# The Impact of Isolation from Mammalian Predators on the Anti-Predator Behaviours of the North Island robin (*Petroica longipes*)

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# Abstract

Conservation in New Zealand has begun to focus heavily on the restoration of degraded mainland ecosystems and the reintroduction of native species that have become locally extinct. In many cases the individuals that are selected for reintroduction are harvested from ‘mammal-free’ offshore islands. This thesis examines the effects of isolation from mammalian predators on the predator avoidance behaviours and predator recognition abilities of New Zealand birds using the North Island robin as a model. It also investigates whether any effects of isolation from mammalian predators has a lasting impact on mainland populations founded by individuals from offshore islands.

Nest site selection behaviours were compared across three populations that are exposed to different suites of predators and have differing translocation histories; Benneydale, Tiritiri Matangi and Wenderholm. Point height intercept and point-centred quarter surveys were used to compare habitat availability between the sites and to compare nest sites with the available habitat. Eight nest characteristic variables were also compared across the three sites using a principle component analysis. Benneydale nests were located higher in the trees and were more concealed than nests at the other two sites. Nests on Tiritiri Matangi were supported by large numbers of thin branches and were located toward the periphery of the nest tree. Unfortunately these differences are very difficult to interpret due to a high degree of variation in the habitat types present at the three sites.

The anti-predator behaviours initiated in response to a model stoat, model morepork and control were used to test the ability of nesting robins to recognise the threat that each of these treatments might pose to nest success. Behavioural variables were compared between Benneydale, Tiritiri Matangi and Wenderholm using a response intensity scoring system and a principle component analysis. The results indicated that isolation from mammalian predators on Tiritiri Matangi has suppressed the ability of robins on the island to recognise the predatory threat posed by a stoat. They also suggest that the intense mammal control carried out at Wenderholm may have inhibited the ability of local robins to produce strong anti-predator responses when faced with a stoat.

North Island robin adult with chick (photograph by T. Lovegrove)

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# CHAPTER ONE

# General Introduction

## *1.1 A Short Evolutionary History of New Zealand*

Since splitting from Gondwana approximately 82 million years ago, the New Zealand archipelago has experienced a unique biological history (Worthy *et al.*, 2006). For the past 60 million years New Zealand has been separated from its nearest neighbour by up to 1500 km of open sea (Cooper and Cooper, 1995). This separation has restricted the potential for biotic colonisation from other landmasses. As a result, much of New Zealand's endemic biota reflects its Gondwanan origins (Chambers *et al.*, 2001). As New Zealand rafted away from Gondwana, it carried with it at least one species of small mouse-like mammal. This mammal lineage disappeared during the Neocene period and has only recently been discovered (Worthy *et al.*, 2006). There is currently no evidence that large mammalian predators were present in New Zealand prior to colonisation by humans. In the absence of mammalian predators many endemic species evolved traits such as gigantism, flightlessness and K-selected life histories. These features have made many endemic species highly susceptible to the environmental disturbances that resulted from human colonisation (Blackwell, 2005; Daugherty *et al.*, 1993)

## *1.2 The Impacts of Human Colonisation*

New Zealand was first colonised by Polynesians approximately 700 years ago (McGlone and Wilmshurst, 1999; Wilmshurst *et al.*, 2008). These early colonisers used fire to modify and manage the New Zealand landscape, burning extensive tracts of forest to create clear sites for living or cultivation (McGlone, 1989; McGlone and Wilmshurst, 1999; Ogden *et al.*, 2003). When the first Europeans reached New Zealand in the 17th and 18th centuries, forest cover had declined from approximately 90% before Polynesian colonisation to 53% (McGlone and Wilmshurst, 1999). European settlers continued to clear what was left of the forests and by the 1990s forest cover had been reduced to just 23% (Ministry for the Environment, 1997). This dramatic and extremely rapid decline in forest cover had a disastrous impact by reducing and fragmenting the ranges of numerous plant and animal species. This factor alone may have made some species susceptible to extinction as a result of environmental stochasticity or increased predator pressure (Blackwell, 2005).

The early Polynesians introduced a number of plant and animal species, including the Pacific rat, or kiore (*Rattus exulans*). These rats became key predators of many of New Zealand's native species, and are thought to have caused the extinctions of the mainland races of the New Zealand snipes (*Coenocorypha* spp), the snipe-rail (*Capellirallus karamu*) and several species of flightless wrens (i.e. *Pachyplichas* spp., *Traversia* spp. and *Dendroscansor* spp.) (Holdaway, 1989; Worthy and Holdaway, 2002). European settlers introduced many more mammalian species, of which at least 10 species are known to prey on native fauna (Blackwell, 2005; Clout and Russell, 2006). New Zealand's isolation from predatory mammals meant that many native bird species became structurally or behaviourally flightless and many of these species foraged or nested on the ground. Moreover, as they had evolved in isolation from predatory mammals, many native birds lacked appropriate behaviours to avoid them (Blackwell, 2005; Holdaway, 1989; Maloney and McLean, 1995). Introduced predatory mammals have been the single biggest cause of many recent bird extinctions (Holdaway, 1989; King, 1984). Significant bird extinctions that are likely to have been caused by predatory mammals introduced by Europeans include the Chatham Island rail (*Rallus modestus*), laughing owl (*Sceloglaux albifacies*), bush wren (*Xenicus longipes*), piopio (*Turngra capensis*), huia (*Heteralocha acutirostris*), and South Island kokako (*Callaeas cinerea cinerea*) (King, 1984; Worthy and Holdaway, 2002). During this period a number of other species were extirpated from the New Zealand mainland, including the shore plover (*Thinornis novaeseelandiae*), kakapo (*Strigops habroptilus*), hihi (*Notiomystis cincta*) and saddleback (*Philesturnus carunculatus*) (Armstrong *et al.*, 1999; Armstrong *et al.*, 2002; Nilsson *et al.*, 1994; Worthy and Holdaway, 2002). Today many native bird species persist only in places where mammalian predators are absent or controlled intensively.

## *1.3 Current Conservation Strategies and their Implications*

Mammalian predators remain one of the major causes of decline for many of New Zealand's native species (Clout, 2001; O'Donnell, 1996; Parkes and Murphy, 2003). As such, contemporary conservation programmes often aim to isolate vulnerable populations from predatory mammals. Historically this has involved the translocation of threatened species to mammal-free offshore islands and intensive predator control in mainland habitats (Clout, 2001; Clout and Russell, 2006). The eradication of mammals from offshore islands began in the early 1900s (Clout and Russell, 2006; Veitch and Bell, 1990). Recently, improved anticoagulant poisons, aerial bait distribution and eradication planning have allowed conservation managers to successfully eradicate rodents and mustelids from islands as large as 11,300 ha (Clout and Russell, 2006; Cromarty *et al.*, 2002; Towns and Broome, 2003).

Marooning small populations of threatened species on offshore islands has been a highly successful conservation strategy for many of New Zealand's endemic bird, reptile and invertebrate species (Atkinson, 1990; Williams, 1977). Some of these species now exist only on offshore islands (Ardern and Lambert, 1997; Armstrong and Davidson, 2006; Elliot *et al.*, 2001; Ewers, 2008; Towns and Ferreira, 2001). Although islands will remain an important tool for New Zealand conservation, the past decade has seen an increasing emphasis on restoring mainland ecosystems through the creation of "mainland islands" (Craig *et al.*, 2000; Lovegrove *et al.*, 2002; Saunders, 1990; Saunders and Norton, 2001). The mainland island strategy attempts to emulate the conservation successes of offshore islands through habitat restoration and intensive predator control (Gillies *et al.*, 2003; Saunders, 1990; Saunders and Norton, 2001). Improved predator control methods have allowed mainland island managers to reduce mammalian predator densities to levels at which some vulnerable species can establish and maintain viable populations (Armstrong *et al.*, 2006; Clout and Russell, 2006; Gillies *et al.*, 2003; Innes *et al.*, 1999; Saunders and Norton, 2001). Innes *et al.* (1999) showed that North Island kokako (*Callaeas cinerea wilsoni*) populations recovered quickly following intensive possum (*Trichosusrus vulpecula*) and ship rat (*Rattus rattus*) control, and Armstrong *et al.* (2006) showed that a declining robin population recovered when ship rats were controlled. Mammalian predator control at other mainland island sites has increased the nesting success of kaka (*Nestor meridionalis*) and New Zealand falcon (*Falco novaeseelandiae*), and increased Kereru (*Hemiphaga novaeseelandiae*) population size (Butler, 2003; Gillies *et al.*, 2003; Innes *et al.*, 1999; Saunders and Norton, 2001).

A key aspect of mainland island restoration is the reintroduction of locally extinct species. Translocations have been common place in New Zealand conservation since the late 1800s (Atkinson, 1990; Griffith *et al.*, 1989; Young, 2004). Historically, these translocations have moved individuals from high risk areas to safe island refuges as a species conservation measure (Atkinson, 1990). However, island refuges are increasingly being used as sources of founding birds for translocations to managed mainland sites (Dimond and Armstrong, 2007). These individuals are therefore moved from places with few or no mammalian predators to places where these predators are controlled but have not been removed completely. Maloney and McLean (1995) showed that individuals within a historically isolated population of New Zealand robins (*Petroica australis*) were unable to recognise and respond to mammalian predators (Maloney and McLean, 1995). Recent translocations of birds between places with very different predator densities provide opportunities to assess predator recognition abilites and anti-predator behaviours. The conservation of New Zealand's robin species (*Petroica* spp.) has involved translocations between sites with a range of predator densities. As such, the robins provide a good model for studying the effect of these translocations on predator recognition abilities. This study investigated how isolation from mammalian predators through translocation affects the predator recognition abilities of North Island robins (*Petroica longipes*).

## *1.4 Conservation and Predator Recognition in New Zealand's Robins*

According to recent phylogenetic analyses New Zealand has four endemic robin species, the North Island robin (*Petroica longipes*), the New Zealand robin (*P.*

*australis*), the black robin (*P. traversi*) and the tomtit (*P. macrocephala*) (Miller and Lambert, 2006). The highly endangered black robin is restricted to two small islands in the Chatham group, while the other robin species occur on the New Zealand mainland as well as on some offshore islands. The North Island robin occurs only on the North Island, while the New Zealand robin occurs in the South and Stewart Islands (Miller and Lambert, 2006). The Department of Conservation follows an older classification and recognises the North Island and New Zealand robins as one species, with three distinct subspecies present on the North Island, South Island and Stewart Island (Heather and Robertson, 1996; Powlesland, 1997; Turbott, 1990). This thesis follows the taxonomic classification used by the Department of Conservation. The tomtit is widespread and relatively common throughout many of New Zealand's larger forested areas and exists in a wide variety of forest types (Knegtmans and Powlesland, 1999). Unlike the tomtit, the robin has a much more local mainland distribution and is restricted to discrete areas of native and exotic forest (Armstrong, 2000). It is not known why the robins were not extirpated from the mainland like many other vulnerable native species, such as the saddleback (*Philesturnus carunculatus*), hihi (*Notiomystis cincta*) and kakapo (*Strigops habroptilus*) (Armstrong, 2000). It is also unknown why robins have been able to persist in some forest fragments but not in others. This patchy distribution has resulted in the North and South Island robins being classified as "regionally threatened" but not "endangered" (Powlesland, 1997). In the early 1970s South Island robins were translocated to several offshore islands in order to test translocation methods for use on the endangered black robin (Armstrong, 2000). During the 1980s and 1990s further translocations were carried out as part of island restoration projects being undertaken at the time. New populations are now thriving on several offshore islands including Motuara, Moturua, Mokoia, Tiritiri Matangi and Mana Islands (Armstrong, 2000).

New Zealand robins are all relatively fearless toward humans and can be trained easily to take food rewards. They are therefore among the easiest birds in New Zealand to find, observe and capture. The relative ease with which robins can be studied and translocated, their ability to persist in mainland sites and their low conservation priority status means that robins are often the first species to be reintroduced to mainland islands (Armstrong, 2000; Armstrong, 2008; Lovegrove *et al.*, 2002). By monitoring their success managers can use robins as an indicator species to test the suitability of restored habitats for more endangered species (Armstrong, 2000).

Maloney and McLean (1995) studied anti-predator behaviours in South Island robins and assessed the ability of robins from two populations to recognise a stoat (*Mustela erminea*), an important predator of many native bird species. One population had naturally persisted in Kowhai Bush on the mainland of the South Island, while the other had been translocated from Inner Chetwode Island to Motuara Island in the Marlborough Sounds in 1973. Stoats had never reached Inner Chetwode Island or Motuara Island, so neither the modern Motuara robins nor their ancestors had ever experienced stoat predation (Maloney and McLean, 1995). The study showed that the Kowhai Bush robins could recognise the predatory threat posed by the stoat and initiated appropriate anti-predator response behaviours. However, the Motuara Island robins lacked the experience necessary to recognise the stoat as a threat and did not display these behaviours as often. This study showed that despite having evolved in the absence of mammalian predators, in the century since stoats were introduced to New Zealand the mainland robins had learned to recognise this predatory mammal as a significant threat to their survival (Maloney and McLean, 1995).

Although mainland robins may be able to recognise the threat posed by mammalian predators it was not known whether this learned recognition ability would be lost when mainland robins were isolated from mammalian predators. This is an important knowledge gap as many reintroductions of threatened bird species to mainland island sites source founding individuals from newly established populations on predatory mammal-free offshore islands (Dimond and Armstrong, 2007). If birds from these protected source populations can not recognise mammalian predators, then the founders reintroduced to mainland sites may be unable to respond appropriately when they encounter them (Griffin *et al.*, 2000).

## *1.5 Aims and Thesis Structure*

This study aims to identify how the translocation of robins from the North Island mainland to Tiritiri Matangi island, and from there back to a nearby mainland site at Wenderholm Regional Park, has affected their mammalian predator recognition abilities and predator avoidance behaviours.

Chapter two examines the issue of habitat differences between the three study sites used during the research; Tiritiri Matangi Island, Wenderholm Regional Park and Benneydale. It provides a brief introduction to the effects of vegetation and habitat structure on the ecology and behaviour of bird species. Then it describes the species composition, maturity and structure of the forests at each site and outlines key differences between the habitats. Chapter two concludes with an outline of the implications that these differences may have for interpretating the research results.

Chapter three investigates how the translocations of robins between areas with different predator densities have affected their ability to select nest sites appropriate to their current predatory environment. It reviews the current knowledge of predator-induced behavioural plasticity and the factors that affect an individual bird's nest site selection criteria. It then outlines the use of nest site characteristics to identify differences in the nest site selection of robins in populations responding to varied predator pressures and with different translocation histories. Nest site characteristics such as nest height, nest concealment and vegetation structure are used to assess whether nest site selection reflects the estimated risk of predation and the suite of predators present in each population.

Chapter four addresses two key issues. Firstly, it aims to identify whether the ability to recognise mammalian predators has been lost in robins that have been isolated from these predators. It then assesses whether any lost predator recognition abilities can be relearned when isolated robins are reintroduced to mainland sites. This chapter begins with a review of the current theory relating to the importance of predator recognition in conservation. It then outlines the use of predator response behaviours to assess predator recognition in robins from three sites with varying predator densities and differing translocation histories. Here taxidermic mounts of an introduced mammalian predator (a stoat) and a native avian predator (a morepork, *Ninox novaeseelandiae*) were presented to nesting robins. The strength of the response behaviours elicited by these models is used to infer the extent to which the birds considered the models a predatory threat.

Finally, Chapter five outlines the conclusions drawn from the above analyses and provides recommendations for the future management of aspects of translocations in New Zealand. It highlights some of the issues associated with implementing pre-release predator recognition training and provides recommendations for future investigations into predator recognition abilities in New Zealand birds.

# CHAPTER TWO

## Habitat Composition and Structure at Three Study Sites; Tiritiri Matangi Island, Wenderholm Regional Park and Benneydale

**Plate 2.1:** An aerial view of Wenderholm Regional Park (photograph by A. Jamieson)

## Abstract

This chapter investigates habitat differences between the three study sites in this thesis; Tiritiri Matangi Island, Wenderholm Regional Park and Benneydale. Vegetation composition and habitat structure play an important role in determining the ecology and behaviour of bird communities. As such, differences between the habitats at these sites are likely to confound the interpretation of behavioural differences between their resident North Island robin (*Petroica longipes*) populations. This investigation uses point-centred quarter and point height intercept survey techniques to provide a detailed description of the species composition, maturity and structure of the forests. All of these habitat characteristics varied between the sites. Benneydale was dominated by mature tawa trees (*Bielschmiedia tawa*), Tiritiri Matangi by pohutukawa (*Metrosideros excelsa*) and Wenderholm by tree ferns (*Cyathea dealbata*). The forests fragments at the Benneydale site were the most mature while the recently replanted Tiritiri Matangi forest was the least mature. The Benneydale forest also featured the tallest canopy and both Benneydale and Wenderholm had a high diversity of tree species contributing to the forest canopy above 4.0 m. The understorey at Benneydale, however was less diverse than the other two sites. These differences made interpreting behavioural comparisons between the sites extremely difficult. The confounding influence of habitat differences between the study sites must be considered to ensure that the interpretation of behavioural results is appropriate.

## 2.1 Introduction

Vegetation is an important component of most terrestrial ecosystems. In both managed and unmanaged systems plants provide a physical structure that can affect the species richness, abundance and distribution of bird communities (James and Wamer, 1982; McArthur and McArthur, 1961; Rotenberry and Wiens, 1980; Roth, 1976). At a smaller scale, it has been suggested that the structure of local vegetation may affect the behaviour and microhabitat distribution of specific bird species. Variations in plant species composition and foliage distribution, for example, have been shown to affect foraging behaviour by altering the availability of specific food resources and the efficiency of foraging tactics (Holmes and Robinson, 1981; Kennedy and Southwood, 1984; Robinson and Sutherland, 1999; Robinson and Holmes, 1984; Whelan, 2001). Predator avoidance behaviours can also be affected by vegetation structure as dense or tall vegetation can hamper the ability of birds to watch for predators. This kind of visual obstruction has been shown to increase vigilant behaviours in a number of bird species (Cresswell, 1994; Metcalfe, 1984; Whittingham and Evans, 2002). Vegetation structure may also affect nest site selection by birds. Parent birds may choose vegetation characteristics that optimise micro-climatic conditions, food availability and concealment from potential predators (Burke and Nol, 1998; Gotmark *et al.*, 1995; Martin, 1998). These examples illustrate that vegetation composition and habitat structure play an important role in determining the ecology and behavioural characteristics of bird communities. As such, studies of avian populations should always consider the structure of the local habitat and its potential influence on the results of the research.

The primary goal of this study was to identify how the translocation of North Island robins from the mainland to an offshore island, and from an offshore island to a mainland island has affected their nest site selection behaviours and mammalian predator recognition abilities. Both of these factors could be influenced by habitat variations among the study sites. Nest site selection behaviours in particular will be constrained by the type of nest sites that are available within the respective habitats. Thus, it is important to gain an understanding of the composition, maturity and structure of the local habitats when interpreting the results of this kind of investigation. The North Island robin is now found in just a few forested areas and their discrete populations often exist within quite different habitats (Armstrong, 2000). This research focuses on North Island robins from Tiritiri Matangi Island, Wenderholm Regional Park and Benneydale in the central North Island. These three sites occur within different landscapes and provide very different habitat characteristics for resident bird populations. The use of these three sites was therefore far from ideal. Differences between their respective habitats had the potential to confound any observed differences in nest site selection behaviours, making it difficult to provide meaningful biological interpretation of the results. The aim of this chapter is to describe the species composition, maturity and structure of the forests present at the three sites. The analysis reveals local habitat differences, which are used to inform the interpretation of a comparison of the nest site selection behaviours of North Island robins within these sites.

# *2.2 Methods*

## 2.2.1 Study Sites

Tiritiri Matangi Island

Tiritiri Matangi is a 220 ha island 4 km east of the Whangaparaoa Peninsula and 25 km north of Auckland City (36°36'S, 174°53'E) (Figure 2.1). Local Maori cleared most of the islands' original forest for cultivation. Following the arrival of Europeans the island was used for grazing domestic livestock (Graham and Veitch, 2002). Tiritiri Matangi has been free of mammalian predators since Pacific rats (*Rattus exulans*) were eradicated in September 1993. Today the island is classified as a Scientific Reserve under the 1977 Reserves Act (Graham and Veitch, 2002). The first translocation of 44 North Island robins to Tiritiri Matangi occurred in April 1992. This was supplemented by a second translocation of 14 birds in June 1993. All of these founders were harvested from a remnant population on the Mamaku Plateau in the central North Island (Armstrong, 1995; Armstrong, 2008a). Since the releases the population has expanded to over 40 pairs (Armstrong *et al.*, 2000). This population has become a useful and productive source of individuals for reintroduction to a number of other sites including some mainland islands (Dimond and Armstrong, 2007).

Benneydale

The township of Benneydale lies 35 km south east of Te Kuiti (38°32'S, 175°22'E) (Figure 2.1). The surrounding landscape is dominated by open farm land. Within this modified landscape a number of native forest fragments have survived, some of which have been able to sustain a metapopulation of North Island robins

(Boulton *et al.*, 2008). This population was recently supplemented by the translocation of a further 135 individuals from nearby pine plantations into 13 forest fragments that did not contain robins (Armstrong, 2008b). Most of these robins dispersed away from their release sites but 36 have established within the 13 fragments targeted in the release. Eleven of these fragments now accommodate at least one breeding pair (Armstrong, 2008b). Predator control in the area includes periodic brushtail possum (*Trichosurus vulpecula*) control and in 2008 rat control was initiated within six of the forest fragments (Armstrong, 2008b). Benneydale is 70 km south-east of the Mamaku Plateau, which accommodates the source population of North Island robins used for the reintroduction to Tiritiri Matangi. The Benneydale population was used in this research instead of the Mamaku Plateau population as an existing robin monitoring programme at the site allowed larger sample sizes to be collected. The Benneydale and Mamaku robins are likely to be genetically similar as some migration is likely to occur between the populations (D. Armstrong pers. comm.).

### Wenderholm Regional Park

Wenderholm Regional Park is a 170 ha managed mainland peninsula 45 km north of Auckland (36°33’S, 174°43’E) (Figure 2.1). Although the area was farmed with cattle and sheep following European colonisation, significant areas of coastal forest survived. In 1965 Wenderholm became Auckland’s first regional park. During the 1980s and 1990s pest control concentrated on the brushtail possum and in 1992 a rodent control programme was initiated. In early 1999, trap lines were installed to target mustelids. Later in 1999, 21 North Island robins were reintroduced to the park from Tiritiri Matangi. This population has persisted and is highly productive.

However, the size of the population is not growing due to high juvenile dispersal out of the park to less intensively managed or unmanaged sink areas where predation risk is high (Andrews, 2007; Lovegrove *et al.*, 2002).

Two satellite populations of North Island robins have established outside of the protected Wenderholm area. A small population of up to four pairs has established 2 km inland from Wenderholm on private land near the lower Waiwera River. Following its establishment a grid of bait stations covering approximately 25 ha was set up to control ship rats (*Rattus rattus*). No attempt was made to control stoats (*Mustela erminea*) or other predators. Approximately 10 km inland from Wenderholm, a second satellite population of up to five pairs established on private land in the Upper Waiwera Valley near Puhoi (Lovegrove, 2008). This population has been monitored since the first pair established in 2003, and rat control was undertaken in individual territories from spring 2003 (Lovegrove, 2008; T. Lovegrove pers. comm.). In May 2007 the Puhoi population consisted of five pairs, however, in July and August 2007 four females were translocated to the Tawharanui Open Sanctuary to rebalance the imbalanced sex ratio in the newly-released Tawharanui population (Lovegrove, 2008). It was expected that more females would be recruited, but in 2008 only one pair was breeding at the Puhoi site. A small grid of poison bait stations and snap traps was maintained to target rats within their territory.

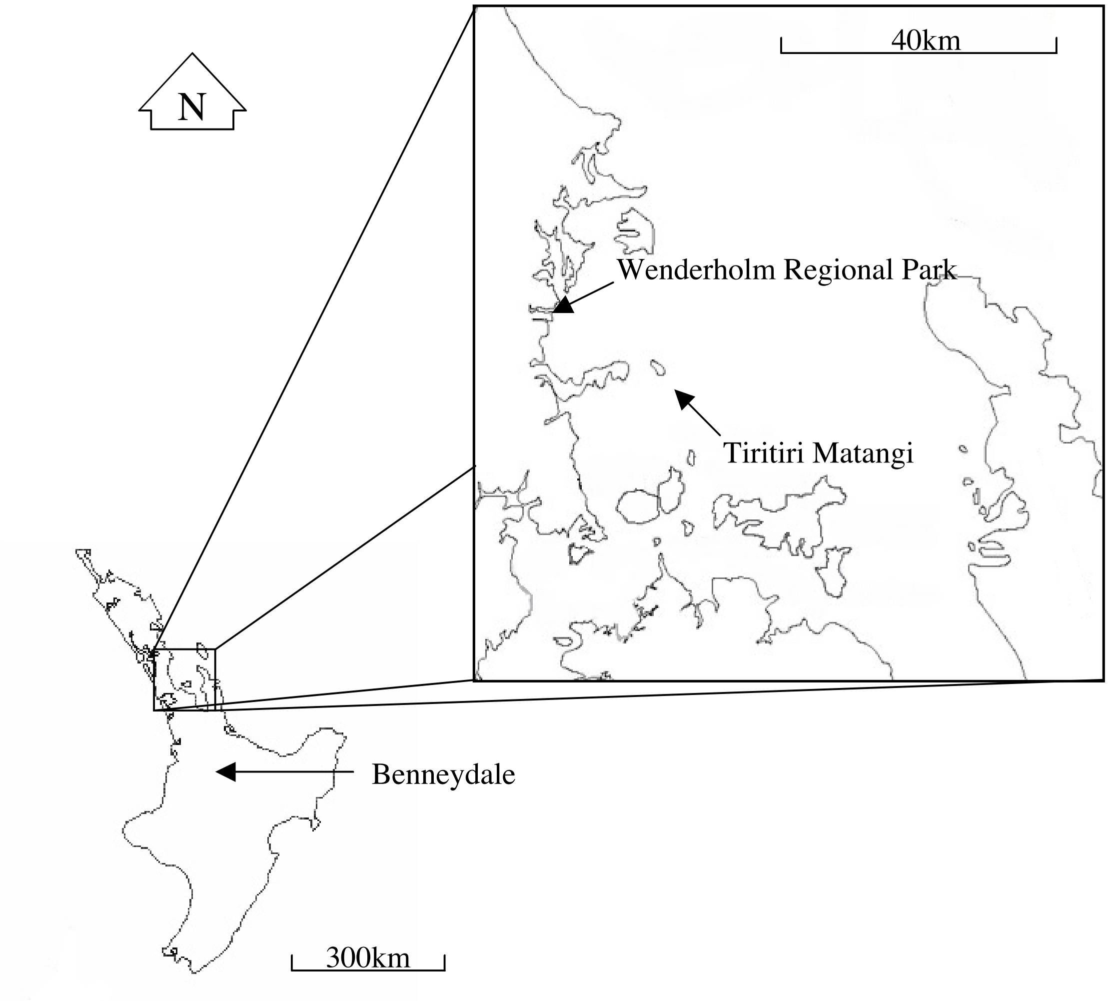


**Figure 2.1:** Map of the North Island of New Zealand, with an enlarged view of the Hauraki Gulf, showing locations of the three study sites.

