invasion in the MIED.

Additional reference information can be obtained from invaded islands larger than the uninvaded reference sites. Given their greater area, such islands can have a higher species diversity of plants, which is helpful in identifying species particularly sensitive to browsing (see below). Such sites may only provide fragmentary information, but they extend information available about the composition of local communities as part of an "ecological memory" (*sensu* Balaguer et al. 2014).

Recolonisation potential

When introduced species are removed, many species can return and recover unaided. This recovery is particularly likely for most species of plants, as long as dispersal mechanisms are available and/or local populations remain. For many plants, dispersal is through birds such as kererū or fruit pigeons (*Hemiphaga novaeseelandiae*), which on these islands are the only species capable of long distance seed dispersal of plants with large fruit including kohekohe (*Dysoxylum spectabile*), taraire (*Beilschmedia tarairi*) and tawāpou (*Pouteria costata*; Table 1). Other forms of distribution are less conventional. For example, the seed pods of *Pisonia* are extremely adhesive, potentially as a means of spread between locations by relatively large seabirds, which would explain the wide distribution of the genus throughout the Pacific (e.g. Burger 2005). Given that most islands in the MIED are now free of introduced mammals, it may be possible for natural dispersal through wind and birds to facilitate dispersal of plants.

Despite impressive flight mobility, seabirds still face some barriers to natural dispersal. Studies of seabird colonies have often indicated high philopatry, with birds behaviourally tied to their original birthplace (Warham 1996). A review of colonisation ability of seabirds around New Zealand found more capacity to colonise new islands than had previously been assumed (Buxton et al. 2014). However, frequency of colonisation declined rapidly with distance from source islands, and natural colonisation by most species became unlikely when source populations were >25 km away. Ellipses based on the 25 km radius around uninvaded, densely populated islands in MIED indicate that Mercury, Ohinau and Aldermen archipelagos are all within a 20 km radius (Figure 2). However, Cuvier is between 20 and 25 km from the nearest large uninvaded islands, and still has only been recolonised naturally by three species of Procellariiformes: grey-faced petrel (*Pterodroma macoptera*), fluttering shearwater (*Puffinus gavia*) and diving petrel (*Pelecanoides urinatrix*) (Borrelle et al. 2015).

Table 1. Native species of plants suppressed by kiore as determined from responses of resident species to rodent eradications (from Atkinson 1964; Towns et al. 1997; Campbell & Atkinson 1999, 2002), with canopy species marked*
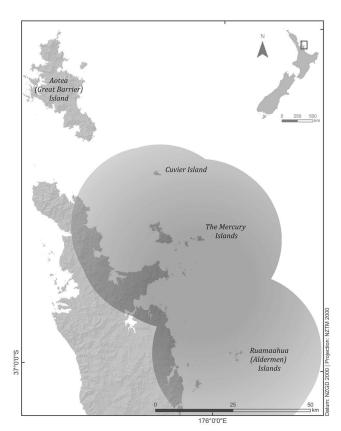
Species	Study site (s)	Status on reference sites
Kohekohe *Dysoxylum spectabile**	Double, Cuvier, Red Mercury	Locally dominant canopy species on larger islands, rare on Middle, unknown from Green
Parapara *Pisonia brunoniana*	Cuvier, Double, Middle Chain	Subcanopy species capable of forming dense thickets but absent from Middle and Green
Karo *Pittosporum crassifolium*	Double, Red Mercury, Middle Chain	Widespread and common small tree in coastal areas on Middle and Green
Tawapou *Pouteria costata**	Double, Red Mercury, Middle Chain	Often scattered on larger islands but rare on smaller seabird islands such as Middle
Karamu *Coprosma macrocarpa*	Double, Red Mercury	Widespread and common small tree; now widespread on most islands
Taupata *C. repens*	Red Mercury	Coastal shrub now common in coastal areas on all islands
Coastal maire *Nestigis apetala**	Cuvier	Coastal tree absent from Mercury Islands
Nikau *Rhopalostylus sapida*	Cuvier	Palm, which can be locally abundant but absent from Mercury Islands
Houpara *Pseudopanax lessonii*	Double, Cuvier, Middle Chain	Shrub or small tree widespread on Mercury Islands
Milktree *Streblus banksii**	Middle Chain	Small tree with extensive areas as canopy on Middle Island and spreading on Stanley
Hymenanthera *Melicytus novae-zelandiae*	Red Mercury	Shrub widespread in coastal areas on Middle

Figure 2. Potential seabird recolonisation ellipses based on 25 km ranges from uninvaded source islands within the Mercury Islands Ecological District.

Effects of invasive species on ecosystem function

Occasionally the effects of invasion are so extreme they are even visible to offshore observers. Examples include extensive vegetation modification and soil loss following decades of browsing by goats (*Capra hircus*) or rabbits (e.g. Merton 1987; Bellingham et al. 2010b). More often the effects are subtle, but even when the invasive species are rodents (e.g. Towns et al. 2006) or ants (e.g. O'Dowd et al. 2003), they can still produce catastrophic changes to ecosystem function.

