Assessing the use of artificial nests for predicting predation pressure in New Zealand forest fragments

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THESIS ABSTRACT

Using artificial nests to predict the predation pressure on natural bird nests has been the subject of over 400 publications, the vast majority quantifying aspects that affect nest success. However, these studies have usually invoked the assumption that artificial nests accurately reflect the success of natural nests. The intention of this thesis was to evaluate the technique of using artificial nests to predict natural nest success, with the aim of establishing the main factors influencing its success as a monitoring technique. This was done by addressing three main questions a) Can artificial nests be used to predict natural nest success in forest fragments?, b) What aspects of the methodology influence the precision, practical application and interpretation of the results from artificial nests in New Zealand forest fragments?, c) What external factors, i.e. habitat structure, confound interpretation of artificial nests results in New Zealand forest fragments?

Artificial nest experiments were conducted concurrently in nine reserves, with estimates of nest success calculated for each reserve using the known fate model in MARK. These estimates were then correlated with the success of North Island Robin nests (estimated using Stanley's (2000) method of stage specific nest success) in the corresponding reserves. General linear modelling was used to fit a log-log relationship between artificial and natural nest success estimates using parametric bootstrapping to account for error in the estimates. The Akaike's Information Criterion (AIC) model selection procedure was used to select the model for estimating both artificial and natural nest success and for selecting the best model for predicting natural nest success using artificial nests.

The evidence from the results revealed that artificial nests could be used to predict natural nest success. However, imperative to achieving this result was having the ability to identify and conduct independent analysis for each predator group (all predators, 'rats and possum', birds and mice). AIC selection procedure selected nest success estimates derived from predation by rats and possum as the most parsimonious model, hence the best at predicting natural nest success.

Investigation of methodology showed that: (1) data from artificial nests left out for one week gave better predictions than data collected over four consecutive weeks; (2) leaving nests out longer than one week before checking increases the chance of the marks becoming obscured, hampering predator identification; (3) adding a quail egg has little effect on predation rate, particularly on the rate of predation by mammals; and (4) it is necessary to include clay eggs in artificial nests as marks left on quail eggs and damage done to artificial nests were not reliable indicators of predator type.

Investigation of external factors revealed: (1) no strong or consistent evidence that the fine-scale habitat at nest sites affected predation on artificial nests; (2) reserve size may affect the rate of rat and possum predation, but not bird predation; and (3) the proximity of artificial nests to a bait station may influence the rate of predation by mammals.

Chapter One

Thesis Introduction

Human modification of habitats has had negative impacts on species diversity and survival (Diamond *et al.*, 1981). Habitat loss, disturbance (Bradbury *et al.*, 2000) and fragmentation (Raherilalao, 2001 see also reviews by; Andrén, 1994; Simberloff, 2000a; Chalfoun *et al.*, 2002b) are currently influencing resource availability (e.g. food supply, suitable nesting sites and living space) and predator community structure (Burkey, 1993; De Santo & Willson, 2001) and heightening exposure to abiotic factors such as severe weather impacting avian nest success (Karr, 1982a). Additionally, for species confined by insularity or restricted in their range, e.g. on offshore islands or fragmented areas of forest, exacerbation of the effect of the previously mentioned factors (Savidge, 1987; Sieving, 1992; Simberloff, 1995; Hernandez *et al.,* 1999; Simberloff, 2000b) can increase the risk of extinction. Among these factors, the single biggest factor leading to decline of bird species in many regions, certainly in New Zealand (King, 1984, 1990), has been introduced predators.

The introduction of invasive alien vertebrates is a major cause of the loss of native biodiversity in many regions of the world. These introductions have been linked to increased nest failure in bird species, along with a variety of impacts including disease, parasitism, competition, habitat destruction and hybridisation (Atkinson & Cameron, 1993; Mack *et al.*, 2000; Simberloff, 2000c). The threats posed by them are especially severe on oceanic islands and other isolated ecosystems. On islands, the association of habitat loss on species extinctions is often miscalculated because introduced species have driven extinctions beyond those caused by habitat loss (Brooks *et al.*, 2002).