### 2.2.2 Sampling

Independent 80 m long transects were placed in random positions throughout the available habitat at each site. Eighteen transects were set up within Wenderholm Regional Park and in the surrounding habitat. Twenty transects were set up at both Benneydale and Tiritiri Matangi. The start point of each transect was identified by placing a grid over a map of the area. The grid points represented potential transect start points. These start points were numbered and selected using a random number generator. The bearing of each transect was determined by blindly spinning a compass dial. The resulting compass bearing became the direction of the transect.

### 2.2.3 Species Composition and Maturity

The species composition of the available forest habitat was assessed using a point-centred quarter (PCQ) survey method (Mitchell, 2007). Ten PCQ sampling points were used, located at 8.0 m intervals along each random transect. This produced a sample size of 180 random sampling points at Wenderholm and 200 each at Benneydale and Tiritiri Matangi. At each sampling point a north-south oriented cross was made on the forest floor to create four quarters (Figure 2.2). The nearest tree in each quarter was identified and its diameter at breast height and distance from the sampling point recorded. A ‘tree’ was defined as any vegetation with a central trunk greater than 5 cm in diameter. If the tree had multiple trunks at breast height, all were recorded separately. These recorded values allowed the frequency, density and basal area of each tree species to be calculated. Mature forests are generally characterised by larger trees that are more dispersed than younger forests (Mark and Dickinson, 1989). It was therefore possible to describe the maturity of the forests based on tree diameter values and the distance of the trees from the sampling point.

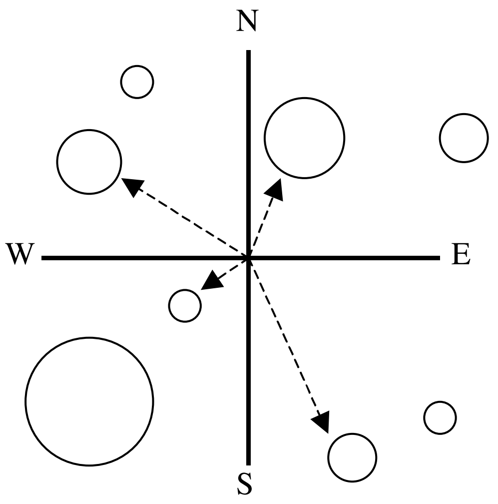


**Figure 2.2:** The point-centred quarter (PCQ) sampling layout. The sampling point is located at the centre of cross. Circles indicate the trunks of trees. Dotted lines indicate which trees would be selected for measurement and the distance to be measured. Figure adapted from Mitchell (2007).

### 2.2.4 Forest Structure

Vegetation structure and complexity was assessed using a basic point height intercept (PHI) survey method (Park, 1973). PHI sampling points were located every 4.0 m along each random transect resulting in a sample size of 360 at Wenderholm and 400 each at Benneydale and Tiritiri Matangi. At each point a 2.0 m high dowel pole was held in a vertical position with one end touching the ground. All live vegetation touching the pole at the base, between 0.0 and 0.2 m high and between 0.2 and 2.0 m high was identified and recorded. The pole was then held two meters off the ground in a vertical position and all live vegetation touching the pole at between 2.0 m and 4.0 m high was recorded. The vertical line was then projected through the canopy. All species intercepting the line at a height greater than 4.0 m were recorded. The highest species that intercepted the line was recorded as the ‘canopy’ species and its height was measured using an electronic clinometer.

## *2.3 Analysis and Results*

### 2.3.1 Forest Composition

The data from the PCQ survey were used to calculate the relative frequency, relative density per hectare and relative basal area of each species observed. The relative frequency is a measure of how the species is distributed within the habitat. It is calculated by dividing the proportion of sampling points that feature a particular species by the sum of the proportions that feature all other species. A high relative frequency value indicates that a species has a uniform distribution (Mitchell, 2007). The relative density of a species is the total number of observations of that species as a percentage of the total number of observations made. The relative basal area is the total basal area of the species represented as a percentage of the total basal area of all the species observed. The sum of these variables provided an ‘importance value’ for each species (Mitchell, 2007) (Tables 2.1-2.3). All of these values were used to describe the species composition of the forests at all three sites.

**Table 2.1:** Results from random point-centred quarter survey at Benneydale.

| Species<br>(Common Name) | Sample Size | Relative Frequency | Relative Density | Relative Basal Area | Importance Value Index |
|---|---|---|---|---|---|
| *Cyathea dealbata*<br>(Ponga) | 422 | 39.04% | 52.75% | 20.49% | 112.28 |
| *Beilschmiedia tawa*<br>(Tawa) | 220 | 24.48% | 27.50% | 52.93% | 104.91 |
| *Melicytus ramiflorus*<br>(Whiteywood) | 51 | 11.78% | 6.38% | 11.94% | 30.09 |
| *Dacrydium cupressinum*<br>(Rimu) | 21 | 4.85% | 2.63% | 6.13% | 13.60 |
| *Fuchsia excorticata*<br>(Fuchsia) | 16 | 3.69% | 2.00% | 1.11% | 6.80 |
| *Knightia excelsa*<br>(Rewarewa) | 8 | 1.85% | 1.00% | 1.99% | 4.84 |
| *Pseudopanax arboreus*<br>(Fivefinger) | 10 | 2.31% | 1.25% | 1.23% | 4.79 |
| *Weinmannia racemosa*<br>(Kamahi) | 11 | 2.55% | 1.38% | 0.61% | 4.53 |
| *Myrsine australis*<br>(Mapou) | 9 | 2.08% | 1.13% | 0.36% | 3.57 |
| *Aristotelia serrata*<br>(Wineberry) | 6 | 1.39% | 0.75% | 0.16% | 2.30 |
| *Carpodetus serratus*<br>(Marbleleaf) | 4 | 0.92% | 0.50% | 0.86% | 2.28 |
| *Prumnopitys taxifolia*<br>(Miro) | 5 | 1.15% | 0.63% | 0.48% | 2.25 |
| *Pseudowintera colorata*<br>(Horopito) | 3 | 0.69% | 0.38% | 0.72% | 1.79 |
| *Pseudopanax crassifolius*<br>(Lancewood) | 4 | 0.92% | 0.50% | 0.13% | 1.55 |
| *Podocarpus totara*<br>(Totara) | 3 | 0.69% | 0.38% | 0.47% | 1.54 |
| *Pinus radiata*<br>(Pine) | 3 | 0.69% | 0.38% | 0.16% | 1.22 |
| *Pittosporum eugenioides*<br>(Lemonwood) | 1 | 0.23% | 0.13% | 0.21% | 0.57 |
| *Dacrycarpus dacrydioides*<br>(Kahikatea) | 1 | 0.23% | 0.13% | 0.01% | 0.37 |
| *Coprosma grandifolia* | 1 | 0.23% | 0.13% | 0.01% | 0.36 |
| *Streblus heterophyllus*<br>(Turepo) | 1 | 0.23% | 0.13% | <0.01% | 0.36 |

**Table 2.2:** Results from random point-centred quarter survey on Tiritiri Matangi.

| Species (Common Name) | Sample Size | Relative Frequency | Relative Density | Relative Basal Area | Importance Value Index |
|---|---|---|---|---|---|
| *Metrosideros excelsa* (Pohutukawa) | 191 | 18.75% | 23.90% | 52.51% | 95.16 |
| *Melicytus ramiflorus* (Whiteywood) | 146 | 18.55% | 18.25% | 10.87% | 47.67 |
| *Cordyline australis* (Cabbage Tree) | 134 | 16.97% | 16.75% | 4.64% | 38.36 |
| *Dysoxylum spectabile* (Kohekohe) | 60 | 5.43% | 7.50% | 8.62% | 21.55 |
| *Coprosma macrocarpa* | 61 | 9.50% | 7.63% | 2.64% | 19.77 |
| *Kunzea ericoides* (Kanuka) | 34 | 4.07% | 4.25% | 5.02% | 13.34 |
| *Cyathea dealbata* (Ponga) | 43 | 5.66% | 5.38% | 1.96% | 12.99 |
| *Leptospernum scoparium* (Manuka) | 30 | 4.30% | 3.75% | 4.35% | 12.40 |
| *Myrsine australis* (Mapou) | 31 | 4.53% | 3.88% | 0.77% | 9.17 |
| *Vitex lucens* (Puriri) | 16 | 2.72% | 2.00% | 4.06% | 8.78 |
| *Pittosporum crassifolium* (Karo) | 14 | 2.49% | 1.75% | 1.41% | 5.65 |
| *Sophora chathamica* (Kowhai) | 14 | 2.26% | 1.75% | 1.39% | 5.40 |
| *Coprosma robusta* | 6 | 1.12% | 0.75% | 0.29% | 2.16 |
| *Coprosma repens* | 4 | 0.91% | 0.50% | 0.13% | 1.54 |
| *Coprosma areolata* | 4 | 0.68% | 0.50% | 0.09% | 1.27 |
| *Pseudopanax arboreus* (Fivefinger) | 3 | 0.68% | 0.38% | 0.20% | 1.25 |
| *Beilschmiedia tawaroa* (Tawa) | 1 | 0.23% | 0.13% | 0.85% | 1.21 |
| *Entelea arborescens* (Whau) | 3 | 0.23% | 0.38% | 0.03% | 0.64 |
| *Melicope ternata* (Wharangi) | 2 | 0.23% | 0.25% | 0.01% | 0.49 |
| *Rhopalostylis sapida* (Nikau) | 1 | 0.23% | 0.13% | 0.12% | 0.47 |
| *Knightia excelsa* (Rewarewa) | 1 | 0.23% | 0.13% | 0.03% | 0.39 |
| *Geniostoma rupestre* (Hangehange) | 1 | 0.23% | 0.13% | <0.01% | 0.36 |

**Table 2.3:** Results from random point-centred quarter survey at Wenderholm.

| Species<br>(Common Name) | Sample Size | Relative Frequency | Relative Density | Relative Basal Area | Importance Value Index |
|---|---|---|---|---|---|
| *Cyathea dealbata*<br>(Ponga) | 251 | 24.41% | 34.91% | 14.88% | 74.20 |
| *Kunzea ericoides*<br>(Kanuka) | 75 | 12.80% | 10.43% | 19.49% | 42.73 |
| *Peischmiedia tarairi*<br>(Taraire) | 93 | 11.85% | 12.93% | 16.41% | 41.20 |
| *Rhopalostylis sapida*<br>(Nikau) | 79 | 11.85% | 10.99% | 8.89% | 31.72 |
| *Vitex lucens*<br>(Puriri) | 16 | 3.08% | 2.23% | 11.49% | 16.79 |
| *Corynocarpus laevigatus*<br>(Karaka) | 21 | 3.79% | 2.92% | 6.45% | 13.16 |
| *Podocarpus totara*<br>(Totara) | 14 | 2.84% | 1.95% | 6.29% | 11.07 |
| *Hoheria populnea*<br>(Lace Bark) | 22 | 3.32% | 3.06% | 2.33% | 8.71 |
| *Sophora chathamica*<br>(Kowhai) | 14 | 2.84% | 1.95% | 3.54% | 8.33 |
| *Coprosma tenuifolia* | 28 | 3.08% | 3.89% | 1.06% | 8.04 |
| *Dysoxylum spectabile*<br>(Kohekohe) | 18 | 1.65% | 2.50% | 2.21% | 6.36 |
| *Dacrycarpus dacrydioides*<br>(Kahikatea) | 13 | 2.13% | 1.81% | 1.70% | 5.64 |
| *Melicytus ramiflorus*<br>(Whiteywood) | 15 | 3.08% | 2.09% | 0.41% | 5.58 |
| *Myrsine australis*<br>(Mapou) | 15 | 3.08% | 2.09% | 0.21% | 5.38 |
| *Beilschmiedia tawaroa*<br>(Tawa) | 7 | 1.42% | 0.97% | 1.01% | 3.40 |
| *Knightia excelsa*<br>(Rewarewa) | 7 | 1.42% | 0.97% | 0.59% | 2.98 |
| *Pittosporum eugenioides*<br>(Lemonwood) | 4 | 0.94% | 0.56% | 0.76% | 2.26 |
| *Coprosma areolata* | 5 | 1.19% | 0.70% | 0.05% | 1.94 |
| *Macropoper excelsum*<br>(Kawakawa) | 3 | 0.71% | 0.42% | 0.33% | 1.46 |
| *Geniostoma rupestre*<br>(Hangehange) | 3 | 0.71% | 0.42% | 0.06% | 1.19 |
| *Agathis australis*<br>(Kauri) | 1 | 0.24% | 0.14% | 0.80% | 1.18 |
| *Schefflera digitata*<br>(Pate) | 3 | 0.71% | 0.42% | 0.02% | 1.15 |
| *Prumnopitys taxifolia*<br>(Matai) | 2 | 0.47% | 0.28% | 0.35% | 1.10 |
| *Cordyline australis*<br>(Cabbage Tree) | 2 | 0.47% | 0.28% | 0.30% | 1.05 |
| *Alectryon excelsus*<br>(Titoki) | 1 | 0.24% | 0.14% | 0.18% | 0.56 |
| *Phyllocladus trichomanoides*<br>(Tanekaha) | 1 | 0.24% | 0.14% | 0.06% | 0.44 |
| *Melicope ternata*<br>(Wharangi) | 1 | 0.24% | 0.14% | 0.03% | 0.40 |
| *Rhabdothamnus solandri*<br>(Kaikaiatua) | 1 | 0.24% | 0.14% | 0.02% | 0.40 |
| *Lophomyrtus obcordata*<br>(Rohutu) | 1 | 0.24% | 0.14% | 0.02% | 0.40 |
| *Pseudopanax crassifolius*<br>(Lancewood) | 1 | 0.24% | 0.14% | 0.02% | 0.40 |
| *Streblus heterophyllus*<br>(Turepo) | 1 | 0.24% | 0.14% | 0.01% | 0.39 |
| *Coprosma grandifolia* | 1 | 0.24% | 0.14% | 0.01% | 0.39 |

## 2.3.2 Forest Maturity

The tree diameter and distance values were not normally distributed. Differences between these values were therefore analysed using a non-parametric Kruskall Wallis test and post-hoc Mann-Whitney *U* comparisons. The mean distance between the sampled trees and their sampling points was found to differ significantly among all three sites (Table 2.4, Figure 2.3). The Benneydale trees were the most distant while the Tiritiri Matangi trees were the closest to the sampling point (Table 2.4, Figure 2.3). The mean diameter of the trees was greater at Benneydale than at Tiritiri Matangi (Table 2.4, Figure 2.4). The diameter of the trees at Wenderholm was not significantly different from either of the other two sites (Table 2.4, Figure 2.4).

**Table 2.4:** Result of Kruskal Wallis Test comparing mean distance from sampling point and mean diameter of the trees sampled at each site, Benneydale (B), Tiritiri Matangi (T) and Wenderholm (W). Test statistics are $H_{\mathrm{df}}$ for Kruskal Wallis and *U* for post-hoc Mann Whitney *U* Tests. Post-Hoc tests were subject to a Bonferroni correction that reduced the significance threshold to 0.016. Statistically significant results are highlighted in bold.

| **Variable** | **Kruskal Wallis Test** | **Mann-Whitney *U* Comparisons** | | |
|---|---|---|---|---|
| | | **Sites** | **Test Statistic** | **$p$ value** |
| Distance from sampling point | $H_{2} = 45.64$<br>**$p < 0.01$** | B vs T | $U = 259511$ | **<0.01** |
| | | B vs W | $U = 250836$ | **<0.01** |
| | | W vs T | $U = 266653$ | **0.01** |
| Diameter | $H_{2} = 10.82$<br>**$p < 0.01$** | B vs T | $U = 289606$ | **<0.01** |
| | | B vs W | $U = 270444$ | 0.04 |
| | | W vs T | $U = 278694$ | 0.30 |

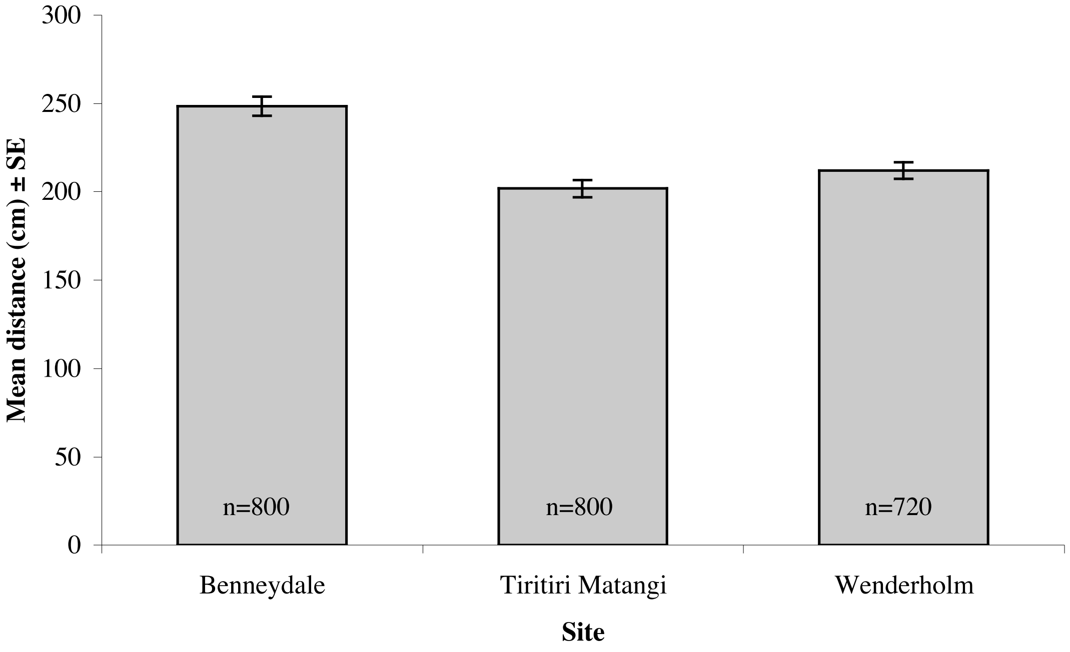


**Figure 2.3:** The mean distance from the sampling point of the trees sampled at each site. Error bars represent ± the standard error.

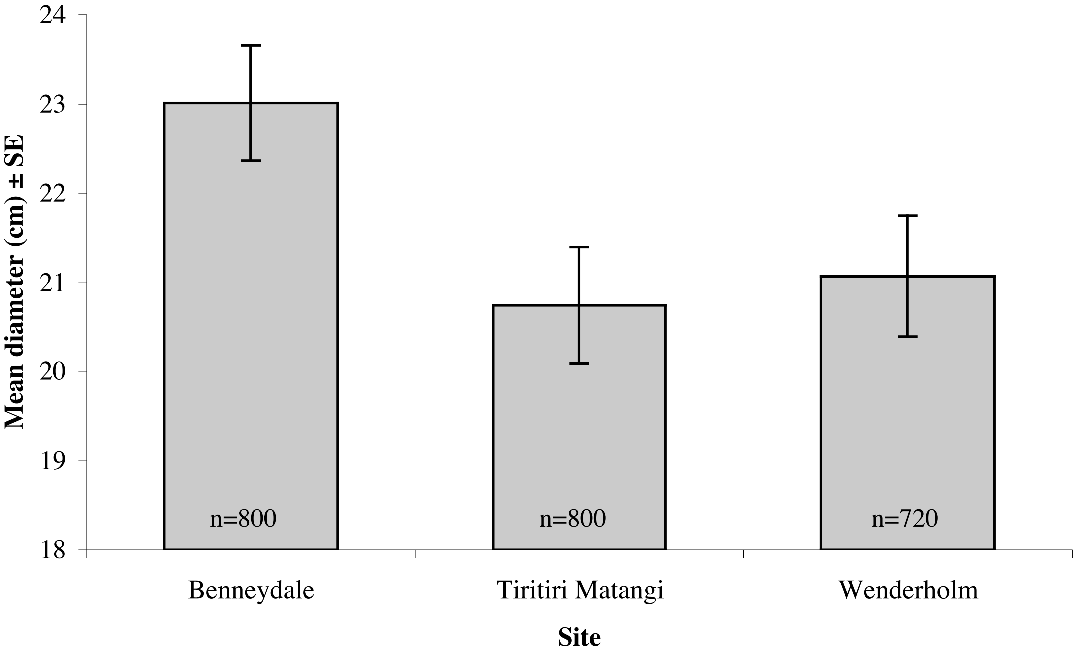


**Figure 2.4:** The mean diameter of the trees sampled at each site. Error bars represent ± the standard error.

### 2.3.3 Forest Structure

Chi-squared analyses were carried out to compare the number of species intercepting the PHI vertical line within each of the five height categories. Vertical forest structure differed significantly between the three sites ($x^2_8$= 176.0, $p$<0.001). The Benneydale forest showed fewer species intercepting the line between 0.2 and 4.0 m while the Tiritiri Matangi forest showed fewer species intercepting the line above 4.0 m (Figure 2.5)

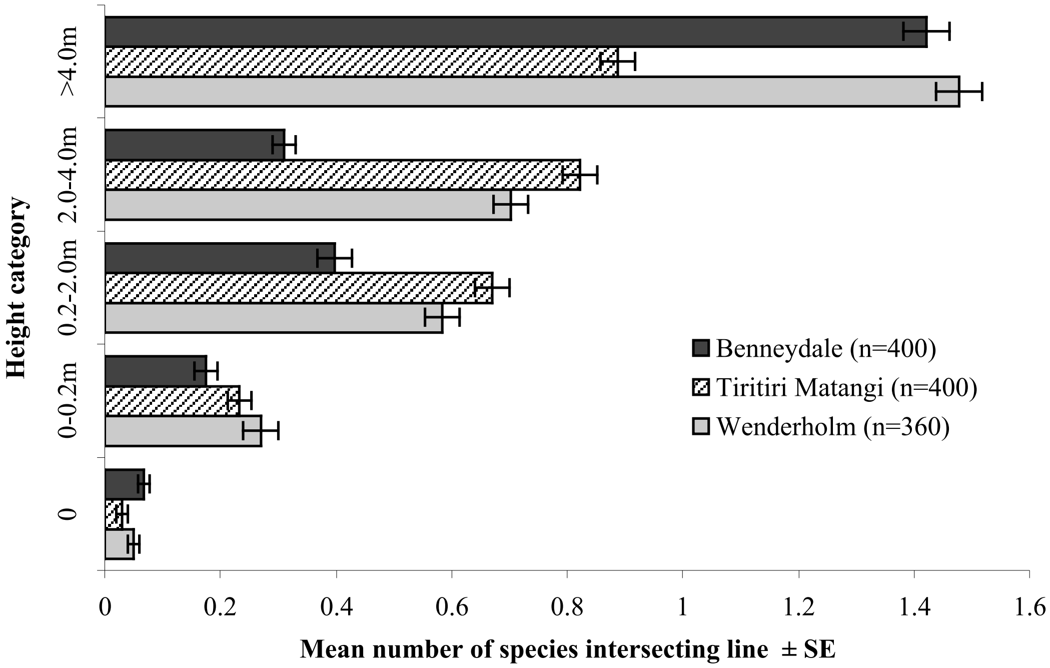


**Figure 2.5:** The mean number of species intercepting the PHI lines in each height category. Coloured bars represent each of the three sites. Error bars represent ± the standard error

A Kruskall Wallis test and accompanying post-hoc Mann-Whitney *U* comparisons were used to compare the mean height of the forest canopy among the sites. There was a significant difference in canopy height across all three sites (Table 2.5). The Benneydale forest canopy was the highest, followed by Wenderholm and Tiritiri Matangi respectively (Figure 2.6).