Studies in New Zealand of the distribution of tuatara (*Sphenodon punctatus*), lizards, invertebrates and plants compared with kiore over a large sample of islands indicate that some species populations are either heavily suppressed by these rats or incompatible with them (Whitaker 1978; Watt 1986; Atkinson 1986; Campbell & Atkinson 1999). A similar comparative approach was used to determine the effects of suppressed seabird populations on island ecosystem function. Nine islands in northern New Zealand (including four in the MIED) with large populations of burrowing seabirds were compared with nine where seabirds were suppressed by introduced rats. On islands with few seabirds, soils had 47% less total C, 45% less total N, 53% less total P and 23% lower marine-derived δ^{15}N than on uninvaded islands (Fukami et al. 2006). Furthermore, on islands with few seabirds, 11 orders of leaf-litter and soil-inhabiting invertebrates were less abundant, foliar and litter N concentrations in several plant species were lower, and litter decomposition rates were slower than on un-invaded islands with large seabird colonies (Towns et al. 2009; Wardle et al. 2009). These studies demonstrate the diverse and subtle effects of seabirds on island ecosystems, and conversely, the extent to which the systems can change when mammalian predators invade. Such studies do not demonstrate cause and effect between mammal invasion and shifts in ecosystem function. They do however, provide a powerful basis for developing hypotheses and conceptual models, which can then be tested experimentally (Veltman 1996; Towns et al. 2009).

Three inferences relevant to islands restoration stem from the above observations. First, introduced species likely have direct negative effects on resident species assemblages. Decades after eradication, the legacy of some invasive mammals, such as kiore, remain on islands, as has been demonstrated by the absence of selected species of seabirds, plants, invertebrates and lizards (Towns 2009). Second, through activities such as burrowing and defecation, seabirds are likely to be one of the most powerful biotic drivers of islands ecosystems around New Zealand (Mulder & Keall 2001) and elsewhere (Mulder et al. 2011). Finally, when invasive species suppress seabird abundance, ecosystem functions engineered by seabirds are suppressed, resulting in a wide range of indirect effects (e.g. Towns & Atkinson 2004; Russell 2011).

Effects of eradicating invasive species

Four sources of information can help us predict the response of native species and ecosystems to the removal of invasive species from islands: 1) studies of the responses of plants and animals after eradication; 2) the use of reference sites that lack invasive species as defined above; 3) using chronosequences of islands from which invasive species have been removed (e.g. Buxton et al. 2016); and 4) paleoecological studies of plant and animal remains in middens, caves, sand-dunes and wetlands (e.g. Towns & Ballantine 1993; Wilmshurst et al. 2014). Direct response studies are most valuable on those islands where a single invasive species was introduced then removed, which avoids complications caused by interactions between invasive species (Towns 2011). An example is provided by tuatara, a species which managed to co-exist with kiore on several islands. In MIED, tuatara were reduced to such low numbers (<20) on kiore invaded islands, their responses to eradication were un-measureable over short timeframes. However, larger numbers of tuatara survived in the presence of kiore in the Marotere Islands, where despite variation between islands, comparisons of recruitment rates of juvenile tuatara before and after kiore eradication demonstrated significant demographic shifts in tuatara populations. Potential competitive effects between kiore and adult tuatara were also revealed by changes in body condition (Towns et al. 2007). Similar comparisons between islands in MIED, using uninvaded islands and those still with kiore, indicated that kiore suppressed 11 of the 17 species of plants studied (Table 1) and that forest composition on the invaded islands had likely been significantly altered (Campbell & Atkinson 2002).

Some apparently extirpated species have reappeared many years after eradications on islands were completed. For example, five populations of geckos and four populations of skinks have reappeared on islands around New Zealand cleared of invasive mammals. One species of gecko, *Dactylocnemis pacificus*, reappeared on at least two the Marotere Islands less than 10 years after the removal of kiore, but the same species has still not been found on any of the Mercury Island Nature Reserves previously inhabited by invasive mammals despite >20 years of monitoring (D. Towns unpublished data).

Restoration goals

All restoration projects require a goal or target (Atkinson 1988). This in itself can be problematic if there is little clarity about what the system previously looked like (Duffy 1994) and since reference sites usually change with time (Simberloff 1990). There are two approaches to defining restoration goals: time or function. A goal could be based on a previous time, such as before the arrival of invasive species, which requires the identification of historic benchmarks (e.g. Atkinson 1988). An alternative is to use ecosystem function as a goal, which does not require the historic reference point, but does require understanding of how key components of ecosystems interact. Such an approach is also greatly assisted if reference sites are available. Now that there is considerable evidence about the engineering role of seabirds (e.g. Mulder et al. 2011), seabird driven island ecosystems as a goal would be a logical option for many islands. This then raises the question of whether intervention is needed.