Management efforts toward restoring declining avian populations are often complicated by complex relationships among habitat, predators and resources. The introduction of alien species has created major management concerns for conservation of bird species, and introduced predatory mammals are recognized as one of the worst groups of offenders (Craig, 2000; Clout, 2002). The devastation following the introduction of mammalian predators is particularly clear on the island archipelago of New Zealand. What makes New

Zealand particularly interesting in terms of conservation is the fact that, before human occupancy, it evolved without any mammalian predators, resulting in a vertebrate biota dominated by bird species. Over the past 200 years, approximately 1,600 species of plants, 33 species of birds and 54 species of mammals have been introduced (Atkinson & Cameron, 1993; King, 1990). Unfortunately, introduced species have acclimatised extremely well in their new environment, so much so that populations of native species are no longer able to compete, causing the extinction or near extinction of several species of birds (40% of the avifauna confirmed as extinct), numerous plants and the change in frequency and distribution of many native flora and faunal communities (Davidson, 1983; Atkinson & Cameron, 1993; Towns & Daugherty, 1994; Atkinson, 1996; Powlesland *et al.*, 1999). The conservation status of many species have elevated to endangered and rare with many bird species now extinct or reduced to small remnant populations on off-shore, predator free islands (Dilks *et al.*, 1996). Of these species introductions, ship rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), brush-tailed possums, (*Trichosaurus vulpecula*) and stoats (*Mustela erminea*) appear to have had the greatest effects on nesting of endemic avian populations, the most notorious being the ship rat (King, 1984; Moors 1985; Innes & Hay, 1991).

In world terms, New Zealand's occupation by man is relatively recent, being one of the last mid-latitudinal land masses of any extent to be occupied. This means that there are historical records dating back to man's arrival tracing the history of this environmental manipulation, recounting events that contributed to extinctions of many endemic species. These records provide conservation bodies with prior knowledge of the natural state of the environment, a template outlining the restoration goal with which to base their conservation strategy on, directing the restoration of New Zealand's native biodiversity towards its natural state. Conservation in New Zealand is largely focused on reducing the impact introduced mammals have on the abundance of indigenous species. Conservation managers have a range of strategies they can employ to control these pests, but the combination that maximizes conservation gains depends on the protection each strategy affords, and the scale at which it can be applied (Choquenot & Parkes, 2001). Vehicles used for this purpose include predator control programmes, ongoing monitoring techniques and the development of offshore and mainland island reserves.

Predator control programmes are used to reduce abundance of nest predators to try to combat local extinction of native bird species within reserves. Common practices include the use of trapping (e.g. Fenn traps, Snares, Snap-traps and leg hold traps), shooting and poison (e.g. Brodifacoum, Cyanide, Cholecalciferol, Phosphorus and Warfarin). Poison may be distributed in bait stations, by hand or by helicopter drops of poison laced bait (Dilks *et al.*, 1996; Innes & Barker, 1999; Powlesland *et al.*, 1999). Predator-proof fences built around the perimeter of areas of forest are also being used as a method of excluding mammalian predators. Translocations of endangered populations to predator-free forest fragments and offshore islands are also used to increase the distribution of and supplement existing populations of threatened species (Armstrong, 2000).

To control predator populations effectively and efficiently, changes in their abundance, density, and re-invasion rates need to be accurately monitored (Clapperton *et al.*, 1999; Morley, 2002). Successful monitoring following predator control is necessary to determine the required intensity and longevity of predator control, preventing unnecessary continuation, thus avoiding unnecessary expense (Alterio *et al.*, 1999; Ruscoe *et al.*, 2001). The outcome of this monitoring determines the fate of the species that you are trying to protect; hence it is important that the technique used is reliable and reasonably accurate. Monitoring can also be used to assess habitat suitability where bird species are absent from patches (e.g. assess risk for translocated populations).

In New Zealand, predator abundance, hence the success of predator control programmes, is often indexed using tracking tunnels (King & Edgar, 1977; Brown *et al.*, 1996b Blackwell *et al.*, 2002; Gillies & Williams, 2002). The technique uses a “run through” tunnel containing two pieces of paper either side of a sponge soaked with a tracking medium (food colouring). The animal picks up the tracking medium on its feet as it passes through the tunnel, then leaves a set of footprints on the paper as it departs from the tunnel.

Relative density indices such as tracking tunnels are susceptible to a number of biases. Sarrazin & Bider (1973) suggested that tracking tunnels do not allow changes in animal abundance to be differentiated from changes in animal activity. This technique is considered to be best suited for providing simultaneous comparisons of the relative abundance of rodents (particularly rats) or mustelids between similar habitat areas (Blackwell *et al.*, 2002), e.g. treatment versus non-treatment, or gross changes in relative abundance over time at a single site. Tracking tunnels can also become "saturated" when rodents or mustelids occur at high densities, making the results difficult to interpret. Identification of the predator type can also be difficult if the sponge has dried out, the food colouring was too dilute, or if the animal has backed out after placing only one foot on the sponge leaving only partial tracks or footprints. The target animals can also exhibit a certain amount of neophobia towards tracking tunnels, resulting in an underestimation of population density (Crowcroft, 1973, cited in Brown *et al.*, 1996). Additionally, baited tracking tunnels are thought to induce target animals to leave their natural home ranges, potentially biasing abundance estimates within given areas (Gillies & Williams, 2002). The fact that tracking tunnels are placed on the ground means that they preferentially target predators with a ground-searching mode of behaviour rather than an arboreal search mode that is required to find and depredate nests. Therefore, rodent monitoring using tracking tunnels does not escape the necessity for concurrent nest-monitoring for assessment of rodent impact on nest mortality.