**Table 2.5:** Result of Kruskal Wallis test comparing the mean canopy height at all sites, Benneydale (B), Tiritiri Matangi (T) and Wenderholm (W). Test statistics are $H_{df}$ for Kruskal Wallis and $U$ for post-hoc Mann-Whitney $U$ tests. Post-hoc tests were subject to a Bonferroni correction that reduced the significance threshold to 0.016. Statistically significant results are highlighted in bold.

| **Kruskal Wallis Test** | **Mann-Whitney *U* Comparisons** | | |
|---|---|---|---|
| | **Sites** | **Test Statistic** | ***p* -value** |
| $H_2 = 499.89$<br>**$p$ < 0.01** | B vs T | $U$ =15407 | **<0.01** |
| | B vs W | $U$ =32803 | **<0.01** |
| | W vs T | $U$ =13481 | **<0.01** |

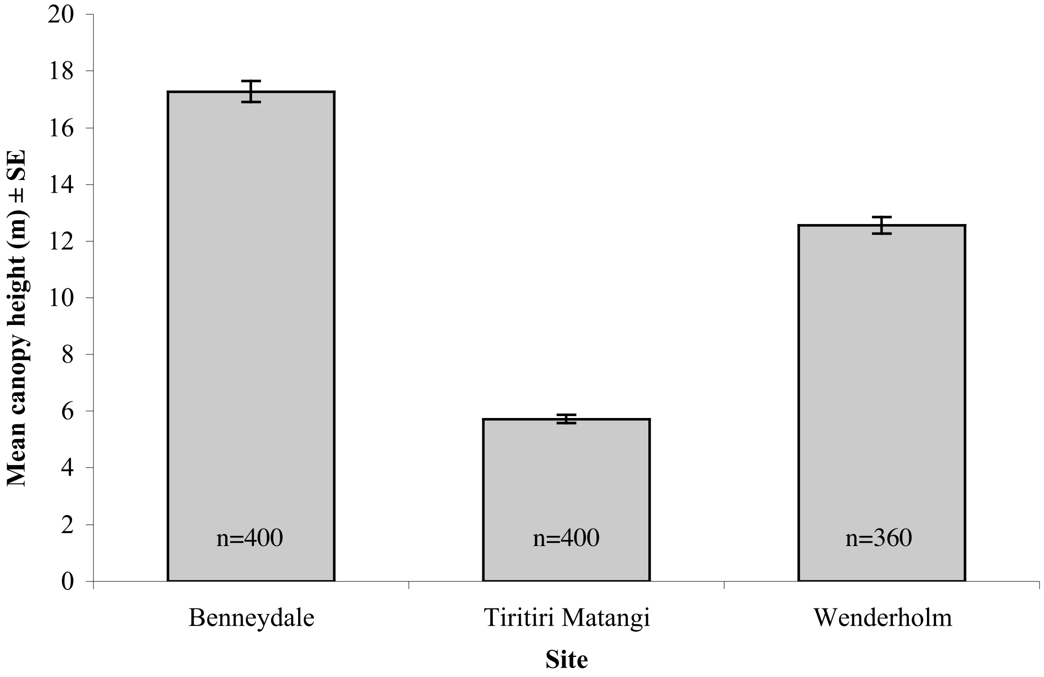


**Figure 2.6:** The mean canopy height at each site. Error bars represent ± the standard error.

**Plate 2.2:** The tawa forest habitat typical of the Benneydale site (photograph by B. Whitwell)

**Plate 2.3:** The regenerating forest of Tiritiri Matangi. The dominant species, pohutukawa, is visible in the centre of the picture (photograph by W. Ji)

**Plate 2.4:** The forest of Wenderholm Regional park. Young nikau palms are visible in the understorey and a puriri trunk dominates the foreground (photograph by T. Lovegrove)

## *2.4 Discussion*

### 2.4.1 Forest Composition

The species composition of the forests was highly disparate among the three sites. Large tawa trees and numerous ponga tree ferns dominated the Benneydale forest patches. Other important species included whiteywood and rimu. Fuchsia, rewarewa, five finger, kamahi and mapou were also common but contributed less in terms of their importance scores. Less common species included marble leaf, miro, horopito, wineberry, totara, lancewood, and pine. *Coprosma grandifolia*, lemonwood, kahikatea and turepo were only recorded once at Benneydale.

The forest on Tiritiri Matangi was dominated primarily by pohutukawa, although whiteywood and cabbage trees were also important. *Coprosma macrocarpa,* kohekohe, kanuka, manuka and ponga ferns were common while puriri, mapou, karo and kowhai were less common. Three other *Coprosma* species (*C. robusta*, *C. repens* and *C. areolata*), five finger, whau and wharangi were rare, while tawa, nikau, rewarewa and hangehange were only recorded once.

The Wenderholm forest was dominated by ponga with other important species including kanuka, taraire and nikau. Puriri, karaka, totara and kowhai also featured prominently. *Coprosma tenuifolia,* lace bark, kohekohe, kahikatea, whiteywood and mapou were present but were encountered relatively infrequently. The least common species recorded in the Wenderholm forest were *Coprosma areolata*, tawa, rewarewa, lemonwood, kawakawa, matai, cabbage tree, hangehange, and pate. Nine other species were only encountered once.

The vast differences in species composition are likely to correspond to differences in the structure of the available habitat. The tawa trees that dominate

Benneydale are typically very tall and sturdy, with dense foliage. The ponga tree ferns that dominate Wenderholm, however, are usually small with an exposed trunk and only a crown of fronds at the top in which a robin can easily conceal a nest (pers. obs.). Variation in the tree species composition of the sites may also affect the invertebrate prey species available to birds such as robins. The species richness of phytophagous insects has been shown to vary between some tree species (Kennedy and Southwood, 1984). Differences in the availability of specific tree species and their associated invertebrate species may affect nest site selection by robins at the study sites. This effect could have important implications for the interpretation of differences in North Island robin nest characteristics.

### 2.4.2 Forest Maturity

The trees sampled at Benneydale had the thickest trunks and were the most widely dispersed of the three sites. In contrast, Tiritiri Matangi trees had the smallest trunks and were generally closer together. The mean diameter of the trees sampled at Wenderholm was intermediate between the other two sites. The spacing between the Wenderholm trees was also intermediate and did not differ significantly from either Benneydale or Tiritiri Matangi. These characteristics indicate that the Benneydale forest was the most mature, while the Tiritiri Matangi forest was the least mature. This finding is consistent with the known history of Tiritiri Matangi Island. The early Maori inhabitants of Tiritiri Matangi cleared most of the original forest on the island (Armstrong and Ewan, 2002). Later, following the arrival of Europeans, the island was converted to farmland for the grazing of livestock (Armstrong and Ewan, 2002). By the time management of the island was taken over by the Hauraki Gulf Maritime

Park Board in 1971 the island was covered almost entirely in pasture with some forest patches remaining in steep gullies (Armstrong and Ewan, 2002; Graham and Veitch, 2002). The revegetation of Tiritiri Matangi only began in 1979 (Armstrong and Ewan, 2002; Graham and Veitch, 2002). As a result, the vegetation on the island is relatively young compared with the other sites in the study. Differences in forest maturity should be taken into account when interpreting differences in robin nest site characteristics across the three sites. More mature forests are likely to provide nest sites with different characteristics than those available in younger forests. In particular, mature forests may offer an increased availability of nest sites that are situated on larger branches or next to thicker trunks. Such sites may be more protected from adverse weather than nest sites in younger forests (Murphy 1983). Mature forests have also been observed to produce more woody debris and leaf litter, which may enhance invertebrate food sources (Diez *et al*., 2001; Evans *et al*., 1993). Variations in the availability of food resources and nest sites that are protected from the elements may alter the nest site selection criteria used by the robins. Such an effect could confound the interpretation of nest site differences in relation to mammalian predation or mammalian predator recognition.

### 2.4.3 Forest Structure

Benneydale and Wenderholm both had taller forest canopies and higher diversities of tree species contributing to the canopy than Tiritiri Matangi. Benneydale also had the lowest diversity of understorey species contributing to the forest structure between 0.2 m and 4.0 m. These differences suggest that the availability of specific nest site characteristics will vary across the three sites. The high canopy at

Benneydale for example, provides higher nest sites than would be available on Tiritiri Matangi. Equally, Tiritiri Matangi and Wenderholm are likely to provide an increased availability of nest sites that are situated in complex and diverse understorey vegetation. These differences need to be considered when comparing the characteristics of North Island robin nests at the three sites.

### 2.4.4 Conclusions

The results of this descriptive study illustrate that the forest habitats at Benneydale, Tiritiri Matangi and Wenderholm are quite different. It is clear that the use of such different habitats as a basis for a comparison of nest site selection in relation to mammalian predation is far from ideal. However, the limited distribution of North Island robins means that it is difficult to avoid using study sites with different forest structures. The habitat differences highlighted in this chapter will pose a significant challenge when attempting to interpret data relating to the nest site selection behaviours of North Island robins. However, by being aware of these differences it will be possible to take them into account when comparing robin nest site characteristics, and ensure that their confounding influences are not overlooked.

# CHAPTER THREE

## The Influence of Isolation from Mammalian Predators on the Nest Site Selection Behaviours of North Island Robins (*Petroica longipes*)

**Plate 3.1:** A robin nest (dark area in the centre of the photograph) concealed amongst the foliage of a tawa tree (photograph by B. Whitwell).

## Abstract

Plasticity in nest site selection behaviours allows birds to respond to changes in predation risk by selecting nest sites that balance this risk against other important factors. Isolation from mammalian predators, however, may result in individuals being incapable of recognising the risk associated with these predators. This study investigates how isolation from mammalian predators has affected the ability of North Island robins to alter nest site selection in response to changes in mammal densities. Point height intercept and point-centred quarter surveys were carried out at random points throughout the available habitat and around robin nests at three sites. Eight nest characteristic variables were recorded and analysed using a principal component analysis. Robins at Benneydale showed a preference for nesting in large tawa trees (*Bieschmiedia tawa*) and nested in areas with low levels of understorey complexity. Robins from Tiritiri Matangi and Wenderholm showed no tree species or forest complexity preferences. Forest maturity did not affect nest site selection. Nests at Benneydale were located in larger trees, were higher off the ground and were more concealed than nests on Tiritiri Matangi Island and at Wenderholm. While this result was expected, due to high mammal densities at Benneydale, it is confounded by the availability of large tawa trees, which were rare at the other sites. Nests at Tiritiri Matangi were supported by many small branches and were located toward the periphery of the trees. This result may be driven by the limited supply of larger trees on the island forcing robins to nest in smaller and shrubbier plants. Nest concealment from the ground was greater than aerial concealment at Benneydale and the opposite was observed on Tiritiri Matangi. However, this finding may again be confounded by habitat variations between the sites.

## *3.1 Introduction*

### 3.1.1 Predator-Induced Phenotypic Plasticity

The term "phenotypic plasticity" describes the ability of organisms to alter their phenotype in response to changes in their surrounding environment (Via and Lande, 1985). Environmental variables within the geographic range of a species are unlikely to be homogeneous in space or time. Phenotypic plasticity therefore offers a tool to allow individuals to maximise their fitness over a range of environments (DeWitt *et al*., 1998; Via *et al*., 1995). Environmental change has accelerated in recent decades as anthropogenic processes such as urban sprawl, deforestation and global warming alter the physical environment and invasion by exotic species alter the communities in which native species must survive (Daehler, 2003; Vitousek, 1994; Vitousek *et al*., 1997). As such, phenotypic plasticity is of considerable theoretical and practical interest to evolutionary biologists, ecologists and conservation biologists alike (Moore *et al*., 2008; Via *et al*., 1995).

Predator-induced phenotypic plasticity refers specifically to alterations in an individual's phenotype in response to changes in predator density or perceived predation risk. In these cases plasticity may involve physical changes in an individual's morphology (Freeman and Byers, 2006; Relyea, 2001) or physiological changes in the production of specific compounds (Harvell, 1990). One of the most frequently studied examples of predator-induced plasticity is the alteration of behaviour in response to changes in predation risk (Lima and Dill, 1990). Predator-induced behavioural plasticity has been documented in a number of taxa including zooplankton (Dobson, 1988), insects

(Juliano and Reminger, 1992; Rufaut and Gibbs, 2003), fish (Magurran, 1993), amphibians (Relyea, 2001), reptiles (Hoare *et al*., 2007) and birds (Eggers *et al*., 2006).

### 3.1.2 Predator-Induced Plasticity in Nest Site Selection

Behavioural studies have illustrated that many bird species show extensive behavioural plasticity in response to changing predator threats, particularly in breeding related behaviours. Plasticity has been documented in nest visitation rates, clutch sizes, inter-specific nesting associations and nest site selection (Eggers *et al*., 2006; Forstmeier and Weiss, 2004; Ghalambor and Martin, 2002; Larson, 2000; Peluc *et al*., 2008). Predation is the primary cause of nest failure for most bird species (Ricklefs, 1969). It is therefore expected that a major factor influencing nest site selection should be the minimisation of predation risk (Martin, 1992). It is often assumed that predation risk decreases with an increase in the density of vegetation immediately surrounding a nest. Greater foliage density is thought to inhibit the transmission of visual, chemical and auditory cues, and therefore conceal the nest from passing predators (Martin, 1993). It is also thought that dense and complex vegetation in the meters around the nest may reduce the ability of predators to locate the nest, even if the nest itself is not well concealed (Martin, 1993). Many authors have attempted to test these hypotheses. A meta-analysis by Martin (1992) found that in the majority of published studies, predation rates were lower for nests that were more concealed.

Although predation is an important cause of nest failure, there are also a number of opposing selection pressures that may act against the selection of nests sites for the prevention of predation. Nest sites that provide the most cover and the most protection from predation are often located high off the ground, or within the dense foliage at the ends of branches (Wilson and Cooper, 1998). In these peripheral sites nests are often supported by small, weak branches and are exposed to damage from high winds (Murphy, 1983; Wilson and Cooper, 1998). Dense foliage cover may also alter the ambient temperature in the nest. During a study of Siberian jay (*Perisoreus infaustus*) researchers found that nest sites selected by birds that had been exposed artificially to the calls of a known predator were located amongst denser vegetation. These nests were also on average 2.3°C colder than nest sites selected by unmanipulated birds (Eggers *et al.*, 2006). When selecting an optimal nest site, birds must therefore balance protection against predation with the risk of weather damage, the thermoregulatory requirements of the eggs and a range of other factors, such as food availability.

Birds are often subject to predation by a diverse suite of predators with differing foraging methods. The ability of a bird to optimise nest predation avoidance is therefore constrained by an inability to minimise the risk of predation by all predators at the same time (Liebezeit and George, 2002). For example, nesting higher in trees to avoid predation by land predators may put the nest at increased risk of predation by aerial predators. To select appropriate nest sites birds must be able to identify which predators present the greatest threat to nest survival. It is then possible to select nest sites that will minimise the risk of detection by those predators, potentially to the detriment of protection against a range of less common predators. The nests of dusky flycatchers (*Empidonax oberholseri*) in areas where they are preyed on primarily by birds have been shown to have different nest concealment and vegetation characteristics than in areas where they are preyed on by mammals (Liebezeit and George, 2002). To maximise nest survival by balancing predation risk against all other variables, nesting pairs must not only be able to identify the total risk of predation but also the types of risk.

### 3.1.3 Risk Assessment and Predator Isolation

The presence of key predators in the environment can have important effects on the behaviour of prey species. Prey individuals may reduce foraging, increase vigilance or alter nest site preferences or clutch size (Eggers *et al.*, 2006). When a prey species becomes isolated from key predators, costly anti-predator behaviours may be eliminated through natural selection. This process has been illustrated in the loss of group size effects from isolated populations of wallabies (*Macropus eugenii*), and in the reduction of flocking behaviour in a number of island bird populations (Beauchamp, 2004; Blumstein and Daniel, 2005; Blumstein *et al.*, 2004). The rate at which anti-predator behaviours can be lost varies considerably, and depends on the cost of the behaviour to the fitness of the actor and the degree to which the genetic basis for the behaviour is tied to other behavioural traits (Griffin *et al.*, 2000). Alternatively, the ability to perform an anti-predator behaviour may remain intact while the ability to recognise the predators for which the behaviour was initiated may be lost. As recognition is often a learned ability, it is likely to be among the first skills to be lost as a result of isolation. Learned abilities like recognition may be lost from a population in as little as one generation, while the genetic potential to perform a behaviour may remain intact (Blumstein, 2006; Kullberg and Lind, 2002).

Predator recognition is a key prerequisite to initiate predator-induced phenotypic plasticity. A prolonged period of isolation may therefore hinder an individual's ability to assess the likely risk of predation and select nest sites that will minimise this risk (Blumstein, 2006; Kullberg and Lind, 2002). Adjusting nest site selection behaviours requires the collection of relevant information about the local environment. If this information is unreliable then an appropriate behavioural response can not be initiated (DeWitt *et al.*, 1998). Similarly, behavioural responses will be impeded if reliable information is incorrectly interpreted due to a lack of recognition ability.

### 3.1.4 Risk Assessment and the North Island Robin

The North Island robin is currently found in a number of areas with very different suites of predators. In unprotected mainland sites robins are exposed to predation by avian predators including harriers (*Circus approximans*), moreporks (*Ninox novaeseelandiae*) and long-tailed cuckoos (*Eudynamys taitensis*, pers. obs.), as well as mammalian predators such as mustelids (*Mustela* spp.), cats (*Felis catus*), rats (*Rattus* spp.) and brushtail possums (*Trichosurus vulpecular*). On protected island sanctuaries such as Tiritiri Matangi, mammalian predators have often been removed and avian predators may be more abundant than at mainland sites (D. Armstrong pers. comm.). Between these two extremes are the ‘mainland island’ protected areas. Here mammalian predators are present, but their density has been reduced through intensive trapping and poisoning programmes (Saunders and Norton, 2001). Some reintroduced mainland robin populations have been founded by birds from mammalian predator free offshore islands. If this history of isolation has affected mammalian predator recognition in the resulting population, it is possible that individual robins may not be able to assess predation risk accurately. These birds may be unable to adjust their nest site selection criteria in response to the presence of mammalian predators. This could cause reintroduced robins to select nest sites that are at an increased risk of mammalian predation compared with naturally occurring mainland robins.

### 3.1.5 Aims and Hypotheses

The aim of this study was to investigate how isolation from mammalian predators has affected the ability of North Island robins to alter their nest site selection behaviours in response to changes in the density of these predators. There were two specific objectives. The first was to identify whether nest site characteristics differ between Benneydale and Tiritiri Matangi in a manner that suggests mammalian predation risk affects nest site selection. The second was to identify whether a history of isolation from mammalian predators has suppressed the ability of North Island robins at Wenderholm Regional Park to select nest sites that are appropriate in an environment where mammalian predators still pose a threat to nest survival. Three hypotheses with associated predictions are outlined below.

Hypothesis One

North Island robins select nest sites with specific characteristics. The tree species composition and structure of the vegetation directly surrounding the nest will therefore differ from that observed during random surveys of the available habitat.

The null hypothesis is that North Island robins select nest sites at random. In this case, the vegetation characteristics directly surrounding the nest will not differ from those observed during a random survey of the available habitat.

### Hypothesis Two

It is expected that the minimisation of predation risk is a major factor influencing nest site selection. The nest site characteristics of North Island robins will therefore differ between sites where mammalian predators are common and where there are no mammalian predators. Differences may include increased concealment and nest height at a site where mammalian predators occur.

The null hypothesis is that mammalian predator density does not affect nest site selection. In this case, nest site selection characteristics will not differ between a site with mammalian predators and one without.

### Hypothesis Three

North Island robins that have been reintroduced to the mainland following a period of isolation from mammalian predators will regain an ability to recognise these predators. They will therefore be able to select nest sites appropriate in an environment where mammalian predators pose a risk to nest survival. Nest site characteristics of reintroduced robins at a site where mammalian predators are controlled will be intermediate between sites where these predators are common and where they are absent.

The null hypothesis is that reintroduced robins will not be able to learn to recognise mammalian predators and will not be able to select nest sites that are appropriate where mammalian predators are present. In this case, nest site characteristics will not differ between sites where robins are isolated from mammalian predators and those where previously isolated robins have been reintroduced to a mainland site.

Predictions

- At all sites the tree species composition and structure of the habitat surrounding North Island robin nests will be different from that observed during random surveys of the available habitat.
- The nest sites of North Island robins at Benneydale will be higher off the ground, closer to the periphery of the tree, more visually concealed and placed in more complex vegetation than nest sites at Wenderholm Regional Park or on Tiritiri Matangi.
- The nest sites of North Island robins at Wenderholm will be higher off the ground, closer to the periphery of the tree, more visually concealed and placed in more complex vegetation than nest sites on Tiritiri Matangi.

## *3.2 Methods*

### 3.2.1 Study Species

This study focuses on the North Island robin. Prior to human colonisation the North Island robin occured throughout most of the North Island. Today, they are patchily distributed in just a few forested areas (Armstrong, 2000). It is unknown why this species has persisted in some forested areas but not others. It is thought however, that the primary cause of population decline among mainland populations is a high rate of predation upon nesting adult females by mammalian predators (Armstrong *et al.*, 2006; Boulton *et al.*, 2008).

### 3.2.2 Study Sites

This study compares the nest site selection behaviours of North Island robins from Tiritiri Matangi, Wenderholm Regional Park and Benneydale in the central North Island (Figure 2.1). Ten robin nests were investigated on Tiritiri Matangi, a site that is free of introduced mammalian predators. As it was founded by robins translocated from the North Island mainland in 1992-93, the Tiritiri Matangi robins represent a population that has become isolated from mammalian predators relatively recently (Armstrong, 2000).

Six nests were investigated in the predator controlled Wenderholm Regional Park mainland site. Four were located within the park while two were on nearby private land where rat control is carried out. The two nests that were outside the park were attended by the same male. As it is the female of the pair that builds the nest they were deemed to be independent of each other for the purposes of this investigation and both were included in the nest site selection analysis (Armstrong *et al*., 2000; Powlesland *et al*., 2000). North Island robins were reintroduced to Wenderholm from Tiritiri Matangi in 1999. As such, these robins represent a population that has become exposed to mammalian predators following a period of isolation from them.

Although rat control was carried out in some of the forest patches at Benneydale no attempt was made to control any other mammalian predators. As such, Benneydale represents a site where mammalian predators are relatively common. Although some of the robins at Benneydale have been translocated from other areas they have never been isolated from the effects of mammalian predators. A total of ten nests were investigated within seven forest patches at Benneydale.

At each site the random transects described in Chapter 2 were used to compare the nest sites selected by the robins with the habitat available. At Benneydale these transects were distributed among forest patches by allocating two random transects for every nest used in a forest patch. If two nests were used in a patch, then four random transects would be allocated to that patch. The transects were therefore representative of the habitat differences between the patches.

### 3.2.3 Forest Composition and Maturity

The species composition of the available forest habitat and the habitat directly surrounding the nests was assessed using a point-centred quarter (PCQ) survey (Mitchell, 2007). Details of the method are provided in Chapter 2. At Wenderholm, a total of 180 sampling points were assessed along 18 random transects. At Benneydale and Tiritiri

Matangi, 200 sampling points were assessed along 20 random transects. One PCQ sampling point was assessed at each of the robin nests resulting in a nest specific sample size of six at Wenderholm and ten each at Benneydale and Tiritiri Matangi. At each nest the sampling point was located on the ground directly below the nest.

### 3.2.4 Forest Structure

Vegetation structure and complexity was assessed using a basic point height intercept (PHI) survey (Park, 1973). Details of the method are provided in Chapter 2. At Wenderholm 360 random sampling points were assessed, while 400 each were assessed at Benneydale and Tiritiri Matangi. Thirteen PHI sampling points were assessed at each of the robin nests, resulting in a sample size of 78 at Wenderholm and 130 each at Benneydale and Tiritiri Matangi. At each nest the first sampling point was located directly below the nest. Three points were then placed 4.0 m apart to the north, south, east and west of the first point (Figure 3.1). The number of species intercepting the PHI line is considered a measure of vegetation complexity, with an increase in species intercepts representing an increase in complexity. Vegetation complexity in the area around the nest is associated with broad-scale nest concealment (Martin, 1993).

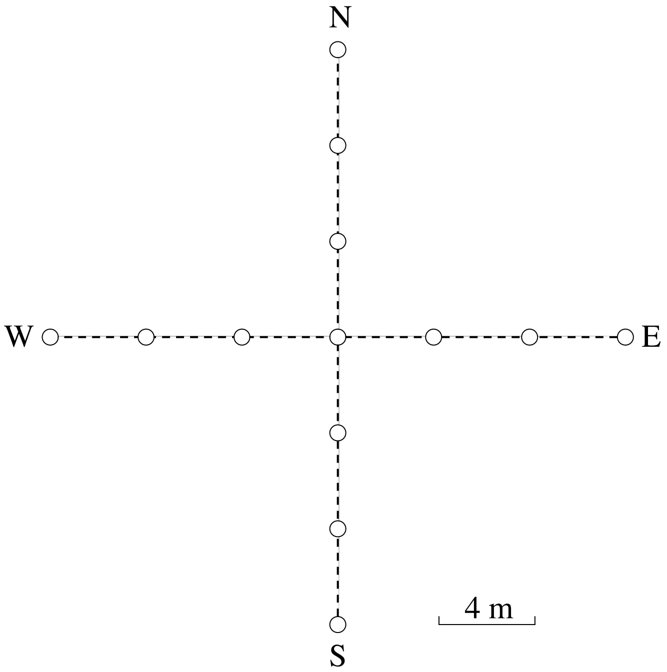


**Figure 3.1:** The orientation of PHI sampling points around the nest. Small circles indicate sampling points. The central point is located on the ground directly below the nest

## 3.2.5 Nest Characteristics

At each nest various nest characteristic variables were recorded in accordance with methods used in previous studies (Martin *et al.*, 1997; van Heezik *et al.*, 2008). These variables are summarised in Table 3.1. The species of the plant supporting the nest was identified and the location of the nest was recorded using a hand-held Garmin etrex GPS. The height of the nest and the tree were measured using an electronic clinometer and the diameter of the trunk at breast height was measured with a diameter tape. The number of branches supporting the nest was recorded while ensuring that only branches that were underneath the nest or woven into the nest were counted. No vertical trunks or branches were included. The mean diameter of the support branches was estimated from a distance by judging them against objects that were close at hand, such as a pencil or fallen branch. The number and size of the support branches provided an indication of small-scale vegetation complexity. The vertical placement ratio was calculated by dividing the nest height by the tree height. This provided a measure of the height of the nest as a proportion of the total tree height. The horizontal placement ratio was calculated by dividing the distance from the nest to the central stem by the distance from the central stem to the outer limit of the plant's foliage at the height of the nest. These distances were measured using a measuring tape on the ground. Nest concealment was assessed using a combination of ten scores that were allocated according to how visible the nest was from various positions. It was assessed how visible the nest would be to a ground predator at a horizontal distance of 8.0 m from four evenly spaced points around the nest (north, south, east and west). At each point a score between 0 and 3 was allocated, 0= nest is very visible, 1= nest is quite visible, 2= nest can be seen with difficulty, 3= nest can not be seen. It was then assessed how visible the nest would be to a predator flying over at a horizontal distance of 8.0 m from the same four points around the nest. Finally, it was assessed how visible the nest would be to a ground predator directly below the nest and to an aerial predator directly above the nest. All ten values were then added together to produce an overall nest concealment score with a maximum of 30 (van Heezik *et al.*, 2008).