If the goal is to restore seabird-driven ecosystems, three pieces of evidence suggest that no further manipulation may be required after eradication at many locations (Buxton 2014). First, Jones (2010) analysed marine-derived nitrogen ($\delta^{13}N$) in soils, plants and spiders (as predatory invertebrates) across islands at different stages of recovery after eradication of mammals. She found increasing evidence of a marine seabird-derived signature with time since mammal eradication and predicted that ecosystems with seabird-driven attributes can recover in a few decades. Second, Buxton et al. (2014) found that the rate of seabird recovery on some islands is higher than might be predicted from the breeding success of residents. They found evidence that existing burrowing seabird colonies attract immigrants, which can be conspecifics, but may also be other species. Finally, where suitable habitat is available, and the density of potential source colonies is sufficient, sites can be identified where natural recovery is most likely (Buxton 2014). In MIED, natural seabird recolonisation potential is high in all archipelagos except Cuvier (Figure 2) (Borrelle et al. 2015).

Given that introduced mammals can extirpate a range of species from within these systems (Table 2), a second option is to extend the functional goal of seabird driven ecosystems to include reintroducing species unable to naturally recolonise. For example, since the above biogeographic analyses support an argument for vicariance within the Mercury islands, restoration could aim to restore seabird-driven ecosystems with community composition typical of the Mercury Islands archipelago. The case study outlined below acknowledges the capacity for natural recovery of seabird populations but also the inability of some species of reptile and invertebrate to re-colonize. For other species, such as the tree wēta (*Hemideina thoracica*) and some species of plants, an overlay of data from reference sites combined with knowledge of the effects of invasive species within the archipelago informed the extended restoration goal.

When is the restoration process complete?

The question of when a restoration project has reached a pre-defined target is of particular interest to conservation managers. The range of unpredictable outcomes and uncertainties involved with island restoration are so numerous that predicting an endpoint for such an exercise is complex and could involve timescales beyond the life span of a researcher. For example, the time to reach carrying capacity for Whitaker's skinks (*Oligosoma whitakeri*) reintroduced to Korapuki Island was estimated as at least 140 years (Miller 2009). On other islands in the archipelago, such as Red Mercury Island, which is over ten times larger than Korapuki, the recovery of reintroduced populations of the same species will inevitably take even longer.

The criteria for successful restoration through

Table 2. Status of species of flightless invertebrates and reptiles present on mammal-free Mercury islands but absent from Korapuki Island before removal of introduced mammals and identified as candidates for reintroduction by Towns & Atkinson (2004)

Name	Ecological role	Reintroduction status	Tolerance of invasive predators
Gastropoda *Rhytida greenwoodi*	Predator of gastropods and earthworms	Still to be reintroduced; known only from Green Island	Does not co-exist with kiore on any Mercury Islands, but occasionally does so elsewhere
Arachnida *Cambridgea mercurialis*	Nocturnal predator	Still to be reintroduced; common in seabird burrows on Middle and Green Islands	No data; does not seem to balloon so may have limited dispersal capabilities (M Fitzgerald pers. comm.)
Orthoptera (Stenopelmatidae) *Hemideina thoracica*	Folivore	52 from Double Island (1997) now widespread and abundant (Green 2005)	Co-exists with kiore on some Mercury Islands but not others
Hemiandrus pallitarsus	Predator of invertebrates	Still to be reintroduced; present on Middle and Red Mercury	Co-exists with kiore on some Mercury Islands but not others
Motuweta isolata	Predator of invertebrates	100 captive reared originally from Middle Island (2007) now locally abundant (unpublished report, Department of Conservation)	Does not co-exist with kiore
Coleoptera (Tenebrionidae) *Mimopeus opaculus*	Algal/fungal grazer	100 from Middle Island (2000-2002) now locally abundant (C. Green pers. comm.)	Rarely co-exists with kiore; absent from other Mercury Islands invaded by kiore
Reptilia (Sphenodontidae) *Sphenodon punctatus*	Apex terrestrial predator of invertebrates, lizards and small seabirds	Still to be reintroduced; dense populations on Middle and Green, relict on Stanley and Red	Coexists with kiore on some other Mercury Islands, but with consistent recruitment failure
(Gekkonidae) *Dactylocnemis pacificus*	Omnivore, nectar, fruit and invertebrates	Still to be reintroduced; common in forested areas on Middle	Does not co-exist with kiore in Mercury Islands but does in other archipelagos
(Scincidae) *Oligosoma alani*	Predator of invertebrates and smaller lizards	14 reintroduced (1992-93) from Green; widely dispersed and locally abundant	Does not co-exist with kiore on any islands
Oligosoma oliveri	Predator of invertebrates	25 reintroduced (1992-93) from Green; breeding	Does not co-exist with kiore on any islands
Oligosoma suteri	Intertidal predator of invertebrates	30 reintroduced 1992 from Green; locally abundant	Can co-exist with kiore on islands with appropriate boulder refuges
Oligosoma whitakeri	Predator of invertebrates	28 reintroduced 1988 from Middle; expanding range and locally abundant	Does not co-exist with any mammalian predators on islands

reintroductions are relatively clear (e.g. Towns & Ferreira 2001), and include complete replacement of the release propagule with locally born offspring (Wolf et al. 1996). For some invertebrates, high reproductive output and rapid turnover means that such criteria may be achieved in <10 years. However, for species such as tuatara, adult life spans of up to 100 years mean that monitoring population replacement will require generations of biologists. In contrast to intervention through reintroductions, passive recovery is undirected and process driven. Nonetheless, passive recovery requires monitoring to assess whether hypotheses about ecosystem development are being met. If success is based on changes in ecosystem function, rather than assemblage composition, progress can be estimated in relatively short time scales (Tables 3 and 4). Measures of the recovery of seabird driven ecosystems can include simple measures of burrow density coupled with additional measures of seabird effects. The study of uninvaded islands and those