A more direct method for assessing the effectiveness of predator control is to monitor natural nest success. However, monitoring natural nests directly is not devoid of bias that can be introduced by human sampling error or nest disturbance. For example, nests detected may be more exposed than the average nest (Martin & Geupel, 1993) and regular visits to monitor nest fates may increase the probability of failure by showing the way to visual (Gutzwiller *et al.*, 2002; Tryjanowski & Kuzniak, 1999) and olfactory-searching nest predators (Whelan *et al.*, 1994). Locating natural nests can also be very time consuming due to their often cryptic appearance and location high in the canopy. In addition, this technique can not be used to assess survival probability in areas of forest where bird populations are absent, so cannot be used to assess risk before translocations.

Artificial nests provide an alternative or additional method of assessing predation risk for native bird species. Artificial nest experiments have been used extensively overseas, particularly in North America (Sugden & Beyersbergen, 1987; Ortega *et al.*, 1998; Wilson *et al.*, 1998; King *et al.*, 1999; Buler & Hamilton, 2000; Davidson & Bollinger, 2000; Thompson & Burhans, 2004), Europe (Part & Wretenberg, 2002), and Australia (Zanette, 2002). Artificial nest experiments have been used to assess variation of predation rates associated with characteristics of location, degree of concealment, predator type, habitat, density and season (Sonerud & Fjeld, 1987; Martin, 1987; Major & Kendal, 1996; Sieving & Willson, 1998; Major *et al.*, 1999; Schmidt & Whelan, 1999; Githiru *et al.*, 2005). Several experiments have recently been conducted assessing whether artificial nests give an accurate index of real predation rates (Wilson *et al.*, 1998; Ortega *et al.* 1998; King *et al.*, 1999; Part & Weidinger, 2001; Wretenberg 2002; Zanette, 2002; Thompson & Burhans, 2004). However, the results have been variable – that is, artificial nests work well in some situations but not in others (see also reviews by; Major & Kendal, 1996; Mezquida & Marone, 2003; Moore & Robinson, 2004). Results suggest that artificial nests that closely mimic natural nests give the most useful data (Janzen, 1978; Martin, 1987). However, it is clearly important to test the effectiveness of artificial nests in any new environment where they are to be used.

Despite the obvious importance of nest predation in New Zealand, and the potential power of artificial nests for studying effects of predation on bird distributions, there has been no published research in New Zealand using artificial nests to date. It is particularly unclear what the results will be in New Zealand, where most of the predation is by mammals, given that previous research has found that artificial nests were preyed upon mainly by birds, whereas real nests were preyed upon by mammals (Willebrand & Marcstrom, 1988; MacIvor *et al.*, 1990;). This has been linked to the fact that avian predators are assumed to use visual cues, whereas mammalian predators are assumed to use olfactory cues absent from artificial nests (Willebrand & Marcstrom, 1988). Therefore the method used is crucial because previous findings show that real and artificial nests attract different predators (Part & Wretenberg, 2002; Moore & Robinson, 2004).

The advantage of artificial nests over other methods is that they can be designed to mimic real nests, reducing neophobia associated with tracking tunnels and traps (Crowcroft, 1973, cited in Brown *et al.*, 1996). They can also be positioned in sites similar to the nest sites used by the avian species that are being monitored, so should be subject to similar conditions and risks. Artificial nests also do not draw predators to the site using strong smelling bait or lures, but present a natural scenario, i.e. nest with eggs. They may therefore be less likely to overestimate the number or type of potential nest predators. Where the bird species of interest are present, artificial nest experiments may be valuable because data can be collected much more quickly than real data, because uncertainty about numbers of nests and laying times is removed, and because confounding factors can be controlled. A correlation between artificial nest depredation rate and bird absence may indicate that the absences are due to differences in predation pressure, whereas lack of such a correlation may indicate that absences are due to other factors. Similarly, a correlation between nest depredation rate and distance to the forest edge may indicate that birds cannot survive in small fragments due to high predation at edges, whereas lack of such a correlation may indicate small fragments (or edges) are unoccupied for other reasons. However, artificial nests will only be a useful technique if it can be shown that the predation rates on artificial nests are an accurate index of predation rates on real nests.

Model species

To assess the degree to which the predation rate on artificial nest reflects that on real nests, we compared artificial rates to real rates for the New Zealand, North Island Robins (*Petroica longipes*) (classification following Holdaway *et al.*, 2001) for multiple sites. Robins are chosen as the model species because: (1) data is available; and (2) robin eggs, young and adult survival are strongly influenced by predator abundance. However, the results will be relevant to all open nesting forest bird species.