**Table 3.1:** Nest characteristic variables

| **Variable** | **Details** |
|---|---|
| GPS location | Recorded using a handheld Garmin etrex GPS |
| Plant species | Species of plant in which the nest was built |
| Nest height (m) | Measured using an electronic clinometer |
| Plant height (m) | Measured using an electronic clinometer |
| Vertical placement ratio | Height of the nest / height of the tree |
| Horizontal placement ratio | Distance from nest to central stem / distance from central stem to plant edge |
| Trunk diameter at breast height | Measured using a diameter tape |
| Number of support branches | Only branches that were underneath or woven into the nest are included |
| Mean diameter of support branches | Estimated by judging sizes relative to objects at hand |
| Concealment | Composite index score with a maximum of 30 |

## 3.3 Analysis and Results

### 3.3.1 Forest Composition and Maturity

Chi-squared analyses were carried out to compare the number of individuals of the most dominant species observed during the random and nest surveys. Only the five most important species identified during the nest surveys at each site were included in the analysis. At Benneydale the tree species composition surrounding the nest was significantly different from the species composition observed during the random surveys ($x^2_4$= 46.5, $p<0.001$). Ponga (*Cyathea dealbata*) were under represented in the nest surveys while tawa trees (*Beilschmiedia tawa*) were over represented (Figure 3.2). At Wenderholm and on Tiritiri Matangi the tree species composition surrounding the nest did not differ significantly from that observed during the random surveys (Wenderholm, $x^2_4$= 0.09, $p=0.999$; Tiritiri Matangi $x^2_4$= 7.75, $p=0.101$) (Figures 3.3 and 3.4 respectively).

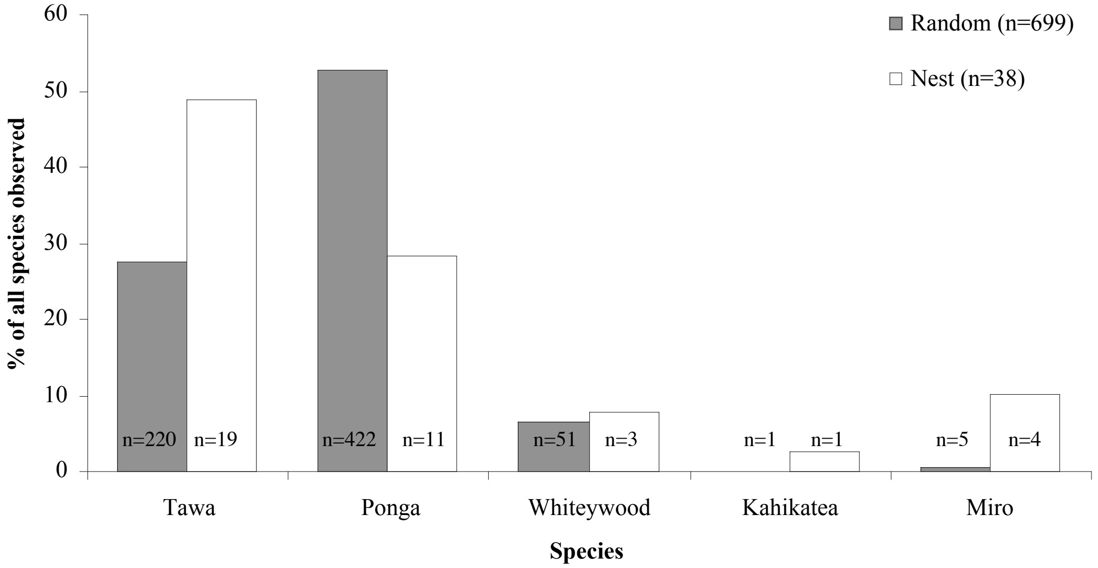


**Figure 3.2:** The percentage of five dominant tree species in the available habitat (Random) and in the area surrounding the robin nests (Nest) at Benneydale.

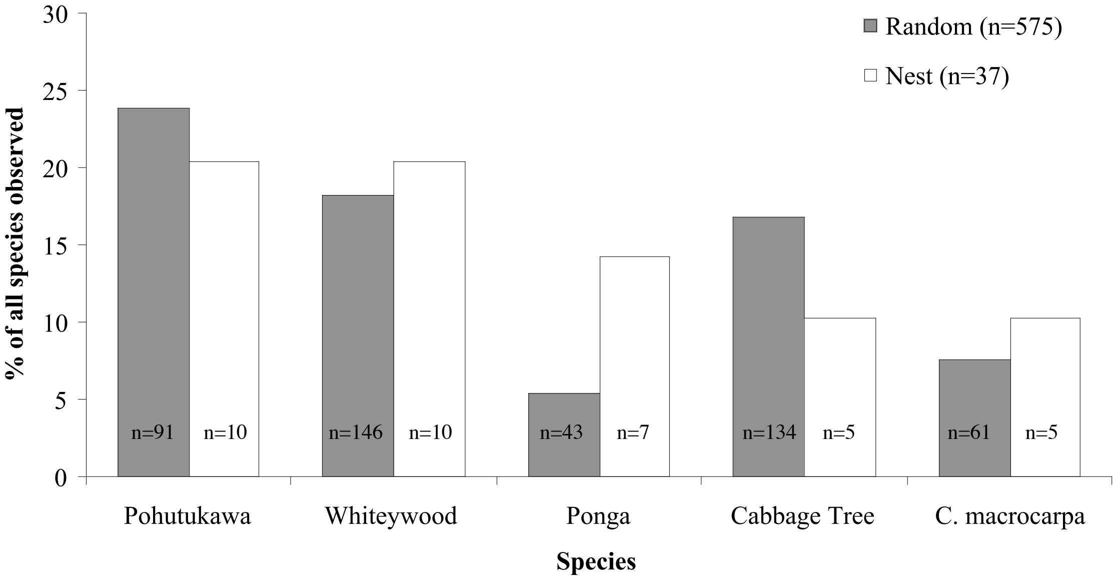


**Figure 3.3:** The percentage of five dominant tree species in the available habitat (Random) and in the area surrounding the robin nests (Nest) on Tiritiri Matangi.

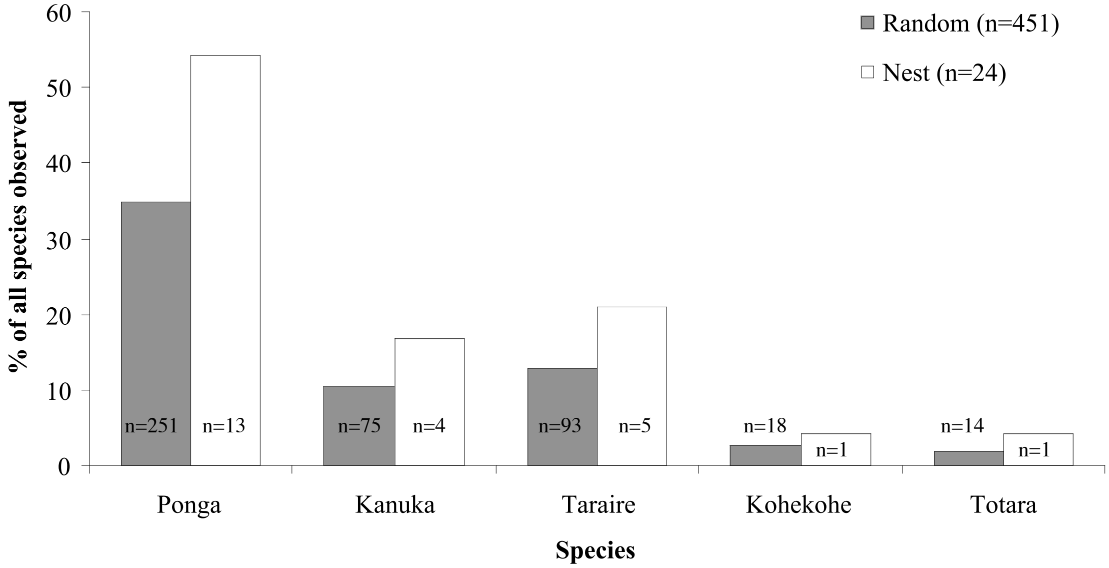


**Figure 3.4:** The percentage of five dominant tree species in the available habitat (Random) and in the area surrounding the robin nests (Nest) at Wenderholm.

The distances between the sampled trees and their sampling points and the diameters of the sampled trees were not normally distributed. As such, these values were compared between the random and nest surveys using non-parametric Mann-Whitney *U* tests. The mean distance of the trees from the sampling points did not differ significantly between the random and nest surveys at any of the sites (Table 3.2). There was also no significant difference between the mean diameter of the trees measured during the random surveys and the nest surveys (Table 3.2).

**Table 3.2:** Results of non-parametric test comparing mean distance from sampling point and mean diameter of the trees sampled during the random and nest surveys at each site.

| Variable | Site | Test Statistic | *p* value |
|---|---|---|---|
| Distance from sampling point | Benneydale | $U$ =14812 | 0.43 |
| | Tiritiri Matangi | $U$ =15322 | 0.65 |
| | Wenderholm | $U$ =8577 | 0.96 |
| Diameter | Benneydale | $U$ =13610 | 0.11 |
| | Tiritiri Matangi | $U$ =15040 | 0.52 |
| | Wenderholm | $U$ =7735 | 0.39 |

## 3.3.2 Forest Structure

Chi-squared analyses were carried out to compare the number of species intercepting the PHI vertical line within each of the five height categories during the random and nest surveys. Vertical forest structure differed significantly between the random surveys and the nest surveys at Benneydale ($x^2_4$= 16.4, p=0.002). On average, more species intercepted the vertical line between 0.2 and 2.0m and above 4.0m at random sampling points than at nest specific sampling points (Figure 3.5). On Tiritiri Matangi, the mean number of species intercepting the PHI lines is not significantly different between the random and nest surveys ($x^2_4$= 8.08, p=0.089) (Figure 3.6). The Wenderholm data also showed no significant difference between the random and nest surveys ($x^2_4$= 5.35, p=0.253) (Figure 3.7).

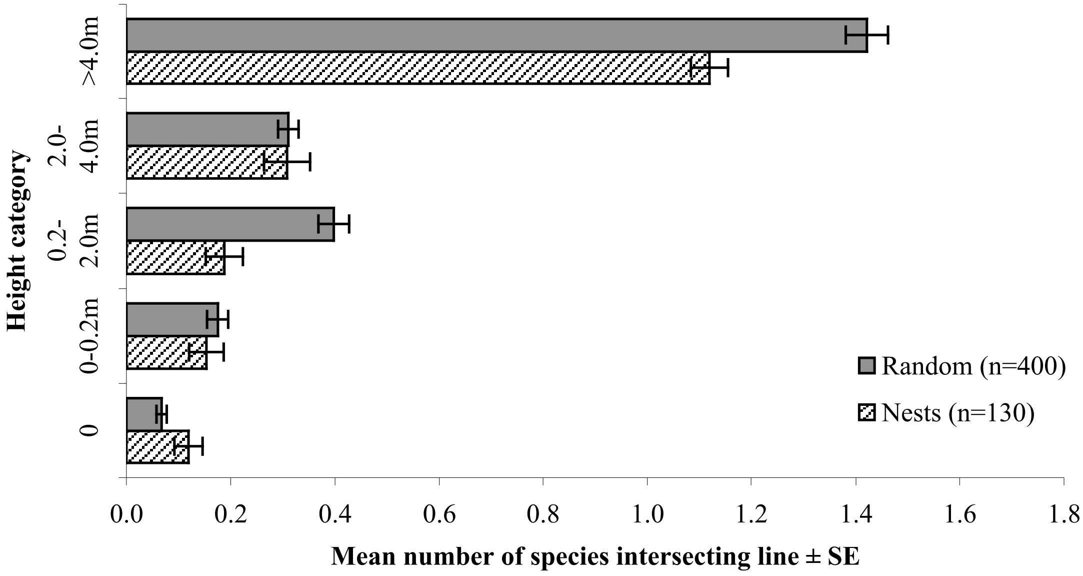


**Figure 3.5:** Mean number of species intercepting the PHI lines at Benneydale. Coloured bars represent the results from random and nest surveys. Error bars represent ± the standard error.

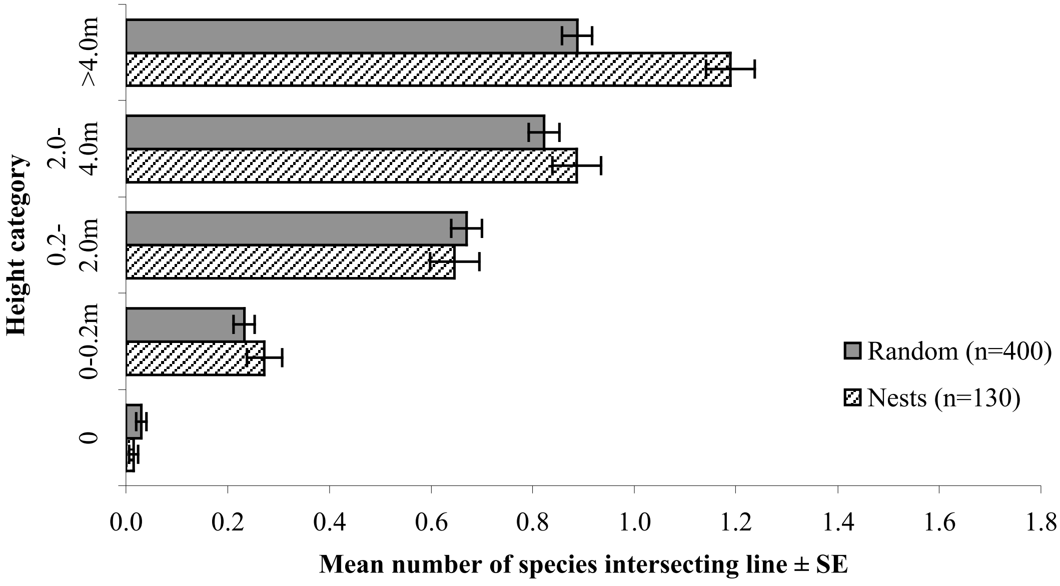


**Figure 3.6:** Mean number of species intercepting the PHI lines on Tiritiri Matangi. Coloured bars represent the results from random and nest surveys. Error bars represent ± the standard error.

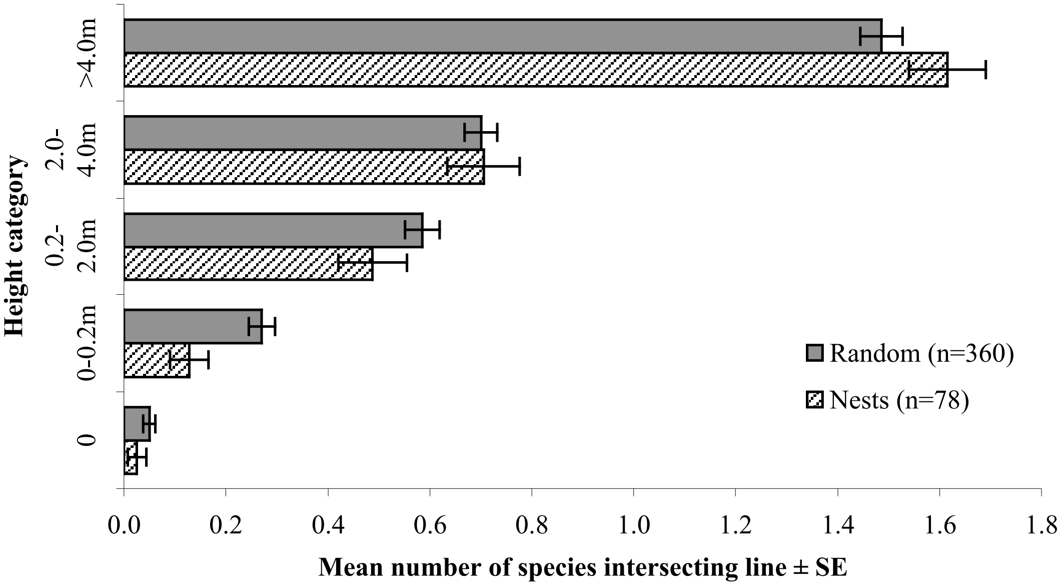


**Figure 3.7:** Mean number of species intercepting the PHI lines at Wenderholm. Coloured bars represent the results from random and nest surveys. Error bars represent ± the standard error.

### 3.3.3 Nest Characteristics

A Principal Component Analysis (PCA) based on a correlation similarity matrix was used to reduce the eight nest characteristic variables to a smaller number of independent components. All principal components with eigenvalues greater than 1.0 are reported (Table 3.3). These two principal components described 68% of the variation in the data. Factor scores resulting from these principal components were then used for further analyses. The PCA included a Varimax rotation of the axes to aid interpretation of the combinations of variables that contributed to each component (Jolliffe, 2002).

**Table 3.3:** Eigenvalues, variance explained and loadings of the original variables in the first two principal components extracted from the eight nest characteristic variables recorded. Variables with principal component values greater than 0.5 are highlighted in bold

| | **PC1** | **PC2** |
|---|---|---|
| Eigenvalue | 3.69 | 1.75 |
| % of variance | 46.07 | 21.85 |
| Cumulative % | 46.07 | 67.92 |
| Plant height | **0.87** | -0.40 |
| Nest height | **0.81** | -0.23 |
| Concealment | **0.76** | 0.40 |
| Trunk diameter | **0.73** | -0.18 |
| Number of support branches | -0.19 | **0.88** |
| Mean diameter of support branches | 0.38 | **-0.78** |
| Vertical placement ratio | -0.34 | **0.72** |
| Horizontal placement ratio | 0.20 | **0.54** |

Principal component 1 (PC1) was strongly correlated with nest concealment, plant trunk diameter, plant height and nest height (Table 3.3). PC2 was strongly correlated with the number and size of the branches supporting the nest and the vertical and horizontal placement ratios (Table 3.3). ANOVA analyses were carried out to determine if the resulting PC values differed significantly among the three sites. The mean of PC1 was significantly higher at Benneydale than at either of the other two sites (Table 3.4, Figure 3.8). This indicates that plant height, nest height, overall concealment and trunk diameter were all higher at Benneydale than at either of the other sites. There was no significant difference in the mean of PC1 between Tiritiri Matangi and Wenderholm (Figure 3.8). The mean of PC2 was significantly higher at Tiritiri Matangi than at Benneydale or Wenderholm (Table 3.4, Figure 3.9). This indicates that the number of support branches, and the vertical and horizontal placement ratios were all higher at Tiritiri Matangi, while the mean diameter of the support branches was lower. PC2 did not differ significantly between Benneydale and Wenderholm (Figure 3.9).

**Table 3.4:** Results of ANOVA analyses and post-hoc Tukey pair wise comparisons assessing differences among the mean values of Principal Components 1 and 2 across the three sites, Benneydale (B), Tiritiri Matangi (T) and Wenderholm (W). Statistically significant results are highlighted in bold.

| **Variable** | **ANOVA** | **Tukey pairwise comparisons** | |
|---|---|---|---|
| | | **Sites** | ***p* value** |
| PC1 | $F_{(2,25)}=11.39$<br>$\boldsymbol{p < 0.01}$ | B vs T | **0.01** |
| | | B vs W | **<0.01** |
| | | W vs T | 0.23 |
| PC2 | $F_{(2,25)}=9.80$<br>$\boldsymbol{p < 0.01}$ | B vs T | **<0.01** |
| | | B vs W | 0.99 |
| | | W vs T | **0.01** |

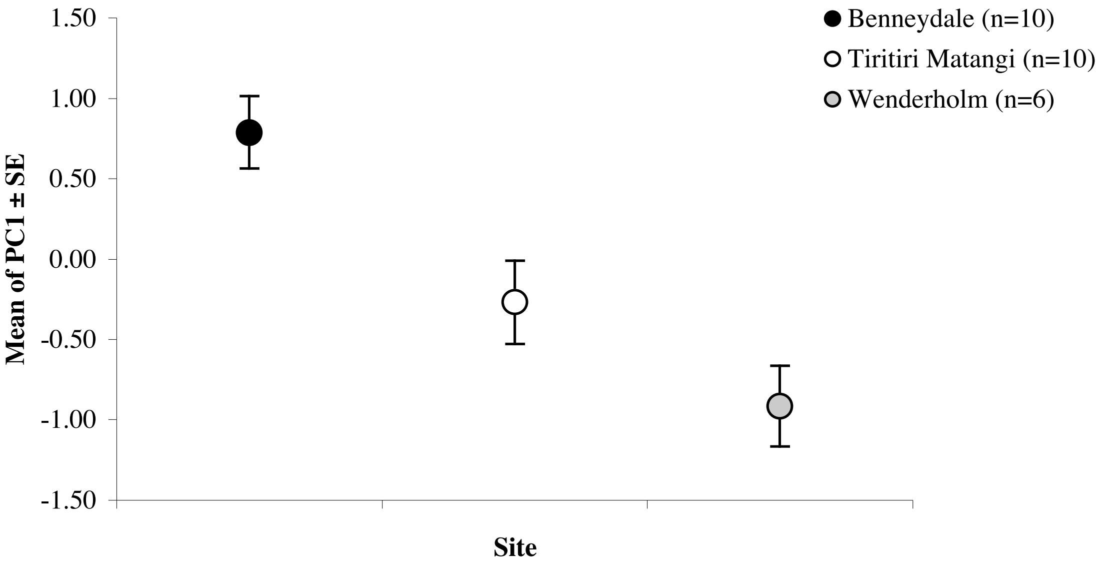


**Figure 3.8:** The mean of PC1 (nest height, plant height, trunk diameter, concealment) at all sites. Error bars represent ± the standard error.

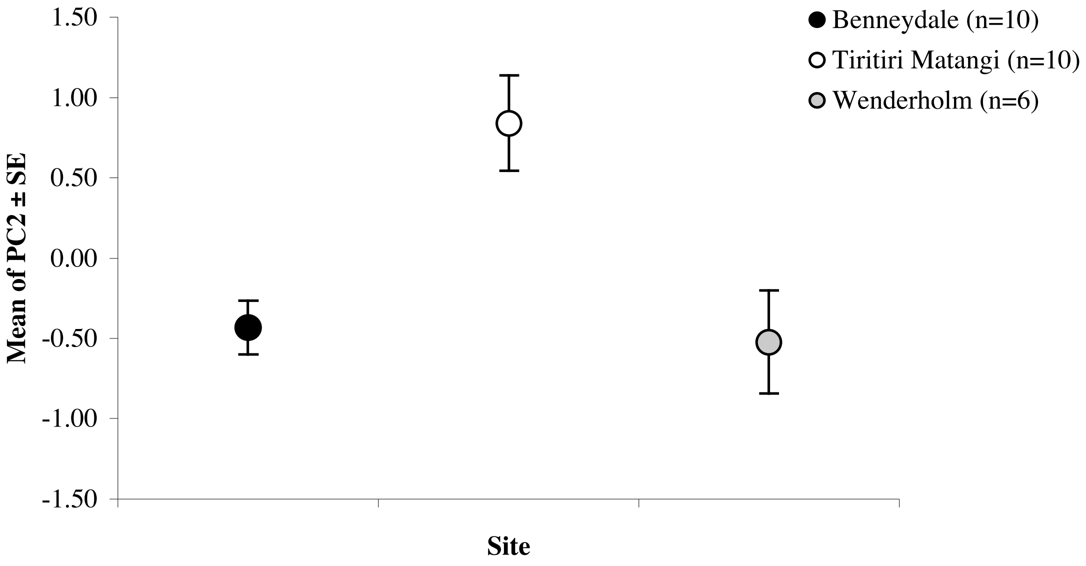


**Figure 3.9:** The mean of PC2 (Number and size of support branches, vertical and horizontal placement ratios) at all sites. Error bars represent ± the standard error.