with seabirds suppressed by invasive mammals (e.g. Fukami et al. 2006; Towns et al. 2009) indicated that soil pH strongly reflects seabird activity. Similarly the measures of C:N and $\delta^{15}N$ used by Jones (2010) indicate the rate at which seabird effects can be measured. Analyses of food webs on islands with and without procellariiform seabirds indicate the likely responses of ecosystem processes to predator removal if these seabirds recover (Figure 4). Present indications from work on Korapuki Island are that islands within the colonisation range of seabirds could demonstrate many of the functional attributes typical of uninvaded seabird islands within 50 years. More sophisticated investigations of invertebrate community and food web structure should contribute to methods for verifying these functional changes (e.g. Orwin et al. in press).

Restoration case study: Korapuki Island

Korapuki was the first island in the Mercury archipelago from which all introduced mammals were removed (kiore in 1986, rabbits in 1987), has been the site where the conceptual and practical impediments to restoration have been tested, and is also the only island in the group with a comprehensive restoration plan (Towns & Atkinson 2004). The restoration target initially proposed for Korapuki Island by Towns et al. (1990) was for a seabird-reptile-invertebrate-plant system similar to that of Middle and Green Islands. The subsequent restoration plan expanded on this target by emphasizing features of the Middle and Green reference sites, including coexistence of very dense populations of small seabirds (particularly diving petrels) with a high diversity of reptiles and many invertebrate species (Towns & Atkinson 2004). For extirpated species such as tuatara, five species of lizards and many species of flightless invertebrates, natural recovery is unlikely (Towns 2002b). The restoration plan thus recommends re-introduction of those species likely to have been lost through the action of habitat modification (fire) combined with the previous presence of kiore and rabbits (Table 3). For the purposes of this review, we focus on changes to the biota of Korapuki Island since the removal of mammals in 1986-87 (Tables 2 and 4), restoration activities implemented (Table 3), predicted and unpredicted outcomes, and the many remaining uncertainties in the recovery trajectory of the island (Table 4).
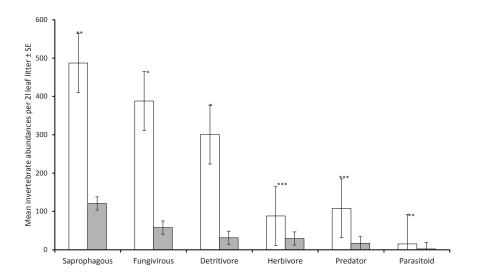
Predicted outcomes

In order to develop hypotheses for the recovery of Korapuki Island after the removal of kiore and rabbits, Towns & Atkinson (2004) constructed conceptual interaction webs. The webs were based on structure of the reference ecosystems of Green and Middle Islands and responses elsewhere in the archipelago to mammal eradications. However, it was not possible at that time to define when various predicted interactions would eventuate, nor were criteria identified as measures of success. Central to the 2004 model was an increasing influence from seabirds adding nutrients to the island's soils, and an increasing density of seabird burrows, which are used as habitat by tuatara and some species of lizards. The speed at which burrow-nesting seabird populations recover was assumed to rest on three aspects of the biology of Procellariiformes: extreme philopatry; low annual reproductive output; and slow development to reproductive maturity (e.g. Warham 1996). In combination with slow population growth by introduced species of reptiles (e.g. Towns 1994), reactivation of the proposed interaction web was assumed to involve timescales of decades or perhaps centuries.

Figure 3. Frequency of forest bird encounters (presence/absence of calls and sightings) at 20 five-minute observation points at 50 m intervals along axial ridges on Korapuki Island in December 2007.

Figure 4. Relative abundance of litter invertebrates from different trophic levels on nine northeastern New Zealand islands invaded by rats and with few seabirds compared with nine islands in the same geographic area never invaded by introduced mammals (for methods and study sites see Towns et al. 2009); Mann-Whitney U Tests were used to compare means with p values identified as * $p<0.05$, ** $p<0.005$, *** $p<0.0005$.

Table 3. Changes to biota of Korapuki Island following the removal of kiore and rabbits.