### 3.3.4 Ground and Aerial Concealment

The nest concealment scores at the three sites were normally distributed with homogeneous variances. As such, paired sample t-tests were used to compare the concealment scores from the perspective of a ground predator with those from the perspective of an aerial predator. At Benneydale the mean of the ground concealment scores was significantly higher than the aerial concealment scores ($t_9$=2.69, p=0.03) (Figure 3.10). On Tiritiri Matangi the mean of the aerial concealment scores was greater than the ground concealment scores ($t_9$=-2.57, p=0.03) (Figure 3.11). There was no significant difference between the aerial and ground concealment scores at Wenderholm ($t_5$=-0.28, p=0.79) (Figure 3.12)

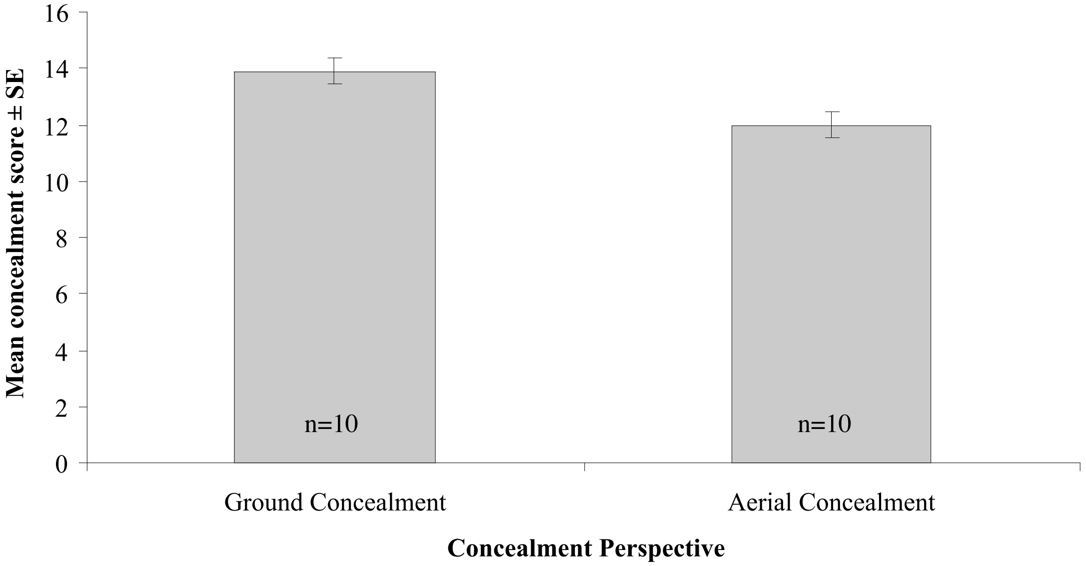


**Figure 3.10:** The mean of the concealment scores given from the perspective of a ground predator and an aerial predator at Benneydale. Error bars represent ± the standard error.

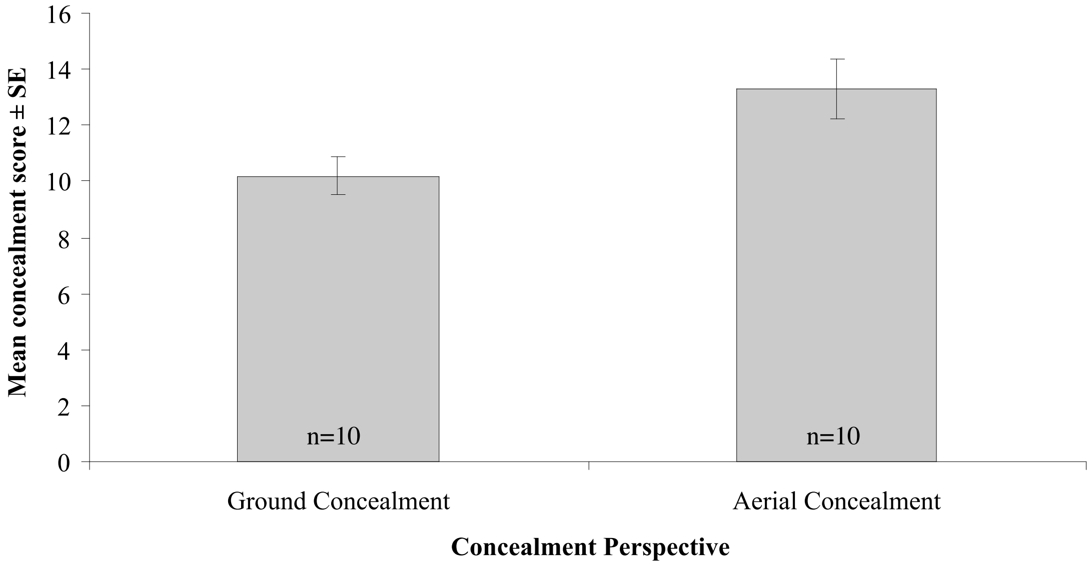


**Figure 3.11:** The mean of the concealment scores given from the perspective of a ground predator and an aerial predator at Tiritiri Matangi. Error bars represent ± the standard error.

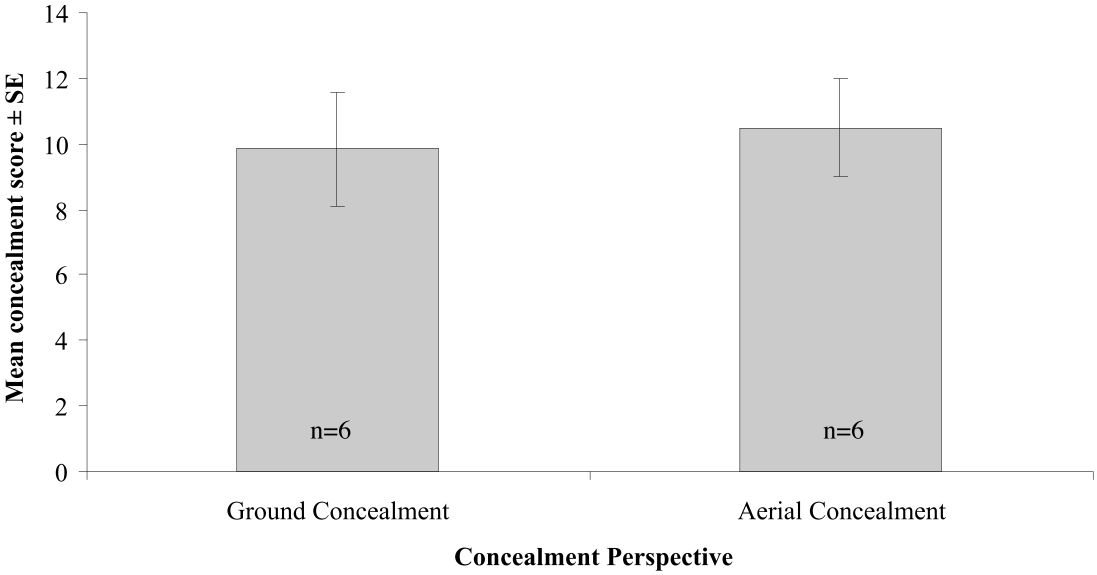


**Figure 3.12:** The mean of the concealment scores given from the perspective of a ground predator and an aerial predator at Wenderholm. Error bars represent ± the standard error.

Differences among the ground and aerial concealment scores recorded at each site were compared using one-way ANOVAs. Ground concealment varied significantly across the three sites ($F_{2,25} = 6.747$, $p = 0.005$). Post-hoc Tukey's HSD tests showed that the Benneydale nests were significantly more visually concealed from the ground than the Tiritiri Matangi or Wenderholm nests. There was no significant difference between the ground concealment scores at Tiritiri Matangi and Wenderholm. There was no significant difference among the aerial conceal scores recorded at the three sites ($F_{2,25} = 1.826$, $p = 0.184$).

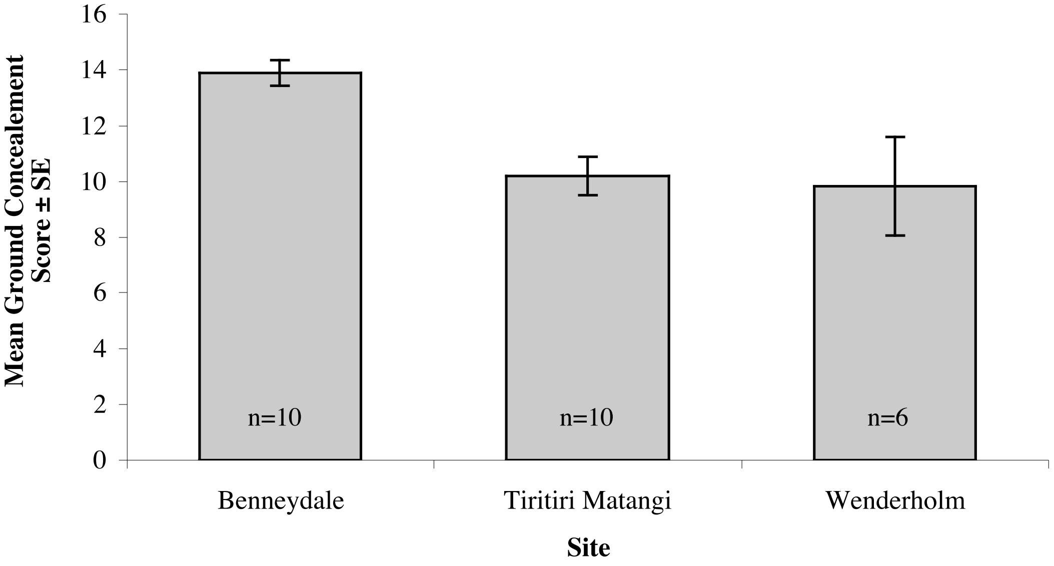


**Figure 3.13:** The mean of the ground concealment scores allocated to nests at each of the three sites. Error bars represent ± the standard error.

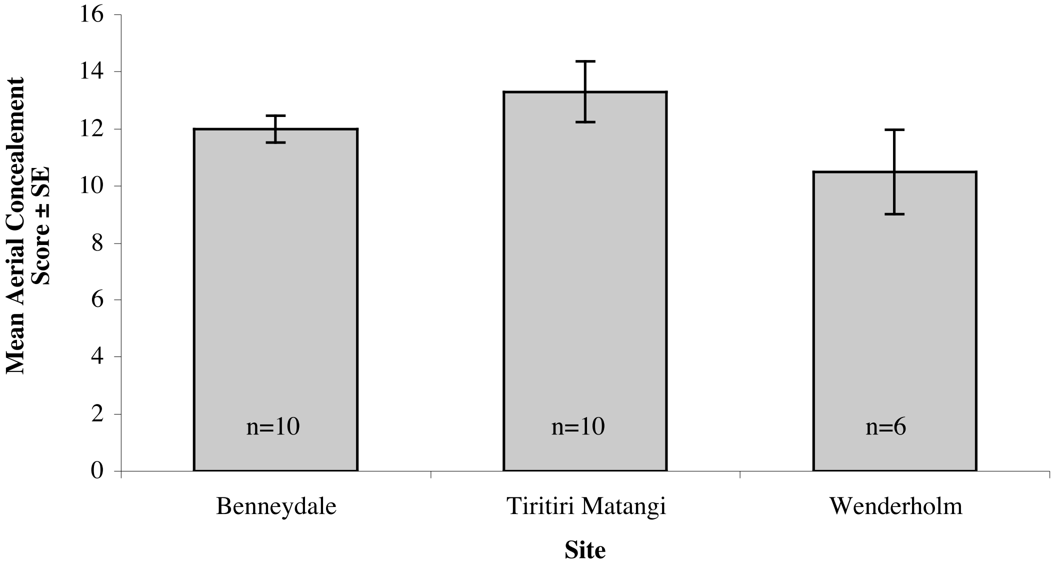


**Figure 3.14:** The mean of the aerial concealment scores allocated to nests at each of the three sites. Error bars represent ± the standard error.

## *3.4 Discussion*

### 3.4.1 Forest Composition and Maturity

The tree species composition differed significantly between the random and nest surveys carried out at Benneydale. This result provides evidence to support the hypothesis that robins select nest sites with specific characteristics, rather than choosing nest sites at random from the available habitat. At Benneydale nests, tawa trees were over represented while ponga tree ferns were under represent. This suggests that Benneydale robins prefer nesting in and around the taller and sturdier tawa trees over the shorter and more delicate ponga. The selection of nest sites that are dominated by tawa trees may reflect differences in food availability and quality. The species richness of phytophagous insect species is likely to vary between tree species (Kennedy and Southwood, 1984). It is more likely, however, that the preference for tawa is associated with a preference for building nests that are higher off the ground than would be possible in the relatively short ponga. Nesting in the tall tawa trees increases the opportunity for birds to nest higher to minimise the risk of predation from ground dwelling predators. In addition, a preference for nests that are associated with tawa trees may be a response to abiotic factors. Being surrounded by a stand of large tawa trees or building nests on the sturdy tawa branches may offer the nest protection from wind and weather damage.

No significant difference was found between the tree species identified during the random and nest surveys at both Wenderholm and Tiritiri Matangi. Robins at these sites did not show measurable preferences for nest sites associated with specific tree species. The robins at all three sites also failed to show measurable preferences for nest sites that are associated with forest maturity. These results suggest that forest composition is not an important nest site selection criterion for robins at Wenderholm and Tiritiri Matangi, while forest maturity is not an important factor at all three sites. It should be noted however, that the relatively small number of nests surveyed might have hindered the detection of statistically significant differences.

The distinct habitats available at the three sites, as described in Chapter 2, make it difficult to interpret differences in nest tree preferences. Tawa, which dominated the Benneydale forest, were rare at Wenderholm and Tiritiri Matangi. It is therefore impossible to identify whether the robins' preference for tawa trees at Benneydale was specific to the Benneydale birds. Robins from Wenderholm and Tiritiri Matangi may have shown the same preference if tawa trees were available.

### 3.4.2 Forest Structure

At Benneydale, the mean number of species intercepting the PHI line was higher between 0.2 and 2.0m and above 4.0m in the random surveys than in the nest surveys. This result suggests that nest site selection is not random in the North Island robin population at Benneydale. The result also indicates that the robins did not specifically select nest sites with greater degrees of canopy or understorey complexity. It has been suggested that high degrees of structural complexity surrounding nest sites may hamper the ability of ground predators to locate the nest (Martin, 1993). It would therefore be expected that Benneydale robins should select nest sites with increased structural complexity to minimise the relatively high risk of mammalian predation at the site. Alternatively, nest site preferences may represent a trade-off between concealment and the ability of parent birds to keep watch for potential predators (Gotmark *et al*., 1995). A study of song thrushes (*Turdus philomelos*) showed that breeding pairs did not select nest sites that maximised concealment. Instead, they selected areas with intermediate concealment, possibly to increase the incubating bird's view of the surrounding environment (Gotmark *et al*., 1995). The present study, however, does not indicate selection for intermediate vegetation complexity, but rather for low complexity. This result suggests that forest structure may not be an important nest site selection criterion for North Island robins. This would be consistent with the findings from Tiritiri Matangi and Wenderholm, where there was no significant difference between the vegetation structure recorded during the random and nest specific PHI surveys. The low complexity at Benneydale nests may be the consequence of a correlation between complexity, forest maturity, tree height and other factors affecting nest site selection, such as food availability or thermoregulatory requirements (Gotmark *et al*., 1995; Liebezeit and George, 2002).

### 3.4.3 Nest Characteristics

Principal component one was strongly correlated with concealment, trunk diameter, plant height and nest height, and was significantly higher at Benneydale than at either of the other sites. Greater plant height and trunk diameter values at Benneydale nests reflect the preference of robins for building nests in large tawa trees. The tawa trees at Benneydale were taller and wider than most of the trees at Wenderholm and Tiritiri Matangi (pers. obs.). As such, this result also reflects the variation in habitat characteristics between the sites. It is possible that robins at Wenderholm and Tiritiri

Matangi would select nest sites with these same traits if they were not constrained by the availability of such traits in their environment. Higher nests and greater nest concealment scores were expected at Benneydale due to the high mammalian predation risk at the site. This result could be interpreted as support for the hypothesis that mammalian predation risk will influence nest site selection by North Island robins. It should be noted however, that the high concealment values observed at Benneydale might simply be an artefact of a correlation between concealment and nest height. PC1 values did not differ between nests at Wenderholm and Tiritiri Matangi. Nests at both of these sites were characterised by being lower to the ground and more poorly concealed than the Benneydale nests. This is not consistent with the prediction that nests at Wenderholm should be higher and more concealed than the Tiritiri Matangi nests. The results of PC1 provide no evidence to support the hypothesis that reintroduced mainland robins will be able to select nest sites appropriate in an environment where mammalian predators pose a threat to nest survival. This finding may be a consequence of the rarity of mammalian predation at Wenderholm. During the breeding season mammal densities in the park are maintained at very low levels through an intensive trapping and poisoning regime (Lovegrove *et al.,* 2002). Where robins are known to breed outside the park, rat populations are controlled with poisons. This pest control regime has been very effective and mammalian predation on robin nests is rare (Lovegrove *et al.*, 2002). Mammalian predation at Wenderholm may therefore have only a limited influence on nest site preferences. It is not known how nest site preferences would develop in a population of naïve robins that is reintroduced into an environment where mammalian predators are not controlled. It is unlikely, however, that naïve robins would survive in such an environment long enough to observe any changes in nest site preferences. The translocation of 15 predator-trained South Island robins (*Petroica australis*) to a mainland site, where no predator control was being undertaken, failed when all the birds disappeared within six months (McLean *et al*., 1999). This issue, combined with the difficulty in obtaining permission for such a translocation, make it unlikely that a field experiment to test the effect of predator density on the development of appropriate nest site selection behaviours could be carried out.

PC2 was positively correlated with the number of branches supporting the nest and the vertical and horizontal placement ratios. It was also inversely correlated with the size of the branches supporting the nest. PC2 was higher at Tiritiri Matangi than at either Wenderholm or Benneydale. Higher vertical height ratios indicate that the Tiritiri Matangi robins nested further toward the tops of trees than the Benneydale and Wenderholm robins. This weakens the finding that Benneydale nests were higher off the ground as it suggests that nest height on Tiritiri Matangi was limited by the height of the trees. Again, the high degree of variation in habitat structure between the three sites has hindered the interpretation of nest site preferences. It is not possible to identify whether the Tiritiri Matangi robins would have nested lower than those at Benneydale and Wenderholm given a similar forest structure. The Tiritiri Matangi nests were also characterised by being supported by a large number of small branches and the nests were placed closer to the periphery of the tree. This finding is unusual since these characteristics are often thought to be typical of birds that are at a high risk of predation by ground predators (Murphy, 1983; Wilson and Cooper, 1998). The results of PC2 therefore provide no evidence to suggest that mammalian predation risk will affect nest site selection behaviours in North Island robins. The relatively high horizontal placement ratios and a large number of nests supported by many small branches on Tiritiri Matangi may again be a consequence of the disparate habitat types present at the three sites. The revegetation of Tiritiri Matangi only began in 1979 (Graham and Veitch, 2002). As a result, the vegetation on the island is relatively young compared with the other sites in the study. Robins on Tiritiri Matangi may therefore be forced to build nests in younger, smaller and shrubbier plants. The use of smaller trees would account for an inflated horizontal placement ratio as any movement away from the central stem would represent an increased proportion of the total distance to the periphery of the tree. The use of shrubbier trees with larger numbers of smaller branches would result in the nests being characterised by a greater degree of small-scale complexity. This explanation is consistent with the dominance of pohutukawa (*Metrosideros excelsa*) and whiteywood (*Melicytus ramiflorus*) on Tiritiri Matangi. Both of these species often have a shrubby structure when they are young (Esler, 1978; Poole and Adams, 1994).

### 3.4.4 Ground and Aerial Concealment

The North Island robin nests at Benneydale were more visually concealed from ground predators than aerial predators. Benneydale nests were also the more concealed from the ground than nests at either of the other sites. Tiritiri Matangi nests were more visually concealed from aerial predators than ground predators, but aerial concealment did not vary significantly among the three sites. This result is interesting as the Benneydale robins are likely to be most at risk from ground dwelling mammalian predators, while the Tiritiri Matangi robins are most at risk from aerial predators. This pattern of nest concealment suggests that the robins at these sites selected nest sites that are concealed preferentially from the suite of predators that poses the greatest threat to nest survival. There was no significant difference between aerial and ground concealment at Wenderholm. This may reflect the intermediate threat posed by both aerial and ground predators at Wenderholm compared with the other two sites. While this concealment pattern is expected given the relative abundances of different predators at the sites, it is far from conclusive evidence that predation risk influences the nest site selection behaviours of North Island robins. As discussed above, the Benneydale nests were typically higher off the ground due to the preferential use of tall tawa trees for nesting. This may have contributed to inflated ground concealment scores. Tiritiri Matangi nests may have been located in smaller and shrubbier trees due to the immature nature of the recently replanted forest. This may have resulted in an increased aerial concealment score relative to the ground concealment score due to the presence of a dense and shrubby canopy. As such, it is possible that the observed differences in concealment from the perspective of aerial and ground predators may reflect fundamental differences in habitat, rather than a difference in nest site selection behaviours.

### 3.4.5 Conclusions

The findings of this study are inconclusive. As predicted, the robin nests at Benneydale were higher off the ground and more visually concealed than the nests at Wenderholm and Tiritiri Matangi. However, both of these results may be influenced more by the dominance of large tawa trees at Benneydale than by any effect of predation on nest site selection. Overall, there is little evidence to suggest that robin nest site selection is affected by mammalian predation risk. The very different habitat types available at the three sites were a strong confounding factor in this study. Characteristics such as nest height and vegetation complexity cannot be compared between sites due to vast differences in the availability of nest sites with these characteristics. Another confounding factor that was not addressed in this study is the effect of nest site competition. Tiritiri Matangi accommodates a higher density of birds than either of the other sites. As a result, robins on Tiritiri Matangi may be unable to select nest sites that are optimal in relation to predation risk due to inter and intra-specific competition for these sites.

The nest site selection criteria of North Island robins may also be affected primarily by factors other than predation. Many authors have suggested a range of different factors that may influence nest site selection, including food availability and quality, temperature and micro-climate, exposure to weather and human disturbance (Boulton *et al*., 2008; Eggers *et al*., 2006; Murphy, 1983; Sanchez-Lafuente *et al*., 1998; Wilson and Cooper, 1998). Complex interactions between these factors make it difficult to identify nest site characteristics that are affected specifically by predation and make the interpretation of nest site selection patterns extremely difficult. Future studies may benefit by assesses the influence of a number of potentially important nest site selection factors simultaneously. It may then be possible to disentangle their effects and gain a better understanding of the effect of each on overall nest site selection.

This study may have been constrained by the small number of nests surveyed at each site. Larger sample sizes would be recommended during any future investigation of the effects of predation on nest site selection in robins, or any other New Zealand forest birds. The survey methods used in the present study could also be improved. The PHI survey would have proved more useful if it had recorded the number of times each species intercepted the line. This would have provided a better illustration of vegetation density and complexity than a simple measure of species diversity within each height category. The nest characteristic variables may also have provided a better insight into nest site selection patterns if they had been compared with potential nest sites selected at random from the available habitat. Future studies may gain more robust results by attempting to manipulate nest site selection within a site, rather that attempting to compare selection behaviours between sites. Eggers *et al*. (2006) for example, manipulated the perceived risk of nest predation in Siberian jay (*Perisoreus infaustus*) using playbacks of calls of known avian predators. Similarly, Forstmeir and Weiss (2004) used known differences in predator densities between years to assess the effect of predation threats on the site selection behaviours of individuals within a single population.

# CHAPTER FOUR

## The Influence of Isolation from Mammalian Predators on Predator Recognition in the North Island Robin (*Petroica longipes*)

**Plate 4.1:** South Island robins carrying out the ‘wing-droop’ display. This particular display was directed toward a human near the nest (Mclean *et al*. 1999) (photograph by I. McLean)

## Abstract

In New Zealand, many native bird species thrive on offshore islands that lack mammalian predators. These healthy populations are often used as sources of founding birds for mainland reintroductions. This study used assessments of anti-predator response behaviours to investigate how isolation from mammalian predators has affected predator recognition in North Island robins (*Petroica longipes*). The anti-predator behaviours of robin pairs from Tiritiri Matangi Island, Wenderholm and Benneydale were assessed in response to a model stoat (*Mustela erminea*), model morepork (*Ninox novaeseelandiae*) and control (a small box). Behavioural variables were assessed using response intensity scores and a principal component analysis. The response to the stoat was highest at Benneydale, lowest at Tiritiri Matangi and intermediate at Wenderholm. During the stoat trials robins wing-flicked and alarm called more frequently and stayed away from the nest for longer at Benneydale and Wenderholm than Tiritiri Matangi. Robins also maintained a greater distance from the model and hopped less frequently during the stoat trials at Benneydale and Wenderholm. These results suggest that isolation from mammalian predators on Tiritiri Matangi Island has suppressed the North Island robin's ability to recognise this predator. The results also suggest that isolated robins, which have been reintroduced to mainland sites, are able to relearn to recognise mammalian predators. However, the strength of the stoat response initiated by reintroduced robins was suppressed compared with those robins that have persisted naturally on the mainland.

## *4.1 Introduction*

### 4.1.1 Predator Recognition and Conservation

The initiation of a biologically relevant behaviour in response to a stimulus is commonly referred to as 'recognition' (Suboski, 1990). The ability to recognise objects or events is an important part of an individual's fitness. Just as foragers need to recognise suitable food sources to feed, prey species must be able to recognise predators to take evasive action or to defend themselves effectively. Anti-predator behaviours may be required when an individual first encounters a new predator. As such, an innate or experience-independent recognition ability would give an individual the greatest advantage (Griffin, 2004). Innate recognition is evident in individuals from isolated populations of Seychelles warblers (*Acrocep halus sechellensis*). These birds can still recognise the Seychelles fody (*Foudia sechellarum*) as a key nest predator, despite having been isolated from them for many generations (Veen *et al.*, 2000). In many cases, however, the proper performance of anti-predator behaviours requires an innate ability to display the relevant anti-predator behaviours and a learned ability to recognise the predator (Blumstein *et al.*, 2002; Griffin, 2004; Maloney and McLean, 1995; McLean, 1997; McLean *et al.*, 1999).