Species or taxonomic group	Before mammal removal	At least 20 years after mammal removal
Plants	Flora of 96 species (Hicks et al. 1975), with 74% native	Flora of 115 species with 79% native immediately after kiore and rabbit removal (1988); 128 species with 81% native by 2002 (Towns & Atkinson 2004)
Selected woody plants sensitive to kiore	Restricted to <10 known individuals or previously listed as uncommon (a few at one or two locations): *Coprosma repens*; *Corynocarpus laevigatus*; *Melycitus novaezealandiae*; *Myoporum laetum*; *Pouteria costata*; *Streblus banksii* (Hicks et al. 1975)	All species except *C. laevigatus* (spreading but <10 individuals) now present throughout island; *P. costata* with > 80 young plants in some areas (Towns et al. 1997; Towns & Atkinson 2004)
Invertebrates	Few large invertebrates (beetles and millipedes) > 10 mm seen; no other data (Hicks et al. 1975)	Reappearance of three species of native cockroaches, small wētā *Neonetus*? sp. large centipede *Cormocephalus rubriceps* (Towns et al. 1997) and honeydew scale *Coelostomidium zealandica* (Towns 2002b); identification of 24 species of terrestrial molluscs (includes one exotic species of slug) and 70 species of spiders (Towns & Atkinson 2004)
Reptiles	Five species of lizards recorded but only four of these seen by Hicks et al. (1975): *Oligosoma aenea*, not seen; *Woodworthia maculata* and *Hoplodactylus duvaucelii* <10 seen; *O. smithi* and *O. moco*, regarded as common	*O. aenea* trapped in all forest habitats by 1999 (D Towns unpublished data); demographic shifts and habitat changes recorded for *O. smithi* (Towns 1991) and *H. duvacellii* (Towns 1996); increased capture frequencies of all five species (Monks et al. 2014); sighting frequencies of *W. maculata* on coast exceeded Middle Island within 15 years of mammal eradication (Towns 2002b)
Seabirds	Eight species listed, seven of which recorded by Hicks et al. (1975): *Eudyptula minor*, throughout; *Puffinus carneipes*, few seen; *P. griseus*, four seen; *P. gavia*, second-most abundant, <19/ha; *P. assimilis*, scattered burrows <6.8/ha; *Pterodroma macroptera*, most common species <36/ha, 600-700 pairs total; *Pelecanoides urinatrix*, scattered, one site ca 30/ha	*Phalacrocorax varius* observed by Hicks et al. (1975) in coastal waters, but now breeding in pōhutukawa on SW coast
Native land birds	Eleven species of native birds and four exotic species recorded by Hicks et al. (1975), with native species classed as abundant: *Cyanoramphus novaeseelandiae*, *Rhipudura fuliginosa*, *Gerygone igata* and *Zosterops lateralis*. Classed as frequent: *Circus approximans*. Classed as uncommon: *Ninox novaeseelandiae*, *Halcyon sancta*, *Anthornis melanura* and *Prosthemadera novaeseelandiae*	*Hirudo tahitica* not recorded by Hicks et al. (1975), but now seen around the entire coastline (Towns & Atkinson 2004); three species classed as uncommon are now widespread and abundant throughout the island but *P. novaeseelandiae* only reported by A Evans (Unpublished data)

Unpredicted outcomes

Avian predators

Many responses to invasive mammal removals from Korapuki were unpredicted, including the resurgence and recolonisation of two avian predators: the kingfisher (*Todiramphus sanctus)* and the native owl (morepork; *Ninox novaeseelandiae*). Both species were regarded as uncommon by Hicks et al. (1975) and only a single pair of kingfishers was recorded by a survey in 1985 (D. Towns unpublished data). However, in 2007 kingfishers were encountered in over half of the survey sites used (Figure 3).

Moreporks were only occasionally sighted during biennial visits between 1985 and 2009, most likely as visitors from neighbouring islands, as there were no observed territorial calls. By 2009 territorial calls were heard, and in March 2011 moreporks calls were heard across the entire island (D. Towns unpublished data). Moreporks and kingfishers feed on lizards, large invertebrates and small birds (Robertson 1985). Recovery and recolonisation by these two avian predators could thus be an indirect measure of the increased abundance of their prey, one item of which for moreporks is tree wētā reintroduced to Korapuki in 1997 (Table 2).

Insect parasites

Honeydew scale insects are parasites of many forest plant species in New Zealand (Morales 1991). Their role in providing a high energy carbohydrate resource for birds and lizards on islands was unknown until the appearance of coastal forest plants infested by scale insects *Coelostomidia zealandica* on Korapuki (Towns 2002a). As these parasites have gradually spread, the importance of honeydew and other sources of sugar to geckos on these islands has also become apparent. Common geckos (*Woodworthia maculata*) are now common around flax (*Phormium tenax*), where they feed from inflorescences and sap.

Table 4. Chronological measures of progress and success for restoration of communities within a seabird-driven ecosystem of Korapuki Island; with projected measures >25 years.

Years since eradication of invasive mammals	Measure	Comment
10	Dispersal to/within island of key canopy plant species	Dominant species of communities on Middle Island as reference site spreading via bird dispersal (Towns & Atkinson 2004) but likely additional species (e.g. kohekohe) yet to establish (Atkinson 2004)
20	Establishment of selected missing invertebrates and reptiles	Five years for establishment of some invertebrates (e.g. Green 2005) and >8 years for some lizards (Towns & Ferreira 2001)
20-25	Recolonisation of top resident avian predator	Moreporks resident (based on territorial calls), but likely contingent on establishment of large invertebrates including tree wētā
50	Marine signature via seabirds within range of uninvaded islands	C:N and δ^{15}N concentrations in soils and plants equivalent to islands with unsuppressed seabird populations (extrapolated from Jones 2010); high density seabird colonies present but localised (Buxton et al. 2016)
50-100	Complete infestation of potential hosts for honey dew scale; time required to define success for reintroductions of tuatara	About 20% of island with honeydew infested karo or ngaio plants (Evans et al. 2015); successful reintroductions with each population composed of F1 or greater (D. Towns unpublished data)
150	Carrying capacity reached for reintroduced reptiles with low annual reproductive output	Modelled time to carrying capacity for Whitaker's skink (Miller 2009) and likely minimum time for tuatara; density of both species linked to seabird burrow density
>300	Replacement of continuous pōhutukawa canopy by diverse coastal species	Likely gradual change from pōhutukawa to karaka (*Corynocarpus laevigatus*) and kohekohe, but may depend on effects of seabirds