In New Zealand, conservation programmes have recently begun to focus heavily on the restoration of degraded mainland ecosystems and the reintroduction of locally extinct native fauna (Saunders and Norton, 2001). The founders used for such reintroductions may be sourced from captive rearing facilities, or from populations that have been isolated from mammalian predation on island sanctuaries (Armstrong, 2000;

Reed, 1994). These individuals have often had little or no experience with key mammalian predators and, as discussed in Chapter 3, may not be able to recognise these predators as significant threats to their survival. This naïvety may result in an inability to initiate appropriate anti-predator behaviours when faced with mammalian predators. Reintroducing naïve individuals into an environment where these predators still pose a threat could therefore put them at a significant survival disadvantage in their new surroundings (McLean *et al.*, 1999; Reed, 2004). It has been suggested that individuals translocated to places where the risk of predation is higher should be provided with some form of pre-release predator training (Griffin *et al.*, 2000; Maloney and McLean, 1995; McLean *et al.*, 1999; Reed, 2004). Such training has been shown to enable previously naïve South Island robins to recognise a stoat (*Mustela erminea*), ferret (*Mustela furo*) and cat (*Felis catus*), all of which are key predators of robins on the mainland. Trained robins were able to display more intense anti-predator behaviours when confronted with these predators than untrained robins (Maloney and McLean, 1995; McLean *et al.*, 1999). However, in practice predator recognition training is not generally applied during reintroductions (Griffin *et al.*, 2000; Seddon *et al.*, 2007).

### 4.1.2 Naivety and the North Island Robin

North Island robins have been translocated from the mainland to mammalian predator free offshore islands, and from predator free offshore islands back to the mainland (Armstrong, 2008). Until this study, no research had been carried out to investigate how different local mammalian predator densities may affect the predator recognition abilities of individuals in new populations. In 1999, 21 robins were reintroduced to Wenderholm Regional Park from Tiritiri Matangi Island, an offshore island that is free of introduced mammals. As the Tiritiri Matangi population had been founded by mainland individuals, it was assumed that the Tiritiri Matangi robins would be 'suitable for translocation' into a mainland environment (Lovegrove *et al.*, 2002). At the time it was not known how isolation on Tiritiri Matangi might have affected the ability of those robins to recognise mammalian predators. New Zealand's endemic birds co-evolved with a range of avian predators (Worthy and Holdaway, 2002). As such, avian predator recognition abilities are likely to be strong in most species, particularly in places where these predators are common. In contrast, most endemic New Zealand birds have only been exposed to the current suite of mammalian predators for less than 200 years (Blackwell 2005). Thus, the learned ability to recognise mammalian predators may not yet have become genetically fixed in the North Island robin's behavioural repertoire. If this is the case, isolation from mammalian predators may result in the loss of mammalian recognition abilities in as little as one generation (Blumstein, 2006; Kullberg and Lind, 2002). As yet there has been no research into the ability of birds to relearn predator recognition abilities following translocation. The Wenderholm robin population has been described as "hanging on but not growing" (Armstrong, 2008), due to high rates of juvenile dispersal from the park, to surrounding unprotected areas (Andrews, 2007; Lovegrove *et al.*, 2002). It is possible that the increase in predation risk associated with this dispersal may be exacerbated by a suppressed ability of dispersing birds to recognise and respond to mammalian predators. Alternatively, the Wenderholm robins may no longer be affected by suppressed recognition abilities, having relearned to recognise mammalian predators during the 10 years since their reintroduction. The reintroduction of North Island robins and other vulnerable species to mainland sites is becoming increasingly common. As such, it is important to gain a better understanding of how isolation from mammalian predators has affected the predator recognition abilities of those candidate species selected for mainland reintroductions.

### 4.1.3 Aims and Hypotheses

This study investigates how isolation from mammalian predators affects the predator recognition abilities of North Island robins. There were two specific objectives. The first was to identify whether the ability of North Island robins to recognise mammalian predators has been lost since their isolation from these predators on Tiritiri Matangi. The second was to identify whether a history of isolation on Tiritiri Matangi continues to suppress the mammalian recognition ability of North Island robins at Wenderholm Regional Park. Three hypotheses with associated predictions are outlined below. The results of this study provide useful information to guide future translocation decisions, as well as providing empirical evidence to recommend pre-release predator training during reintroductions.

Hypothesis One

The mammalian predator recognition abilities of North Island robins are likely to be learned. As such, isolation from mammalian predators for more than one generation will result in the loss of these abilities. Individuals in North Island robin populations that are isolated from mammals will therefore display a reduced ability to recognise mammalian predators.

The null hypothesis is that mammalian predator recognition abilities are innate. In this case, isolation from mammalian predators will have no effect on North Island robins. Individuals from isolated populations will have the same ability to recognise these predators as mainland individuals.

### Hypothesis Two

Robins that are unable to recognise mammalian predators can gain this ability when they are reintroduced to an environment where these predators are present. Individuals within a reintroduced mainland population will therefore display mammalian predator recognition abilities that are equivalent to those displayed by naturally occurring mainland individuals.

The null hypothesis is that having lost the ability to recognise mammalian predators, individuals within a reintroduced mainland population will be unable to regain this learned ability. These individuals will therefore display a reduced ability to recognise mammalian predators.

### Hypothesis Three

North Island robins have co-evolved with avian predators. Avian predator recognition ability should therefore be equally strong among individuals from all of the populations tested during this study.

The alternative hypothesis is that the ability of North Island robins to recognise avian predators will vary among the populations.

Predictions

- Robins from Benneydale (a mainland site), Tiritiri Matangi (an island) and Wenderholm (a mainland site) will all initiate strong anti-predator response behaviours when confronted with a model morepork, a native avian predator that is present at all sites.
- Robins from Benneydale and Wenderholm will initiate strong anti-predator behaviours when confronted with a model stoat, a mammalian predator present at Benneydale, controlled at Wenderholm but absent from Tiritiri Matangi.
- Robins from Tiritiri Matangi will display reduced anti-predator behaviours when confronted with a model stoat.
- Robins from Benneydale, Tiritiri Matangi and Wenderholm will display limited anti-predator behaviours when confronted with a control model (small box).

# 4.2 Methods

## 4.2.1 Study Sites

This study compares the predator recognition abilities of North Island robins from Tiritiri Matangi, Wenderholm Regional Park and Benneydale in the central North Island (Figure 2.1). Tiritiri Matangi is free of introduced mammalian predators and none of the robins that were translocated to the island from the mainland in 1992-93 are still alive (D. Armstrong pers. comm.). As such, the population is composed entirely of birds that have never been exposed to mammalian predators. At the Wenderholm site mammalian predators are controlled but still present in low numbers. The Wenderholm robin population was founded by a transfer of 21 birds from Tiritiri Matangi in 1999, and at least one of the original founding birds is still alive (T. Lovegrove pers. comm.). The Benneydale population is a relict of a much wider distribution of robins on the North Island mainland and has never been isolated from the suite of predatory mammals that were introduced during European settlement in the 19th century. Ten nests were investigated at both Benneydale and Tiritiri Matangi. As mentioned in Chapter 3, six nests were studied at Wenderholm but two were presided over by the same male. These nests were deemed to be non-independent for the purposes of this study and only one was included in the analysis. This resulted in a sample of five nests at Wenderholm.

The sites used in this study represent three types of predator control regimes and three North Island robin translocation histories. This experimental design is not ideal as only one replicate for each predator control regime and translocation history is used. With only one replicate for each type of site the results are open to possible confounding factors. Differences between the predator response behaviours of robins on Tiritiri Matangi and at Benneydale may be unrelated to their mammal recognition abilities. Instead, they may be a result of their different habitats (see Chapter 2). This was an unavoidable logistic limitation of working with a species that occurs in only a few discrete locations in the North Island. This issue is taken into consideration in the analysis and discussion.

### 4.2.2 Nest Finding

At all three sites, North Island robins have been studied intensively for a number of successive breeding seasons. Most birds had been individually colour banded and fed regularly. As a result, most were individually recognisable and would often approach humans expecting food rewards. Robin nests were located by researchers from independent research groups who were employed to monitor robin breeding success. These researchers located nests by feeding mealworms (*Tenebrio molitor*) to the resident male and observing his behaviour. During incubation the male would call the female off the nest and feed her. It was usually possible to find the exact location of the nest by following the female as she returned to continue incubating. An incubating female will usually stay off the nest for a maximum of about seven minutes (Armstrong *et al*., 2000). During the nestling stage both the male and female may take mealworms from the observer and carry them to the nest. When nestlings are being fed it is usually possible to hear their begging calls.

### 4.2.3 Timing of the Experiment

This study was carried out during the nestling stage of the breeding cycle for two key reasons. Firstly, many birds show more intense anti-predator behaviours as the breeding cycle progresses (Redondo, 1989). Pairs with nestlings are therefore likely to show stronger and more observable anti-predator responses than pairs that are still incubating. To prevent the correlation between response intensity and chick age biasing the results, all experiments were conducted over two consecutive days. Secondly, there is less risk of the pair deserting nestlings than an unhatched clutch (I. McLean pers. comm.).

### 4.2.4 Experiment Set Up and Equipment

The Models

The three models used for the experiment included taxidermic mounts of a stoat, a morepork and a small brown cardboard box as the control. The stoat was selected to represent the mammalian predators because it is a known predator of a wide range of native birds, including robins (Brown *et al.*, 1998; Murphy and Dowding, 1994). Also, Maloney and McLean (1995) used a stoat to test predator recognition in South Island robins. The use of the stoat therefore allowed direct comparisons between the two studies. Due to the large distances between the sites, two teams of researchers and field assistants carried out the experimental work simultaneously and two sets of models were required. Two stoat mounts and one morepork mount were prepared especially for the project (DoC permit AK-23567-DOA). The stoats were posed in exactly the same position (Figure 4.1(a and b)). The second morepork was borrowed from another project and did not exactly match the pose of the first morepork, however both birds were perched in an upright stance (Figure 4.1(c and d)). The cardboard boxes were identical and measured 7.0 cm x 14.0 cm x 5.5 cm (Figure 4.1(e and f)). The moreporks and controls were mounted on natural branches 19 cm long. The stoats were mounted on branches 25 cm long. All the branches were between 3 cm and 5 cm in diameter. A frame made from a green plastic-coated coat hanger, with a loop at the top, enabled the models to be attached to the hoisting gear (Figure 4.1).

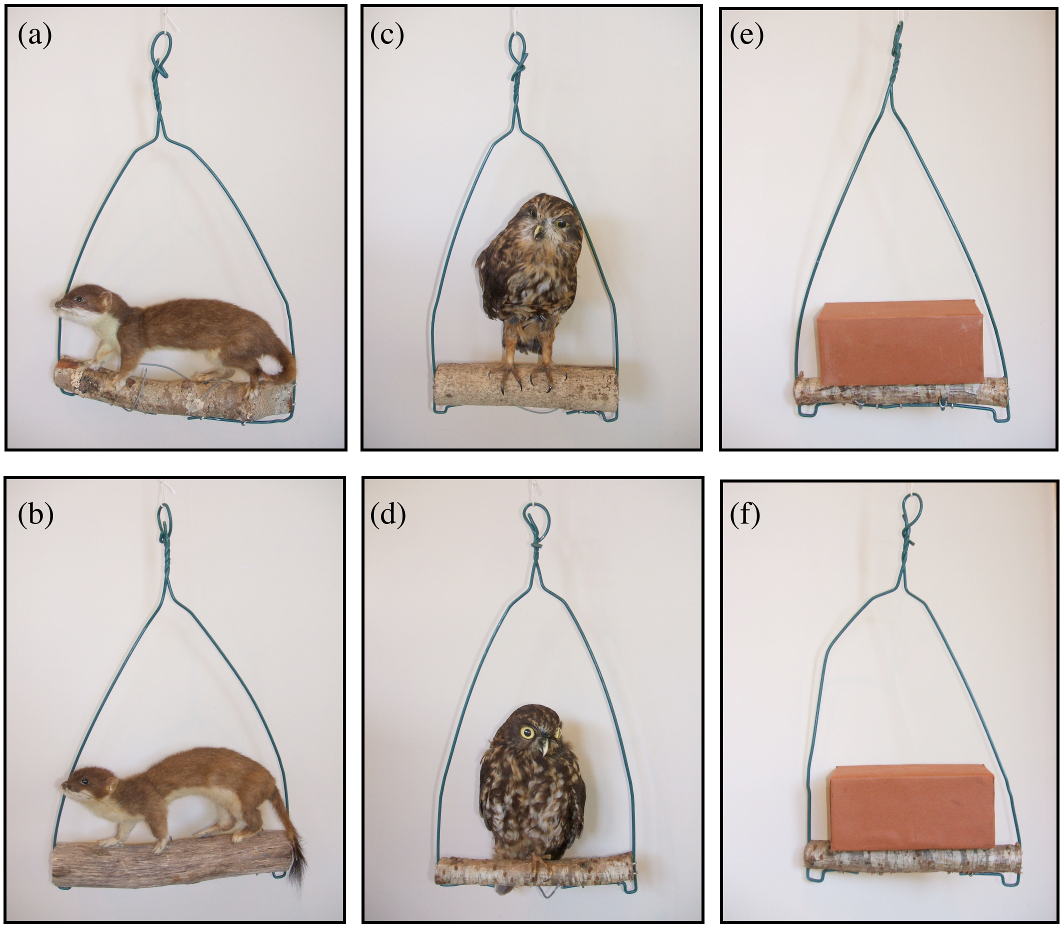
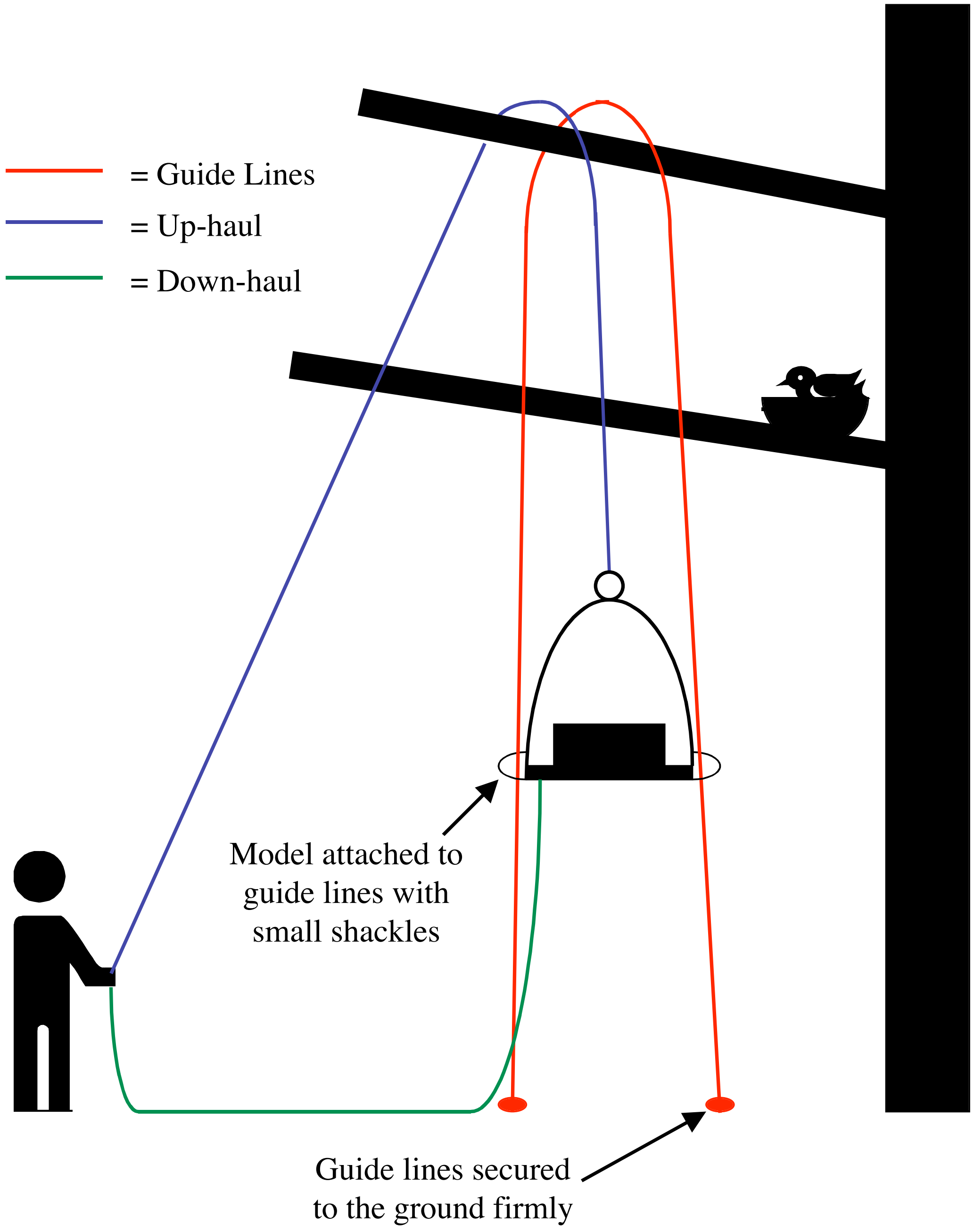


**Figure 4.1:** The models used in the experiment. Stoats (a) and (b) and morepork (c) were prepared especially for the experiment. Morepork (d) was borrowed from another research project. Models (e) and (f) are the controls.

### The Hoisting Rig

The hoisting rig was set up at least one day before the experiment began for all but one of the nests. This allowed time for the parent birds to acclimatise to physical changes near their nests. At one nest logistical constraints forced the rig to be set up on the morning the experiment began. At this nest the robins appeared to be behaving normally within a few minutes of the rig being put in place (pers. obs.). The hoisting rig consisted of three lengths of 1mm thick nylon braid. Two lengths of cord ran from the ground at the base of the nest tree, over a branch that was higher than the nest, and back to the ground (Figure 4.2). One length was pulled tight and secured firmly to the ground at each end to create two guide lines. These guide lines ran through two small shackles on either side of the model and prevented it from spinning as it was hoisted. The guide lines also provided greater control over the direction the model faced when it reached the nest. One end of the second length of cord was tied to the loop at the top of the model frame, while the other end was tied to a branch near the observer's vantage point. This line became the 'up-haul'. By pulling the up-haul the observer was able to hoist the model into the tree (Figure 4.2). A third cord was tied directly onto the model. This cord became the 'down-haul' and allowed the observer to pull the model down if it became snagged on a branch (Figure 4.2). With lower nests a ladder or long stick was used to hook the cords over the branch. A slingshot was used to fire a line over branches that were beyond easy reach.



Model attached to guide lines with small shackles

Guide lines secured to the ground firmly

**Figure 4.2:** Diagram of the hoisting rig. Cords are colour coded according to the key above.

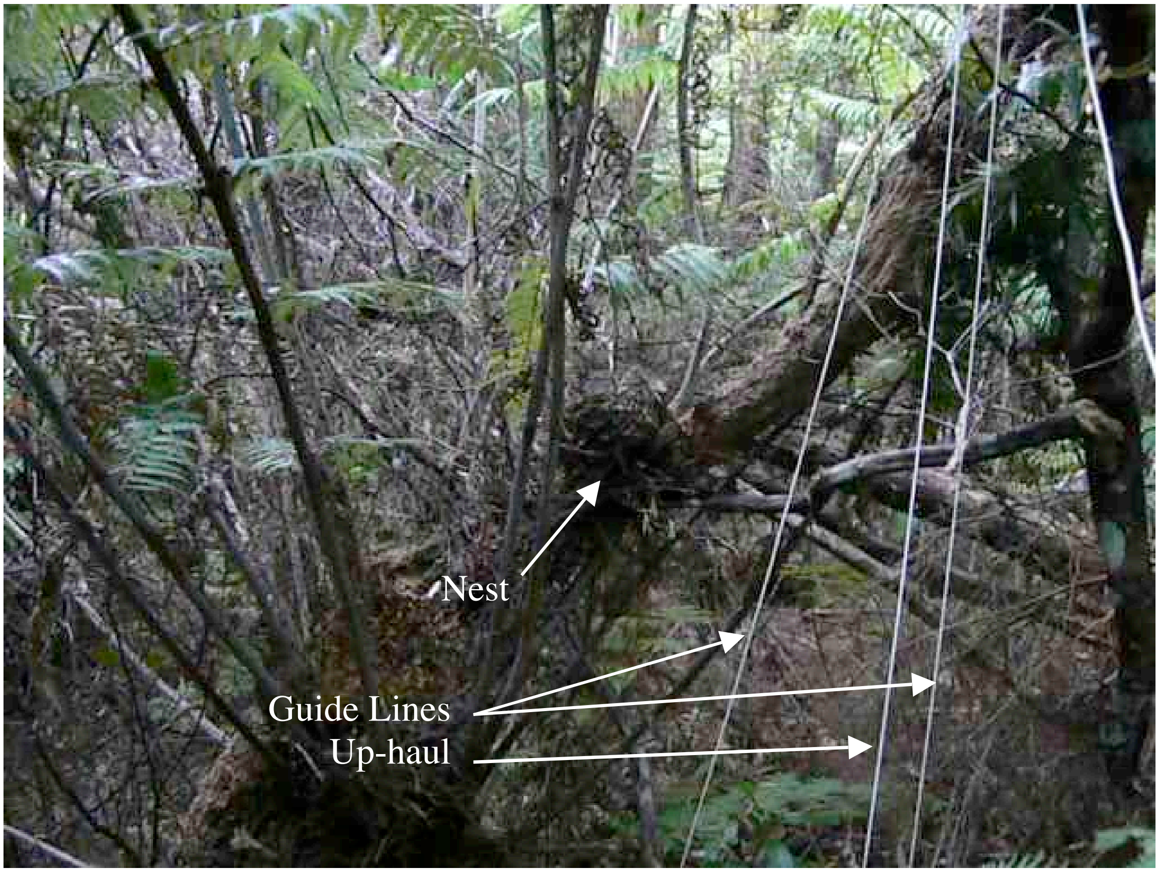


**Plate 4.2:** The hoisting rig in place near a nest at Wenderholm. The nest and the cords are labelled (photograph by B. Whitwell)

## 4.2.5 Experimental Procedure

For each pair the experiment comprised four sessions spread across two days. Session one was the 'initial observation' and usually took place in the morning. This session was used to establish the baseline movements and behaviours of the pair when no models were present. The observer arrived and attached the first model to the hoisting rig. The order of presentation of the models was randomly allocated at each nest. The model was then covered with a piece of army style camouflage fabric to keep it hidden from the parent birds. Once in place, the observer waited quietly for 10 minutes before beginning the 15-minute observation period.

Session two took place immediately after session one. As soon as both birds were out of sight the first model was hoisted into position, level with or slightly higher than the nest and 0.5-2.0 m from the nest rim. The observation period began once either bird had come into view of the observer and responded to the model. When the first bird returned the observer would tug the down-haul, to cause the model to move and catch the bird's eye. It was usually possible to identify precisely when the bird had seen the model. Once a bird had seen the model the experiment would run for five minutes. After five minutes the model was lowered and covered with the fabric. A post-treatment observation period then continued for a further five minutes. If neither parent had fed the nestlings by the end of the post-treatment observation the observer would stay in position and record the time at which either parent first returned to the nest. Session three took place between four to six hours after the end of session two. The observer arrived, attached the model to the hoisting rig, covered it and sat quietly for 10 minutes. The session then followed exactly the same procedures as session two. Session four took place the next morning and followed the same procedures as before.

### 4.2.6 Methods of Recording and Scoring Responses

The methods used for recording and scoring responses in this study are identical to those used by Maloney and McLean (1995). Observations in the field were recorded using a hand held Olympus Pearlcorder S701 dictaphone. If both birds were in sight, then the behaviour of the bird showing the most intense response was recorded. It was possible to observe and record the behaviour of only one bird at a time. The key behaviours and details that were recorded are summarised in Table 4.1. The per minute rate of flights, hops and wing-flicks were used in the analysis so that responses of birds seen only briefly could be compared directly with birds that were observed for longer periods.

Each of the behaviours, time interval characteristics and distance variables described in Table 4.1 were used to produce a composite score, which measured the intensity of the response relative to the bird's 'normal' behaviour. To produce each response intensity score, a scale of 0-2 was used across all eight behavioural variables (Table 4.2). These criteria were based on both the perceived degree of predation threat to the bird being observed and how different the behaviour was from that recorded during the initial observation period (Maloney and McLean, 1995). Maloney and McLean (1995) assumed that the degree of risk would increase if a bird approached the predator, if it approached the nest while the predator was present or if it used behaviours that would make it more conspicuous to the predator. The same criteria were used during this study as Maloney and McLean (1995) found that they produced meaningful results. It also allowed a direct comparison between the two studies. The sum of these intensity scores gave an overall response intensity score. Each pair was given three intensity scores, one for each treatment. Scores could range from 0 (very low response intensity) to 16 (very high response intensity).

**Table 4.1:** Definition of behaviours, distances and time intervals of interest used in this study, following Maloney and McLean (1995).

| Behaviour of the robin | Description of behaviour |
|---|---|
| **Body movements** | |
| Flights | Movements > one body length in distance and requiring the use of wings |
| Hops | Movements < one body length in distance and not requiring the use of wings |
| Wing flicks | The rapid opening and closing of wings while not in flight |
| **Calls** | The number and type of calls eg. males song and/or alarm calls |
| **Body displays** | |
| Head feather displays | Display of frontal spot with head feathers raised |
| Wing droop displays | Wings spread out in full distraction display |
| **Distance from stimulus (m)** | Estimated to the nearest 0.5m |
| **Time intervals** | |
| Time exposed to stimulus | Pre-set to 5 min |
| Time in view of the observer | Proportion of the 5 min experimental period in which the observer could see at least one of the parent birds |
| Natural nest visitation intervals | Time between approaches to the nest prior to the test |
| Test nest visitation intervals | Time before first nest approach once model in place and the following time between approaches to the nest |
| Post test nest visitation intervals | Time between approaches to the nest after model removed |

**Table 4.2:** Response intensity scoring criteria for all response variables (Maloney and McLean, 1995).

| Behaviour of the robin | Intensity Score | | |
|---|---|---|---|
| | 0 | 1 | 2 |
| **Body movements** | | | |
| No. Flights | < Average of initial obs | ≥1 but <2 time initial obs | ≥ 2 times initial obs |
| No. Wing flicks | < Average of initial obs | ≥1 but <2 time initial obs | ≥ 2 times initial obs |
| No. Hops | < Average of initial obs | ≥1 but <2 time initial obs | ≥ 2 times initial obs |
| **Nest visitation** | | | |
| Goes to nest | Within the first 1 min of experiment | After 1 min but while model still in place | After model had been removed |
| **Distance from stimulus** | | | |
| Minimum approach distance | >1m | ≤1m and ≥0.5m | <0.5m |
| **Calls and displays** | | | |
| Alarm calls | None | Once | >Once |
| Head feather displays | None | Once | >Once |
| Wing droop displays | None | Once | >Once |

## *4.3 Analysis and Results*

### 4.3.1 Testing for Confounding Factors

The three most common behaviours observed during the experiment were flights, hops and wing-flicks. These ‘movement behaviours’ were used to test for an effect of the number of birds present during the trial (1 or 2) on behavioural responses. At Benneydale, one bird was observed during 12 observation sessions and two birds were observed during the remaining 18. On Tiritiri Matangi, one bird was observed during eight sessions and two were observed during 18. During the remaining four sessions it was not possible to identify whether the observed behaviours were carried out by different birds or the same bird returning to the nest multiple times. These treatments were not included in this analysis. At Wenderholm, one bird was observed during nine sessions and two were observed during the remaining six. The data from all three sites showed no significant differences in the mean movement behaviour frequencies when one or two birds were observed (Table 4.3). The three movement behaviours were also used to test for any effect of the order of presentation of the model (first, second or third) on behavioural responses. There was no significant difference between the frequencies of the movement behaviours in relation to presentation order (Table 4.4).

The response intensity scores and principal component (PC) scores produced by a principal component analysis were also tested for any confounding effects of presentation order and the number of birds present. There was no significant difference between the mean response intensity scores or PC scores when one or two birds were observed

(Tables 4.5 and 4.6). There was also no significant difference among the mean response intensity scores or PC scores in relation to the order of presentation (Tables 4.5 and 4.7).

The mean age of the chicks was also compared across the three sites. Although there was some variation in chick age among the sites these differences were not statistically significant (Kruskal-Wallis test $H_2$=4.49, $p$=0.29) (Figure 4.3).

**Table 4.3:** Results of statistical tests comparing the mean frequency of movement behaviours when one or two birds were observed. Test statistic '$t_{DF}$' = two sample t-test, '*U*' = Mann-Whitney *U* test.

| Site | Behaviour Variable | Test Statistic | *p* value |
|---|---|---|---|
| Benneydale | Flight | $t_{(28)}$=-0.07 | 0.95 |
| | Hop | $t_{(28)}$=-0.41 | 0.68 |
| | Wing-flick | *U* =91.0 | 0.47 |
| Tiritiri Matangi | Flight | $t_{(24)}$=0.05 | 0.96 |
| | Hop | $t_{(24)}$=0.38 | 0.71 |
| | Wing-flick | *U* =62.0 | 0.51 |
| Wenderholm | Flight | *U* =13.0 | 0.11 |
| | Hop | *U* =13.0 | 0.11 |
| | Wing-flick | *U* =23.5 | 0.69 |

**Table 4.4:** The results of tests comparing the mean frequencies of movement behaviours across the three possible treatment presentation orders (first, second or third). Test statistic '$H_{DF}$' = Kruskal-Wallis, '$F_{DF}$' = ANOVA.

| Site | Behaviour Variable | Test Statistic | *p* value |
|---|---|---|---|
| Benneydale | Flight | $F_{(2,27)}=0.68$ | 0.51 |
| | Hop | $F_{(2,27)}=0.22$ | 0.81 |
| | Wing-flick | $H_{(2)}=0.20$ | 0.91 |
| Tiritiri Matangi | Flight | $F_{(2,27)}=0.16$ | 0.85 |
| | Hop | $F_{(2,27)}=1.68$ | 0.20 |
| | Wing-flick | $H_{(2)}=1.01$ | 0.60 |
| Wenderholm | Flight | $H_{(2)}=0.38$ | 0.83 |
| | Hop | $H_{(2)}=0.07$ | 0.97 |
| | Wing-flick | $H_{(2)}=2.37$ | 0.31 |

**Table 4.5:** The results of tests comparing the mean response intensity scores when one or two birds were observed (t-test) and across the three possible treatment presentation orders (ANOVA). Test statistics '$t_{DF}$'= two sample t-test, '$F_{DF}$'= ANOVA.

| Site | Confounding Factor | Test Statistic | *p* value |
|---|---|---|---|
| Benneydale | Number of Birds Observed | $t_{(28)}=-0.12$ | 0.91 |
| | Order of Presentation | $F_{(2,27)}=1.00$ | 0.38 |
| Tiritiri Matangi | Number of Birds Observed | $t_{(24)}=-1.77$ | 0.09 |
| | Order of Presentation | $F_{(2,27)}=3.23$ | 0.06 |
| Wenderholm | Number of Birds Observed | $t_{(13)}=-0.69$ | 0.50 |
| | Order of Presentation | $F_{(2,12)}=3.23$ | 0.52 |

**Table 4.6:** Results of statistical tests comparing the PC scores when one or two birds were observed. Test statistic '$t_{DF}$' = two sample t-test, '$U$' = Mann-Whitney $U$ test.

| Site | Principal Component | Test Statistic | *p* value |
|---|---|---|---|
| Benneydale | PC1 | $t_{(28)}=1.24$ | 0.23 |
| | PC2 | $U=78.0$ | 0.20 |
| | PC3 | $t_{(28)}=0.84$ | 0.41 |
| Tiritiri Matangi | PC1 | $t_{(24)}=0.41$ | 0.68 |
| | PC2 | $t_{(24)}=-0.74$ | 0.46 |
| | PC3 | $t_{(24)}=0.12$ | 0.91 |
| Wenderholm | PC1 | $U=26.0$ | 0.91 |
| | PC2 | $U=13.0$ | 0.10 |
| | PC3 | $U=15.0$ | 0.16 |

**Table 4.7:** The results of tests comparing the mean PC values across the three possible treatment presentation orders (first, second or third). Test statistic '$H_{DF}$' = Kruskal-Wallis, '$F_{DF}$' = ANOVA.

| Site | Principal Component | Test Statistic | *p* value |
|---|---|---|---|
| Benneydale | PC1 | $F_{(2,27)}=0.21$ | 0.81 |
| | PC2 | $H_{(2)}=0.34$ | 0.84 |
| | PC3 | $F_{(2,27)}=1.26$ | 0.30 |
| Tiritiri Matangi | PC1 | $F_{(2,27)}=1.12$ | 0.34 |
| | PC2 | $F_{(2,27)}=0.17$ | 0.85 |
| | PC3 | $H_{(2)}=1.31$ | 0.52 |
| Wenderholm | PC1 | $H_{(2)}=0.02$ | 0.99 |
| | PC2 | $H_{(2)}=0.14$ | 0.93 |
| | PC3 | $H_{(2)}=0.96$ | 0.62 |

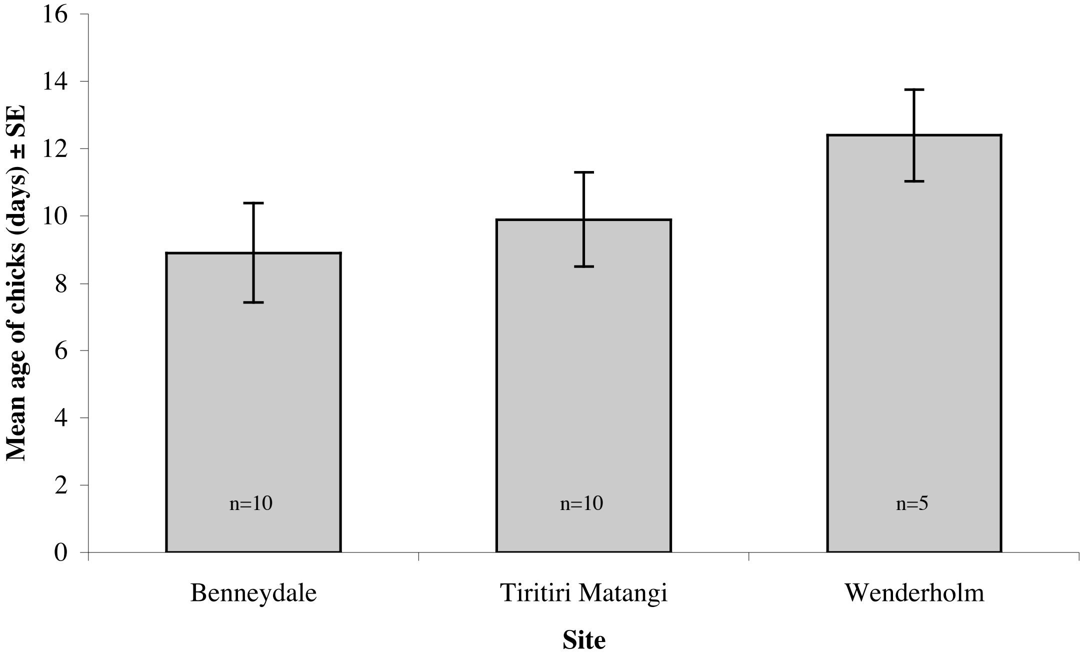


**Figure 4.3:** The distribution of the estimated age of the chicks on the first day of the experiment. Error bars represent ± the standard error.

## 4.3.2 Response Intensity Score

The distribution of the response intensity scores was not significantly different from a normal distribution. A two-way mixed factorial ANOVA was carried out to determine the effect of the three treatments (within subject factor), and the sites (between subject factor), on the response intensity scores produced from each trial. The treatment factor was found to have a medium strength effect on response intensity ($F_{(2,44)}=29.35$, $p<0.01$, $eta^2=0.57$). A post-hoc Bonferroni pair wise comparison showed a significant difference between the morepork treatment and both the stoat and the control treatments ($p<0.01$ for both comparisons). There was no significant difference between the stoat and control ($p=0.07$). The site factor had a statistically significant but small effect on response intensity ($F_{(2,22)}=7.43$, $p<0.01$, $eta^2=0.40$). A post-hoc Tukey HSD multiple comparison showed a significant difference between Benneydale and Tiritiri Matangi ($p<0.01$), but no significant difference between Wenderholm and either Benneydale or Tiritiri Matangi ($p=0.06$, $p=0.83$ respectively). The interaction effect of treatment and site was also found to be significant but small, indicating that responses to the models did not vary consistently among the sites ($F_{(4,44)}=4.37$, $p=0.01$, $eta^2=0.28$).

At Benneydale, the response intensity scores were high for both the morepork and the stoat treatments and low for the control (Figure 4.4). At Tiritiri Matangi and Wenderholm, response intensity scores were high for the morepork and low for both the control and the stoat treatments (Figure 4.4). Morepork response intensity scores were also higher at Benneydale than at either Tiritiri Matangi or Wenderholm (Figure 4.4). Response scores for the stoat trials were higher at Benneydale than at Wenderholm, and higher at Wenderholm than on Tiritiri Matangi (Figure 4.4). Control response intensity scores did not vary among the sites (Figure 4.4).

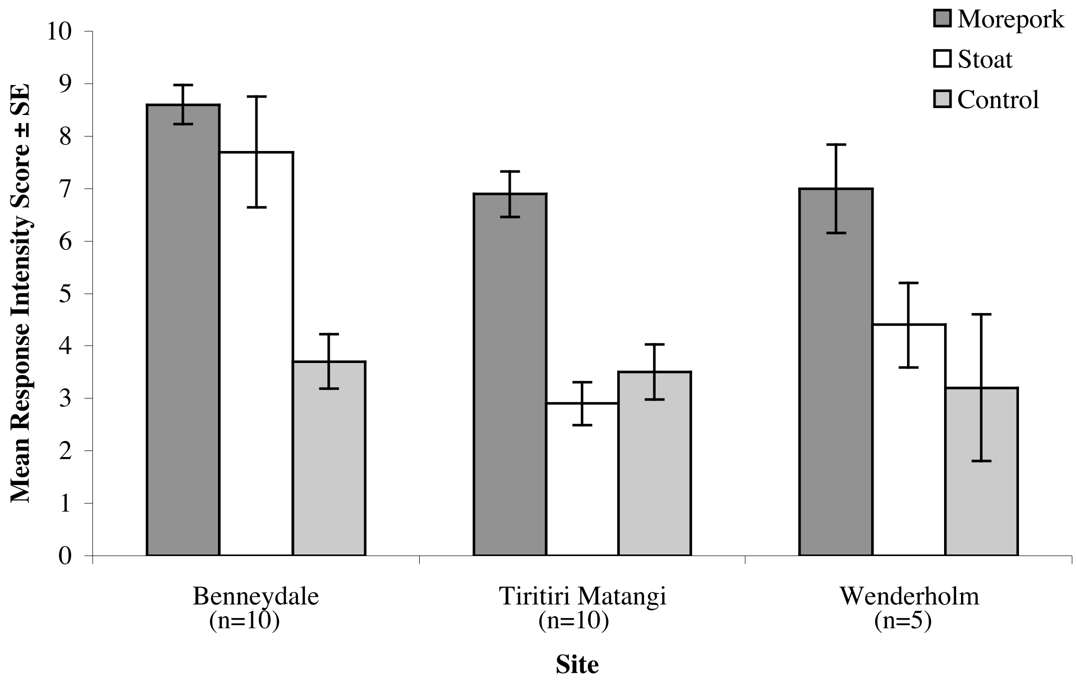


**Figure 4.4:** Mean composite response intensity scores for all three treatments carried out at all three sites. Error bars represent ± the standard error.

### 4.3.3 Principal Component Analysis

A correlation matrix principal component analysis (PCA) with a Varimax rotation was used to reduce the recorded variables to a smaller number of independent components. No raised head feather displays were observed so this behaviour was not included in the analysis. All principal components with eigenvalues greater than 1.0 are reported (Talbe 4.8). These three principal components described 63% of the variation in the data (Table 4.8). The resulting factor scores were used for further analysis.

**Table 4.8:** Eigenvalues, variance explained and loadings of the original variables in the first three principal components extracted from the seven anti-predator behaviour variables recorded. Variables with principal component values greater than 0.5 are highlighted in bold

| | **PC1** | **PC2** | **PC3** |
|---|---|---|---|
| Eigenvalue | 1.89 | 1.38 | 1.13 |
| % of variance | 26.99 | 19.71 | 16.12 |
| Cumulative % | 26.99 | 46.70 | 62.82 |
| Wing-flick frequency | **0.81** | 0.07 | -0.05 |
| Alarm call frequency | **0.74** | 0.06 | -0.13 |
| Latency to return | **0.62** | -0.07 | 0.22 |
| Wing-droop frequency | -0.08 | **0.85** | 0.19 |
| Flight frequency | 0.15 | **0.78** | -0.31 |
| Hop frequency | 0.39 | 0.08 | **-0.62** |
| Minimum approach distance | 0.28 | 0.02 | **0.80** |

PC1 was correlated strongly with the frequency of wing-flicks and alarm calls and the latency of return to the nest following exposure to the treatment (Table 4.8). PC2 was correlated strongly with the frequency of wing-droop displays and flights (Table 4.8). PC3 was correlated negatively with the frequency of hops, and positively with the minimum distance between the robin and the model (Table 4.8).

A two-way mixed factorial ANOVA was used to identify the effects of both the treatment (within subject factor), and the site (between subjects factor), on each of the PC variables. As the data did not fit the assumption of homogeneity of covariance, the ANOVA's F test was corrected using the Greenhouse-Geisser adjustment to increase conservativeness (Kinner and Gray 2004). The treatment factor had a medium strength main effect on PC1. There were also significant site and interaction effects on PC1

(Table 4.9). Neither of the factors was found to have a significant effect on PC2. Both the treatment and site factors had significant main effects on PC3, but had no interaction effect (Table 4.9).

**Table 4.9:** Results of two-way mixed factorial ANOVA on Principal Component values produced by the PCA. One missing value resulting from a recording error reduced the Benneydale sample size to 9 for all treatments. Sample sizes for Tiritiri Matangi and Wenderholm were 10 and 5 respectively for all treatments. *p*-values less than 0.05 are highlighted in bold.

| Principal Component | Factor | Test Statistic | *p* value | eta$^2$ |
|---|---|---|---|---|
| PC1 | Treatment | $F_{(1.3,29)}=30.19$ | **>0.01** | 0.58 |
| | Treatment * Site | $F_{(2.6,29)}=5.06$ | **0.01** | 0.32 |
| | Site | $F_{(2,22)}=10.21$ | **>0.01** | 0.48 |
| PC2 | Treatment | $F_{(1.3,29)}=0.62$ | 0.48 | 0.03 |
| | Treatment * Site | $F_{(2.6,29)}=2.54$ | 0.08 | 0.19 |
| | Site | $F_{(2,22)}=1.11$ | 0.35 | 0.09 |
| PC3 | Treatment | $F_{(1.4,31)}=4.10$ | **0.04** | 0.16 |
| | Treatment * Site | $F_{(2.8,31)}=1.65$ | 0.20 | 0.13 |
| | Site | $F_{(2,22)}=4.00$ | **0.03** | 0.27 |

At Benneydale, the mean of PC1 was greater during the morepork trials than the stoat trials. PC1 was also greater during stoat trials than control trials at Benneydale (Figure 4.5). At both Tiritiri Matangi and Wenderholm, the mean of PC1 was higher in response to the morepork than the stoat or control. PC1 was also higher in response to the morepork at Benneydale than at Tiritiri Matangi or Wenderholm. The mean of PC1 was lower during the stoat trials on Tiritiri Matangi than at Benneydale or Wenderholm.

There was no significant difference among the control PC1 values at all three sites (Figure 4.5).

The mean of PC2 appears to be higher during the stoat trials at Benneydale than during any other trials. However, there were no significant main or interaction effects on PC2 (Figure 4.6, Table 4.9).

The mean of PC3 was greatest during the stoat trials at both Benneydale and Wenderholm (Figure 4.7). On Tiritiri Matangi PC3 was greatest during the morepork trials. PC3 was also lower during the stoat trials on Tiritiri Matangi than at Benneydale or Wenderholm, and greater during the control trials at Benneydale than on Tiritiri Matangi or Wenderholm (Figure 4.7).

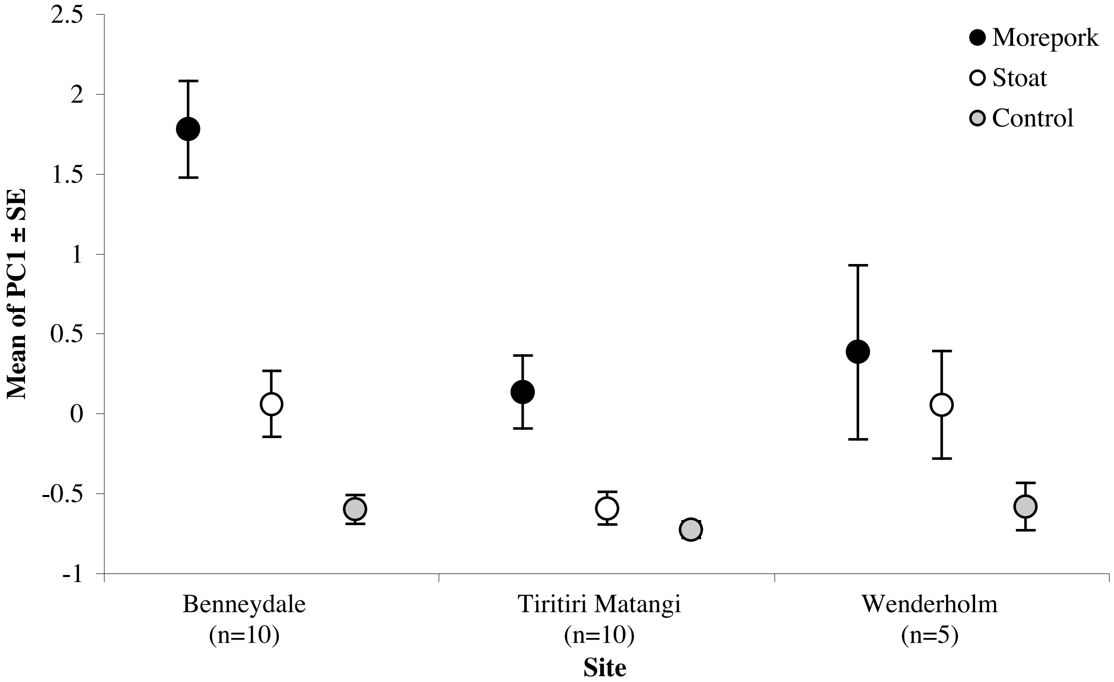


**Figure 4.5:** Mean of PC1 (Wing-flicks, Latency of return, Alarm calls) across all sites and treatments. Error bars represent ± the standard error.

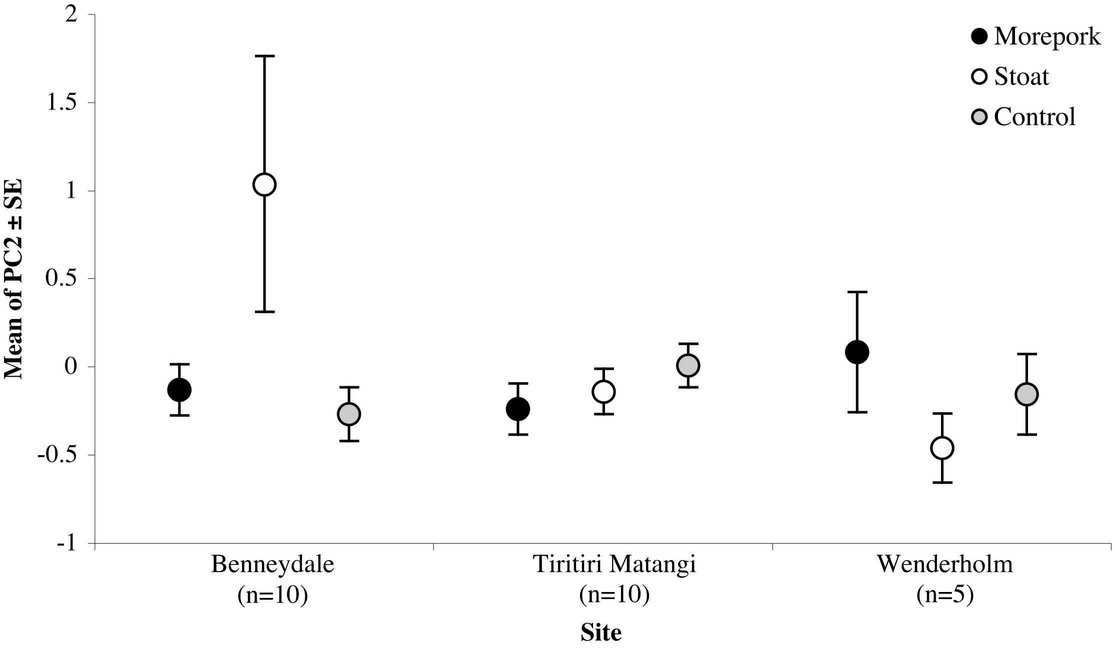


**Figure 4.6:** Mean of PC2 (Flights, Wing-droops) across all sites and treatments. Error bars represent ± the standard error.

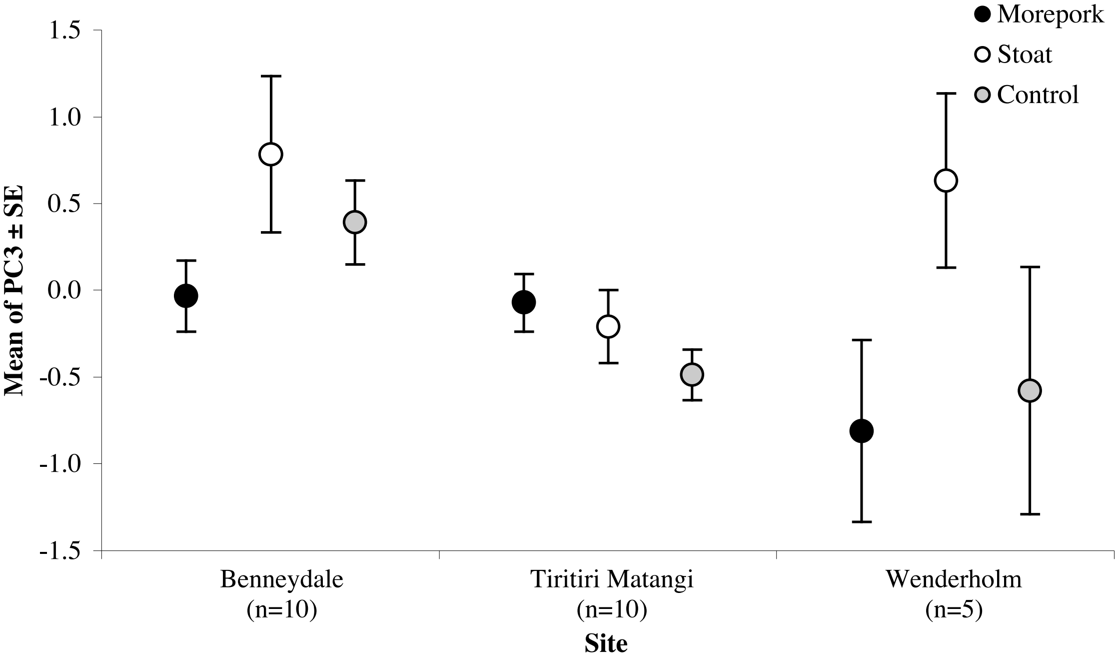


**Figure 4.7:** Mean of PC3 (Hops, Minimum approach) across all sites and treatments. Error bars represent ± the standard error.