Duvaucel's geckos (*Hoplodactylus duvaucelii*) and common geckos are also found on the host trees for honeydew scale, although Duvaucel's geckos are the more abundant at such sites (Evans et al. 2015). Furthermore, bellbirds (*Anthornis melanura*) are often now seen feeding on the honeydew and vocally defending productive scale-infested karo (*Pittosporum crassifolium*) trees (D. Towns unpublished data).

Seabird recovery and recolonisation
The speed at which seabirds have recolonised and influenced restored island ecosystems in New Zealand has confounded assumptions based on philopatry and low immigration rates (Croxall et al. 2012; Kappes & Jones 2014). Through studies of C:N ratios and the concentration of δ^{15}N in soils, foliage and spiders, Jones (2010) concluded that ecosystem recovery on northeastern New Zealand islands may be achieved in decades. These conclusions were supported by Buxton et al. (2014), who found that on islands <25 km from other dense seabird colonies, intra− and interspecific social attraction can stimulate immigration to previously depleted colonies or establish new ones. These findings were particularly relevant to Korapuki Island, which at the longest time since eradication of mammals (then 22 years) had the highest soil and plant δ^{15}N and lowest C:N of the islands sampled (Jones 2010). In contrast to the scattered low density colonies recorded 10 years before mammal eradication (Hicks et al. 1975), seabird colonies now extend over 70% of surveyed areas on the island (Buxton et al. 2016).

Mysterious declines and disappearances
Surprisingly, we found changes in the abundance and distribution of resident species initially thought to be resistant to the effects of kiore and rabbits. For example, the diurnal shore skink (*Oligosoma smithi*) was regarded as abundant in the presence of kiore and rabbits (Hicks et al. 1975).

However, surveys revealed changes in distribution, increases in mean body size, and increased capture frequency soon after mammals were eradicated (Towns 1991, 1996; Monks et al. 2014). Conversely, recent samples indicate declines in the capture rates of shore skinks, while captures of other species of resident and translocated lizards continue to increase at the same sites (D. Towns unpublished data). Whether the current declines of shore skink captures is related to competition or predation from other species of lizards or the increased density of kingfishers as predators remains unclear.

In their early surveys of Korapuki Island, Hicks et al. (1975) observed few large day-flying insects and noted that the only species observed were cicadas and wasps. We assume that the latter were introduced *Vespula* wasps, since these were still present during our visits 10 years later (C. Green pers. comm.). In New Zealand, these wasps compete with birds for honeydew, can kill nestling birds, and prey heavily on spiders and caterpillars, resulting in modified invertebrate community structure (Beggs 2011). Within five years of the mammal eradication these wasps disappeared and have not been seen since (Bellingham et al. 2010a). Similar disappearances have now been observed on other islands after eradication of rats, including very large islands where *Vespula* wasps were once extremely abundant (T. Lovegrove pers. comm.).

Failed colonisations and unknown consequences
Numerous uncertainties remain about the composition and dynamics of communities on Korapuki Island. For example, seed dispersal will inevitably shape forest composition, which for some species requires kererū visiting from neighbouring islands (Towns & Atkinson 2004). The presence of tawāpou and taraire provides evidence of kererū visitation to Korapuki. However, not all species imported by kererū survive. In 1986, three taraire plants appeared to be thriving on the southwestern part of Korapuki; however, all plants succumbed after a drought

in the early 1990s and none have been seen since. Other species that are dispersed to the island may germinate only to be destroyed by drought, trampling or clipping by seabirds.

The relatively rapid increase in seabird activity brings additional uncertainties for longer term successional processes. In some areas of Korapuki, seabird burrow density is high under a canopy of 100-year old pōhutukawa (*Metrosideros excelsa*) that developed as a result of burning and the activities of rabbits (Atkinson 2004). Long term, this canopy would likely be replaced by a variety of coastal species, but the intense seabird activity could suppress seedling growth and arrest succession. Because Korapuki has a wide range of habitats and soil depths (Towns & Atkinson 2004) such effects are likely to be localised.