## 4.4 Discussion

### 4.4.1 Confounding Factors

The most common behaviours were the movement behaviours hop, flight and wing-flick. These three behaviours, the response intensity scores and the PC scores were all used to test for the influence of potential confounding factors on the results. None of the movement behaviours were influenced by the number of birds present during the observation, or by the order in which the treatment was presented. There was also no significant effect of order of presentation or the number of birds observed on the response intensity or PC scores. As such, these factors are not considered to have had a confounding effect on the results. There was no significant difference between the estimated ages of the chicks across the three sites. There was, however, some variation in the distribution of chick ages, with the Wenderholm chicks being slightly older than the chicks from Benneydale and Tiritiri Matangi. As a result, there is some potential for a correlation between anti-predator response intensity and chick age to artificially inflate the observed response intensities at Wenderholm. However, the chicks at Wenderholm were, on average, only three days older than those at Benneydale and two days older than those at Tiritiri Matangi. The confounding effects of these differences in chick ages are therefore likely to be minimal. The lack of a significant difference among the control response scores at the three sites also suggests that the variation in chick ages did not have an important effect on the results. Since all three treatments were carried out within a two-day period, the increasing age of the chicks is also unlikely to have confounded results across the three treatments at each nest. Due to the intense concentration required when recording the rapid and variable behaviours, it was often impossible to read band combinations during the observation period. As a result, the sex of the birds could not always be identified and it was not possible to assess behavioural differences between male and female robins. However, Maloney and McLean (1995) found no significant variation in behavioural responses between the sexes of South Island robins.

### 4.4.2 Response Intensity

As predicted, the response intensity scores were high during the morepork trials at all three sites. This illustrates that all robins were able to recognise the threat moreporks pose to nest survival. The morepork response intensity scores were higher at Benneydale than that at Wenderholm and Tiritiri Matangi. This may be a result of an increased overall risk of predation at Benneydale compared with the other sites. It has been suggested that in an environment where predation risk is temporally variable, an individual should show the most intense anti-predator behaviours when predation risk is elevated (Lima and Bedenkoff, 1999). The same may be true when predation risk is spatially variable, in which case elevated predator responses would be expected at the high risk Benneydale site. However, Tiritiri Matangi may also be considered a high risk site due to increased predation rates by avian predators (D. Armstrong pers. comm.). If avian predation rates on Tiritiri Matangi were equivalent to mammalian predation rates at Benneydale, then high morepork response intensity would be expected at both Benneydale and Tiritiri Matangi. The cause of the increased morepork response intensity at Benneydale will require further investigation. Response intensity scores during the control trials were low and did not differ between sites. This is consistent with the results of Maloney and Mclean (1995), and illustrates that robins do not produce a generic anti-predator response when faced with any novel object near the nest. These responses are used only when a specific predator is recognised.

The mean of the stoat response intensity scores did not differ from the morepork scores at Benneydale. This reiterates Maloney and McLean's (1995) finding that mainland robins have learned to recognise stoats as important threats to nest survival. On Tiritiri Matangi, however, the stoat response intensity scores did not differ from the control. This finding supports the hypothesis that isolation from mammalian predators has resulted in the loss of mammalian recognition ability among these North Island robins. What this study does not address is the length of time required to lose this recognition ability. The Tiritiri Matangi population has been isolated from mammalian predators for 15 years. This is considerably longer than the mean life expectancy of robins and none of the mammalian predator-experienced founder birds are still present on the island (D. Armstrong pers. comm.). Other researchers have shown that learned behaviours have become lost from isolated populations within just one generation (Blumstein, 2002). As such, the ability to recognise a stoat as a predatory threat may have been absent from the Tiritiri Matangi population for several years. It would be informative to repeat this experiment on a population newly translocated to an offshore island over several years, in order to track the decline of predator recognition abilities. It is also unknown whether previously experienced birds can lose the ability to recognise mammalian predators following isolation. This process of forgetting or 'behavioural extinction' has been demonstrated in naïve animals that have been trained to recognise specific predators (de Azevedo and Young, 2006; Hazlett *et al.*, 2002). Rheas (*Rhea americana*) were shown to retain the ability to recognise predators for just three months after training. This kind of behavioural extinction may also occur in naturally experienced birds (Bouton, 1994). Alternatively, these birds may retain their recognition ability until they die, and are then replaced by the next generation of inexperienced birds. Further investigation is required to identify the mechanisms involved in the loss of predator recognition abilities from isolated bird populations. A similar analysis of another offshore robin population is required to test whether the apparent inability of the Tiritiri Matangi birds to recognise mammalian predators is due to their isolation from these predators, and not the result of a confounding factor unique to the island.

The mean stoat response intensity score at Wenderholm was not significantly different from the control. It is possible that this may be a consequence of the small sample size at Wenderholm. This is supported by a significant difference between the mean stoat response intensity scores observed at Wenderholm and Tiritiri Matangi, despite the sites having very similar control responses. This difference supports the hypothesis that a reintroduced mainland population, that was founded by naïve robins, can relearn to recognise mammals as predatory threats. However, stoat response intensity was lower at Wenderholm than at Benneydale, where it was equivalent to the morepork response. There are two possible explanations for this finding. Only some of the robins at Wenderholm may have survived an encounter with a stoat, and thus only some would be able to recognise the stoat model. This could result in some birds responding strongly the stoat model while others do not respond at all. The resulting mean response intensity score would therefore be intermediate with a relatively large variance. Alternatively, all the robins may have learned to recognise the stoat, but do not consider it as great a threat to nest survival as the morepork. In this case, all the birds would produce medium strength responses, resulting in an intermediate mean response intensity score with a small variance. Due to the low sample size at Wenderholm, it is difficult to identify whether one or other, or both, of these processes is at work. In either case, it appears that the low mammalian predator density at Wenderholm may have lowered the ability of the robins to produce strong anti-predator responses when confronted with a stoat. A low incidence of contact with stoats could produce a population where only some of the individuals can recognise them, or a population where robins consider the stoat a rare and relatively small threat. Individual robins may regain the ability to produce strong anti-predator responses to stoats more quickly in an environment where stoat densities are high. As discussed in Chapter 3, the translocation of naïve robins to an environment where mammalian predators are not controlled has a higher chance of failure. Translocations to such sites are not recommended and are unlikely to be undertaken. This means that it may not be possible to study the effect of increased mammalian predation risk on the development of anti-predator responses in the field.

### 4.4.3 Principal Component Analysis

Principal component one (PC1) was greater during the stoat trials than the control trials at both Benneydale and Wenderholm but did not differ between the control and stoat trials on Tiritiri Matangi. PC1 was strongly correlated with the frequency of wing-flicks and alarm calls and the latency of return to the nest. This result is consistent with the findings of Maloney and Mclean (1995), who showed that experienced robins wing-flicked more frequently and stayed away from the nest for longer when exposed to a model stoat compared with the control. This result is also consistent with the results from the analysis of response intensity scores described above. Similar frequencies of wing-flicks and alarm calls and latency of return during the stoat and control trials at Tiritiri Matangi provides further evidence to support the hypothesis that the Tiritiri Matangi robins are not able to recognise the stoat as a threat. Increases in these same behaviours during stoat trials compared with the control at both Benneydale and Wenderholm support the hypothesis that the Wenderholm birds have regained some ability to recognise the stoat.

At Benneydale, wing-flick and alarm call frequencies were elevated and the birds took longer to return to the nest during the morepork trials compared with the stoat trials. This suggests that the Benneydale robins recognise the morepork as a greater threat than the stoat. Intensified responses to the morepork may be the result of greater morepork density at Benneydale than was anticipated. Moreporks prey on a variety of taxa including invertebrates, birds and small rodents, particularly mice (Haw and Clout 1999). Rats and mice are absent from Tiritiri Matangi and controlled intensively at Wenderholm. Although there has been some recent rat control in a selection of forest patches at Benneydale, rats are probably more abundant there than at the other two sites. This may result in increased morepork population at Benneydale as a consequence of increased food availability. A similar argument was used when the high density of moreporks on Lady Alice Island was attributed to a high availability of kiore (*Rattus exulans*) (Saint Girons *et al*., 1986). However, the importance of rats and mice in the morepork diet has been disputed and it is thought that they are rarely taken by mainland moreporks (Haw and Clout, 1999). Recent research suggests that morepork abundance is higher in areas with low rat numbers (Fraser and Hauber, 2008). The morepork density on Tiritiri Matangi has increased substantially over the last 15 years, and morepork predation is thought to be a major cause of robin nest failure on the island (D. Armstrong pers. comm.). This would suggest that morepork responses should in fact be higher on Tiritiri Matangi than at Benneydale. Further work is needed to determine the cause of the increased frequency of wing-flicks and alarm calls and slower return to the nest during the morepork trials at Benneydale.

Principal component 2 (PC2) was correlated with the frequency of wing-droop displays and flights and was not influenced by either the site factor or the treatment factor. The wing-droop display was a very rare behaviour, observed during just 8 of the 75 trials carried out across all sites. The low numbers of wing-droop displays observed made identifying site, treatment or interaction effects more difficult. The lack of any main effects on PC2 could suggest that the treatments did not affect the frequency of flights during the responses. However, this contrasts with Maloney and McLean (1995), who noted that experienced robins flew more frequently when exposed to the stoat treatment than the control treatment. This kind of simple comparison may be inappropriate and misleading in this case. When multiple behaviours are included in an analysis, the results should be treated as exploratory. The PCA analysis is most useful for drawing patterns from a large number of behavioural variables (Jolliffe, 2002)

Principal component 3 (PC3) scores were greater during stoat trials than morepork trials at both Benneydale and Wenderholm. As PC3 was correlated with the minimum approach distance to the model this result indicates that robins at these two sites maintained a greater distance from the stoat model than the morepork model. While moreporks are active predators of robin chicks, they take adult birds less often (Brown *et al.*, 1998; Haw and Clout, 1999). As such, moreporks present less of a threat to an adult bird than stoats, which are active predators of both adults and chicks (Brown *et al.*, 1998; Murphy and Dowding, 1994). Adult robins should therefore maintain a greater distance from the stoat to reduce their risk of direct predation and increase their chances of future reproductive success. A similar result was observed in the anti-predator responses of nesting lapwings (*Vanellus vanellus*) (Elliot, 1985). Parent lapwings would attack a model crow near the nest. However, when presented with a model fox they would maintain a safe distance while circling over-head or performing distraction displays on the ground (Elliot, 1985). This result and the results of the present study indicate that, in general, the closeness of the approach to a predator should be negatively correlated with the threat that predator poses to the survival of the adult bird (Elliot, 1985). However, this effect is likely to be influenced by other factors such as the hunting mode of the predator and the potential benefits of mobbing behaviours. PC3 was also negatively correlated with the frequency of hops made during the observation period. The results show that the robins hopped less in the presence of the stoat at Benneydale and Wenderholm. Stoats are very efficient visual predators. As such, conspicuous movements like hopping may be inappropriate stoat responses as they may attract the stoat's attention. By this logic it may be assumed that conspicuous vocal behaviours like alarm calling would also attract the stoat, and should have decreased during the stoat trials. However, Spurr and O'Connor (1999) showed that stoats are not attracted to the alarm calls of other birds. During the stoat trials on Tiritiri Matangi, hop behaviours were more frequent and the robins approached the model more closely than at either

Benneydale or Wenderholm. This again supports the hypothesis that the robins on Tiritiri Matangi are incapable of recognising the predatory threat posed by the stoat. Robin hopped less and stayed further away during the control trial at Benneydale than at the other two sites. This may indicate increased wariness toward any foreign objects at Benneydale where adult predation risk is highest.

By indicating that robins that can recognise a stoat hop less and stay further away from the model, the results of PC3 illustrate a significant flaw in the response intensity score procedure used in this experiment. If hops should increase when a morepork is near, but decrease when a stoat is near, then the response intensity scoring criteria should not be the same for all predators. Future studies need to develop separate scoring criteria according to the anti-predator behaviours that are most appropriate for each predator used in the experiment.

### 4.4.4 Conclusions

This study provides clear evidence to support the hypothesis that isolation on mammal-free islands for more than one generation suppresses the ability of North Island robins to recognise and respond to mammalian predators. Although this finding is limited to just one species it represents a useful first step in understanding the effects of isolation on the predator recognition abilities of New Zealand's native bird species. It is hoped that these results will stimulate similar research on other species that are potential candidates for mainland island reintroduction programmes. This study also illustrates that the issue of naïvety should be considered when translocating individuals from both historically mammal-free islands, and islands where mammals have been eradicated.

The results of this study also support the hypothesis that North Island robins that have been reintroduced to the mainland following a period of isolation, will relearn to recognise mammalian predators. While this is an encouraging finding, this study also indicates that the strength of the anti-predator responses given by reintroduced individuals in the presence of a stoat was suppressed compared with naturally occurring mainland robins. Due to the small sample size of Wenderholm birds, it is difficult to draw strong conclusions from this result. It is possible, however, that the low mammal density at Wenderholm has reduced contact with stoats to a level that has allowed only a few individuals to learn to recognise the stoat. A low incidence of stoat encounters may also encourage a perception among robins that stoat predation is rare and therefore less important. In either case, predator control may have prevented the full expression of anti-predator behaviours in response to mammalian predators in the Wenderholm robin population.

Pre-release predator training uses the Pavlovian conditioning process to teach naïve animals about the threats posed by novel predators (Griffin, 2004; Griffin *et al.*, 2000; Heyes, 1993; McLean, 1997; Mineka and Cook, 1993; Suboski, 1990). The 'releaser-induced recognition' learning model describes how recognition can develop as a result of an experience in which there is a conjunction between an unconditioned stimulus (which elicits a response) and a conditional stimulus (that does not yet elicit a response). In the wild, a bird that has never encountered a stoat may hear the alarm call of a nearby conspecific (the unconditioned stimulus). This alarm call releases innate response behaviours such as freezing or increased vigilance. The bird then becomes aware of a stoat, which it does not recognise (the conditional stimulus). As the stoat has been seen in conjunction with the alarm call, the bird learns that the stoat is a threat. Next time a stoat is encountered the bird will recognise it as a threat and be able to initiate the response without the input of a conspecific (Suboski, 1990). In birds, the unconditioned stimulus may include aural cues such as alarm calls, or visual signals such as a predator holding a dead or struggling conspecific (Griffin, 2004). By recreating this association between an unconditioned and conditional stimulus in a captive environment, predator training has the potential to replicate the natural learning process. This process has been shown to result in the expression of strong anti-predator responses in previously naïve robins (McLean *et al.*, 1999). Implementing predator training during translocations could therefore enhance the natural relearning process. Whether the strong anti-predator responses learned during this training will be maintained in an environment where contact with mammalian predators is rare will need further investigation.

# CHAPTER FIVE

# Implications for Management and Future Research

**Plate 5.1:** Releasing North Island robins at Wenderholm Regional Park (photograph by T. Lovegrove)

## 5.1 Introduction

Historically, species translocations in New Zealand have focused on moving individuals from vulnerable mainland populations to islands free of introduced mammalian predators. In recent decades, there has been a realisation that these islands do not cater for all of the needs of many of New Zealand's threatened species (Saunders and Norton, 2001). As a result, there has been a shift in focus toward the restoration of so called "mainland island" sites (Craig *et al.*, 2000; Saunders and Norton, 2001). One of the primary goals of these mainland islands is to reintroduce native species that have become locally extinct. Often, candidates for reintroduction are harvested from the thriving offshore island populations that have been isolated from the effects of mammalian predation for some time (Dimond and Armstrong, 2007). Until this study, there had been no research into how this period of isolation may have affected the mammalian predator recognition abilities of these individuals. As a result, the issue of mammalian predator naivety has not been seriously addressed in some reintroduction projects (Lovegrove *et al.*, 2002). During the translocation of North Island robins to Wenderholm Regional Park the birds sourced from Tiritiri Matangi were assumed to be suitable for translocation to a mainland environment (Lovegrove *et al.*, 2002). It was thought that because some of the candidate birds in the translocation were offspring of the mainland birds that founded the Tiritiri Matangi population, these birds would have some predator recognition ability (Lovegrove *et al.*, 2002; T. Lovegrove pers. comm.). It was unknown how isolation from mammalian predators on Tiritiri Matangi may have affected the robins' ability to recognise and respond to these predators in their new environment.

This chapter summarises the findings of this research and their implications for future management of translocation projects in New Zealand. It will discuss the potential for implementing pre-release predator training during translocations and provide a number of recommendations for the direction of future research.

## 5.2 Key Findings and Implications

The results of this study suggest that North Island robins from the Tiritiri Matangi population have lost the ability to recognise a stoat as a significant predatory threat. When exposed to a stoat model these birds wing-flicked and alarm called less frequently and returned to the nest more quickly than expected. Tiritiri Matangi robins also failed to maintain an increased distance between themselves and the stoat model, as was observed in the Wenderholm and Benneydale populations. The overall response intensity of these birds toward the model stoat was not significantly different from the control. These findings have important implications for future translocations of North Island robins from mammal free islands to mainland sites. It is no longer appropriate to assume that offshore populations that were founded by mainland individuals will be suitable for translocation to the mainland without addressing the issue of predator naivety (Lovegrove *et al.*, 2002).

The results of the present research also suggest that North Island robins from the reintroduced population at Wenderholm Regional Park may have regained some ability to recognise the stoat as a predator. These birds showed increased rates of wing-flicking and alarm calling in response to the stoat model, and maintained a greater distance from the stoat model than the other treatments. However, their overall response intensity was lower than expected when compared with the experienced mainland robins from Benneydale. It is possible that this depressed ability to display strong anti-predator behaviours when encountering a mammalian predator is a result of the low mammal densities at Wenderholm. Reduced contact with mammalian predators could restrict the number of individuals within the population that have experienced mammalian predation directly. Equally, low mammal densities could promote a perception that mammalian predation is rare and therefore only a minor threat to nest survival. This result suggests that conservation managers should not rely on the natural relearning ability of reintroduced robins to produce a population that is fully equipped to deal with mammalian predators. To avoid the issue of predator naivety, future mainland reintroductions may choose to harvest individuals from other mainland sites where mammalian predators are common. Alternatively naïve robins from offshore island populations may be taught to recognise mammalian predators prior to translocation. Previously naive New Zealand robins have shown an ability to produce strong anti-predator responses to model stoats, ferrets and cats following predator recognition training (Maloney and McLean, 1995; McLean *et al.*, 1999). As such, pre-release training offers a valuable tool to boost anti-predator behaviours in translocated populations that may struggle to regain the full expression of these behaviours without assistance.

## 5.3 Pre-release Predator Training

For many years conservation biologists have advocated the use of pre-release predator training during the reintroduction of naïve individuals into new environments

(Griffin *et al*., 2000; Maloney and McLean, 1995; McLean *et al*., 1999; Reed, 2004). In practice, however, this kind of training is not generally applied. Resistance to the use of pre-release training is based on several key issues. These include the ethical requirements to minimise stress during translocation, a lack of evidence to illustrate that training will ultimately increase survival and a belief that intensive predator control eliminates the need for translocated individuals to be taught to recognise key predators.

The process of translocating wild or captive raised animals can be extremely stressful for the individuals involved. In some species this stress can reduce the heath and reproductive potential of the founding individuals and can result in high mortality within the first few days of release (McLean *et al*., 1999; Sims, 2000; Teixeira *et al*., 2007). As such current ethical guidelines recommend that translocation procedures should be developed to minimise the stress experienced by the animals (Groombridge *et al*., 2004; Woodford, 2000). As predator training requires the intentional elicitation of stress responses in target individuals, its implementation would be contrary to the current translocation best practice. However, the negative effects of stress can be highly varied. New Zealand's robin species appear to be relatively robust and show few ill effects during translocation. Following translocation to Tiritiri Matangi in 1992-93 and to Tawharanui Open Sanctuary in 2008, the founding North Island robins survived well and bred successfully (Armstrong *et al*., 2000; Lovegrove, 2008). In 1994, 10 South Island robins that had undergone predator training were reintroduced to a mainland site where predator control was not being carried out (Armstrong, 2008; McLean *et al*., 1999). All of these birds survived the translocation but disappeared within six months (McLean *et al*., 1999). The high initial survival of these trained individuals was considered a partial success of the translocation and suggests that the increased stress of predator training was not the cause of failure (McLean *et al.*, 1999). For a resilient species it may be argued that failing to provide training is less ethical than subjecting individuals to increased stress, as it deprives them of the ability to protect themselves effectively in their new environment (McLean *et al.*, 1999). The high degree of variability in the stress tolerance of target species makes it inappropriate to suggest that pre-release predator training should be applied during all reintroductions. It is clear, however, that in some cases the potential for pre-release predator training to improve post-release survival may out-weigh the negative effects of increased stress. The suitability of pre-release training should be assessed during the planning stages of future reintroduction projects based on the potential impact of key predators on the population, the risk of reduced fitness as a result of increased stress and the effectiveness of training to promote strong anti-predator responses (Blumstein, 2000).

Some managers may also resist the implementation of pre-release predator training due to a lack of evidence showing that training will ultimately decrease predation rates and increase the survival of translocated individuals. Many studies have shown that a variety of species can be trained to recognise novel predators (Ellis *et al.*, 1977; McLean *et al.*, 1999; McLean *et al.*, 2000; Miller *et al.*, 1990; Mirza *et al.*, 2006; White *et al.*, 2005). However, few have been able to demonstrate that this learned ability increased the post-release survival of translocated individuals (van Heezik *et al.*, 1999). Founder individuals may die for many different reasons, including, disease, malnutrition, extreme weather events or predation by a range of different species. It is extremely difficult to tease apart these different causes of mortality to identify differences in the predation rates of trained and untrained individuals by specific predators (McLean *et al.*, 1999). This issue, combined with the relatively small sample sizes typically used during translocations, makes it extremely difficult to test the survival benefits of pre-release predator training for most species (McLean *et al.*, 1999). As such, the lack of evidence of a survival benefit from pre-release training may be an illustration that this benefit is difficult to detect, not that it does not exist. It has therefore been suggested that pre-release predator training should be applied in situations where there is merely the potential for improved predator recognition abilities to increase the survival of translocated individuals (McLean *et al.*, 1999).

It may also be argued that pre-release predator training will not be required when naïve individuals are translocated into an environment where key predators are controlled intensively (D. Armstrong pers. comm.). Predator control is an important part of conservation in New Zealand. Recent developments in predator control techniques have allowed mammalian predators to be suppressed to levels at which some vulnerable species are able to establish viable populations (Armstrong *et al.*, 2006; Clout and Russell, 2006; Gillies *et al.*, 2003; Innes *et al.*, 1999; Saunders and Norton, 2001). However, intensive predator control is expensive and is usually limited to discrete 'mainland island' sites. As such, the dispersal of individuals to areas outside of the predator controlled site is likely to occur (Andrews, 2007; Bellingham *et al.*, 2008). Pre-release predator training would allow translocated individuals to gain the knowledge required to recognise and respond to specific predators if they encounter them outside the predator controlled area. If this training allows translocated birds to survive predator attacks in uncontrolled areas they, or their offspring, may be able to return to the predator controlled site and contribute to the population. Equally, as the population expands and inter and intra-specific competition for territories increases, trained birds may be able to persist in peripheral areas where predators might encroach into the controlled site.

## *5.4 Future Research Directions*

The results of this study raise a number of questions that require further investigation. Firstly, a repeat of this study using a different mammalian predator should be carried out. Rats are another significant predator of many native New Zealand species. Pacific rats were present on Tiritiri Matangi for 17 months after robins were translocated to the island and preyed on robin nests during the first breeding season. However, none of the birds surviving on Tiritiri Matangi today has any experience of rat predation. The island was declared mammal free in September 1993 while the oldest surviving robin was born in November 1993 (D. Armstrong pers. comm.). It is suspected that the Tiritiri Matangi robins will have lost the ability to recognise all mammalian predators, including rats. However, this hypothesis should be tested.

There is a need to carry out a similar investigation of predator recognition abilities in a range of other native species that have been marooned on offshore islands. As the mainland island restoration process develops other species will become candidates for mainland reintroductions. It will be important to have a clear understanding of the predator recognition capabilities of these species before such reintroductions occur. If similar naivety as found in this study can be demonstrated, then attempts should be made to determine the capacity of these species to learn to recognise important predators though predator recognition training. Hihi (*Notiomystis cincta*) have recently been reintroduced to the mainland near Auckland. Initial reintroductions of hihi from Tiritiri Matangi to the predator controlled ‘Ark in the Park’ site in the Waitakere Ranges were carried out in April and June 2007 (Bellingham *et al.*, 2008). These translocations failed when all of the founding birds and their off-spring disappeared within two years (Armstrong, 2008). A second reintroduction of hihi to the site occurred in May 2008. Unfortunately, it is unlikely that the population will persist, despite the implementation of an intensive predator control regime at the site (Armstrong, 2008). Hihi could therefore be an excellent study species to continue the investigation of predator recognition abilities in New Zealand birds. If hihi sourced from offshore islands show similar naivety as that demonstrated in North Island robins, future reintroductions may benefit from pre-release predator training.

It might also be valuable to monitor the mammalian predator recognition abilities of individuals that have been translocated from mainland sites to mammal-free offshore islands. By regularly testing the recognition abilities of the founding birds and their offspring it may be possible to identify the time required for these abilities to be lost. Such an investigation should also attempt to identify whether experienced founding individuals will lose their recognition abilities over time.

Very little is known about the retention of recognition abilities that have been learned through artificial training or what effect a lack of retention may have on the resulting anti-predator behaviours (Griffin *et al.*, 2000). It may be interesting to investigate retention by including mammalian predator recognition training in future reintroductions of North Island robins from offshore islands to mainland sites where mammalian predators are controlled. Recognition abilities and the strength of anti-predator behaviours could then be tracked through time. This would allow researchers to identify whether the ability to respond strongly to mammalian predators can be maintained in an environment where contact with these predators may be rare.

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