Finally, the recovery trajectory of Korapuki will likely be affected by external influences (Towns 2002b), such as climate change, ocean pollution, and other conservation actions. The latter could include success with mammal eradications on other islands in the archipelago. If the eradication of invasive mammals from Great Mercury in 2014 proves to be successful (Supplementary Data), all Mercury Islands will be free of introduced mammals. It is likely that kererū numbers will correspondingly increase, which in turn will increase the frequency of their movements between islands. The resulting seed dispersal could include species currently absent from islands such as Korapuki, with outcomes that at present are unknown. Another conservation action that may elicit indirect consequences on the recovery trajectory of Korapuki is the protection of New Zealand fur seals (*Arctocephalus forsteri*) following heavy exploitation in the 19th century (Harcourt 2005). The species is now reclaiming its former range, which includes sightings in 2012 of male fur seals ashore on Korapuki Island (A. Evans unpublished data). Rookeries may be established on Korapuki Island at some stage, which could significantly modify coastal vegetation, as well as contribute nutrient subsidies to the ecosystem. How fur seals might influence the function of these warm temperate ecosystems remains unclear.

Discussion

Invasive mammals have been eradicated from seven of the islands in the MIED. These eradications included some of the earliest campaigns against rodents, beginning with kiore (and rabbits) on Korapuki Island in 1986, and eventually leading to cats and rats on the eighth and largest of the islands (Great Mercury; 1872 ha), which began in 2014. With almost 30 years free of introduced mammals, Korapuki Island has been invaluable for testing concepts associated with island restoration as well as methods for species reintroductions. For example, a restoration target to "extend the area of unique seabird-reptile-invertebrate-plant communities" typical of the Mercury Islands was proposed soon after eradications were completed on Korapuki (Towns et al. 1990), but was not developed into a completed restoration plan until much later (Towns & Atkinson 2004). Empirical support for the pivotal role of seabirds, as implied in the restoration target, is even more recent (e.g. Fukami et al. 2006; Mulder et al. 2011). The evolution of ideas and collection of supporting data for restoration of these islands was built around four components: biogeography; ecosystem function; the effects of invasive species; and outcome measures (Figure 5). For example, through testing biogeographic theory, our work suggests that

assemblage structure may be most easily predicted on islands previously part of the mainland, but especially those once interconnected.

We have also found that ecosystem function can be determined from two sources: the way resident species respond when invasive species are removed and the use of comparative data from reference sites never occupied by invasive mammals. Reference models are likely to be most instructive when on islands of similar size to the site being restored. As island size increases, reference sites uninvaded by introduced mammals become increasingly rare and for islands >1000 ha do not exist (Parkes & Murphy 2003). However, on some of the larger islands, past assemblage composition can be revealed from the bone fragments, pollen and ancient DNA used for archaeological and palaeoecological studies (Bellingham et al. 2010a; Wilmshurst et al. 2014).

Regardless of the availability of reference sites, the amount of restoration effort required is determined by recolonisation ability; this may vary for seabirds according to the distance from source populations but is consistently poor for reptiles and some terrestrial invertebrates. Finally, restoration endpoints can be defined by combining biogeographic origin, post eradication responses and ecosystem function. For example, a restored seabird-driven ecosystem on Korapuki Island with high ecological integrity typical of the archipelago acknowledges historic vicariance, high rates of natural recolonisation by plants and seabirds, but the extirpation of key reptiles and large flightless invertebrates. However, despite the three decades of reintroductions and recovery on the island, measures of progress towards the restoration endpoints are still in development.

In sum, ecological restoration in the Mercury Islands indicates that the "Humpty Dumpty" problem raised by Duffy (1994) and others who have examined the ambiguity of island restoration (Simberloff 1990) can be addressed within a defensible framework. However, our studies have also revealed many unexpected responses to invasive mammal removal. There are also unpredictable consequences of the previous presence of mammals, responses of species such as kererū to conservation actions elsewhere and the effects of recolonisation of the islands by fur seals. Conversely, there is developing clarity about how these seabird driven systems vary under different climatic and biogeographic regimes and the extent to which they can be modified by introduced animals. Insights have come from comprehensive studies of the general relationships between seabird activity, nutrient subsidy, and vegetation composition beginning in the 1950s (e.g. Gillham 1956a, b), complemented locally by analyses of seabird-soil-plant relationships on Middle Island in the Mercury Group (Atkinson 1964), and extended by studies across islands in northern New Zealand (Fukami et al. 2006) and globally (Mulder et al. 2011). The studies by Jones (2010) and ourselves in the Mercury Islands indicate that removal of predatory mammals can lead to reactivation of the seabird influence on island ecosystems, as long as the birds can recolonise. Furthermore, Buxton et al. (2014) show that there is frequently natural recolonisation of islands <25 km from other large seabird colonies. Collectively, these recent studies indicate that seabird-driven ecosystems in some locations can recover rapidly, but they have also identified markers that can be used to measure the extent of that recovery.

Given that the seabird-driven ecosystem on Korapuki appears to be recovering naturally (Jones 2010; Buxton et al. 2016), is restoration based on pre-determined assemblage composition justified? For example, the ecosystem on Korapuki
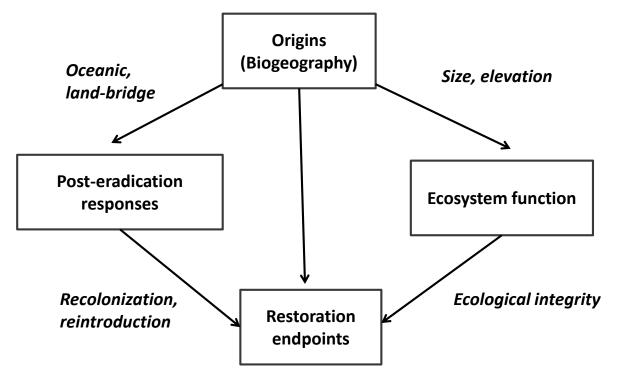
Figure 5. Summary of the relationship between four key components of island restoration.

will not cease to function in the absence of tuatara, which will simply be replaced by Duvaucel's geckos as top reptile predator (Towns 2002b). Furthermore, should we be concerned if ecosystems on islands beyond the natural colonisation range of seabirds enter alternative stable states unlike those with invasive mammals but no longer driven by the engineering effects of seabirds (e.g. Mulder et al. 2009)? Such questions lead us into the realm of value judgements. By phrasing his problem in the context of a children's nursery rhyme, Duffy (1994) implies a social component to restoration, as there is with all conservation biology (e.g. Lawton 1997). One social dimension applied to our study at the outset: a legal framework (i.e. a statutory expression of values) within which to conduct the eradications and attempt ecosystem restoration. Work in the Mercury Islands began on sites administered as Nature Reserves, which mandates the removal of all exotic species where possible (Reserves Act 1977). We therefore assumed that the implicit goal of the reserves is protecting or promoting the highest possible ecological integrity (*sensu* Lee et al. 2005), which on Korapuki includes reintroduction of invertebrates and reptiles (Towns & Atkinson 2004). Nonetheless, even with a legal mandate, when multiple stakeholders are involved there can still be heated debate when invasive species eradications are proposed, as was the case before the removal of kiore from Hauturu (Little Barrier) Island Nature Reserve (Towns et al. 2006). Accordingly, our summary of the essential elements to be considered when undertaking restoration of islands (Figure 5) is a simplified view that excludes the complex regional social issues that may be involved.

Having acknowledged uncertainties about the successional consequences of natural recovery supplemented by reintroductions, our approach on Korapuki has been to allow the ecosystem to develop at its own speed. By facilitating the return of only those components unable to recolonise unaided, we assume that the system will eventually follow a trajectory typical of other regional islands of equivalent size (Simberloff 1990; Towns 2002b). What still remains unclear from the Korapuki study is whether the strong ecosystem engineering effects of seabirds apply on larger islands, or whether such locations develop into more heterogeneous environments than are found on our small reference islands, such as Middle. Consequently, a great deal is still to be learned from the processes of recovery on other Mercury Islands such as Red Mercury, which is over 20 times larger than their available reference sites within the archipelago.

Acknowledgements

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Supplementary Data. Rodents and associated species eradicated from Islands in Mercury Islands Ecological District (McEwen 1987) in chronological sequence updated from Towns & Broome (2003).

Location	Area (ha)	Status	Date	Rodent	Other eradications	Method used against rodents	References
Korapuki	18	Wildlife Sanctuary (Nature Reserve)	1986	Kiore	Rabbits	Ground-based: kibbled maize in silos; prefeed followed by maize dosed with bromodialone (0.005% by wt)	McFadden & Towns (1991)
Double	8 (West) +19 (East)	Nature Reserve	1989	Kiore	None	Ground-based: kibbled maize in silos; prefeed with aniseed added followed by maize dosed with bromodialone (0.005% by wt) on West Double. Hand broadcast 4 g pellets of STORM containing flocoumafen (0.005% by wt) at 18.5 kg/ha on East Double	McFadden (1992)
Stanley	100	Nature Reserve	1991	Kiore	Rabbits	Aerial spread by helicopter using modified monsoon bucket; 0.8 g cereal pellets of TALON 20 P containing brodifacoum at 20 ppm with follow-up hand spread of TALON 50WB (wax blocks) containing brodifacoum at 50 ppm; total of 17 kg/ha	Towns et al. (1993)
Red Mercury	225	Nature Reserve	1992	Kiore	None	Aerial spread by helicopter using modified monsoon bucket; TALON 20 P with follow-up hand spread of TALON 50WB; 15 kg/ha	Towns et al. (1994)
Middle Chain	23	Nature Reserve	1992	Kiore	None	Aerial spread of TALON 20 P by helicopter using modified monsoon bucket; 15 kg/ha	
Cuvier	170	Nature Reserve	1993	Kiore	None	Aerial spread of TALON 20 P by helicopter using bait spreader; 15 kg/ha	Towns et al. (1995)
Ohinau	43	Iwi (Ngati Hei)	2005	Kiore, mice	Rabbits	Aerial spread of PESTOFF 20R containing brodifacoum in two operations by helicopter using bait spreader; 8+8 kg/ha	R Chappell (pers. comm.)
Great Mercury	1872	Private	2014	Kiore, ship rats	Goats, cats	Aerial spread of PESTOFF 20R containing brodifacoum in two operations by helicopter using bait spreader; 8.8+13.2 kg/ha	P Corson (pers. comm.)

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