The North Island Robin is a predominantly ground-foraging insectivorous passerine that nests in trees, making them extremely vulnerable to both ground dwelling and arboreal predators. It stands approximately 10 cm tall and weighs around 26-32 g (Berggren *et al.*, 2004). They generally form monogamous pairs throughout consecutive years and are ardently territorial, often aggressively defending and establishing territories throughout the year (Armstrong *et al.*, 2000). The breeding season extends from late August to early February and pairs will commonly produce 2-3 broods per season. Robins are an open-nesting species that builds tightly woven nests approximately 20 cm wide and 15 cm deep that are made using mainly mosses, fern scales and small sticks. Nests sites can be found anywhere from 1.5 to 20 m, typically in forks of trees or on the crown of tree ferns (Flack, 1985). The female lays a clutch of 2-3 white to mottled brown eggs. Incubation lasts approximately 19 days and the chicks take 19-21 days to develop before leaving the nest and a further 4-7 weeks of bi-parental care before becoming completely independent (Armstrong *et al.*, 2000). Following a predation event Robins will re-build in a new location within their territory. This process has been known to occur multiple times within one breeding season (Flack 1985; pers. obs.). Robins are found to occupy both native and pine forests (Bull, 1984), with populations surviving in both small and large forest patches. Classed as regionally threatened, robins are frequently translocated into areas of bush as part of a reintroduction programme aimed at establishing sustainable populations throughout New Zealand (Armstrong, 2000).

Thesis outline

The intention of this thesis was to evaluate the technique of using artificial nests to predict natural nest success, with the aim of establishing the main factors influencing its success as a monitoring technique. This was done by addressing three main questions:

1. Can artificial nests be used to predict natural nest success in forest fragments?

2. What aspects of the methodology influence the precision, practical application and interpretation of the results from artificial nests in New Zealand forest fragments?

3. What external factors, i.e. habitat structure, confound interpretation of artificial nest results in New Zealand forest fragments?

This thesis was written with the view of presenting three separate papers, the separation of which was based on the audience that they were aimed at. Chapter 2 was written for an international audience streamlined to include the methodological and statistical techniques required to use artificial nests to predict natural nest success within forest fragments. Chapter 3 was written with the purpose of assessing the influence of components of the methodological technique used. While the methods are relevant to an international audience, the results may be relevant only in New Zealand forest fragments. Chapter 4 was written with the purpose of assessing additional external factors that may confound interpretation of the results from artificial nests. Again, the results may be relevant only to circumstances found in New Zealand forest. For the purpose of this thesis only, references were made between chapters to avoid unnecessary repetition of methods common between chapters.

Chapter Two

Using artificial nests to assess predation pressure in forest fragments

ABSTRACT

Using artificial nests to predict the predation pressure on natural bird nests has been the subject of numerous publications, the vast majority quantifying aspects that affect nest mortality. However, these studies have usually invoked the assumption that artificial nests accurately reflect the success of natural nests. The aim of this research was primarily to determine the extent to which artificial nests can be used to predict natural nest success within forest fragments. Artificial nest experiments were conducted concurrently in nine reserves, with estimates of nest success calculated for each reserve using the known fate model in MARK. These estimates were then correlated with the success of natural nests (estimated using Stanley's (2000) method of stage-specific nest success) in the corresponding reserves. General linear modelling was used to fit a log-log relationship between artificial and natural nest success estimates using parametric bootstrapping to account for error in the estimates. Akaike's Information Criterion (AIC) was used to select the best models for estimating artificial and natural nest success, and for selecting the best model for predicting natural nest success using artificial nests. The results revealed that artificial nests could be used to predict natural nest success. However, imperative to achieving this result was the ability to identify and conduct independent analysis for each predator group (all predator, 'rat and possum', bird and mouse). Estimates derived from predation by 'rats and possums' were best for predicting natural nest success. Confounding factors (i.e. a diverse range in habitat structure, area and location, predator control and community) introduced through reserve choice weakened this relationship, highlighting factors important to consider when using artificial nests as a monitoring technique.

INTRODUCTION

Using artificial nests to predict the predation pressure on natural bird nests has been the subject of over 400 publications (Moore & Robinson, 2004), the earliest studies dating back to the 1960s (Matschke, 1965; Henry, 1969). The majority of this research has focused on measuring the aspects affecting nest mortality such as the influence of habitat characteristics and habitat loss, most frequently the influence of edge effect and fragmentation (Andrèn & Angelstam, 1988; Gardner, 1998; Hartley & Hunter, 1998; Matthews *et al.*, 1999; Soderstrom, 1999; Lahti, 2001; Maina & Jackson, 2002; Chalfoun *et al.*, 2002a, b; Bàtàry & Baldi, 2004). The influence of microhabitat (Crabtree *et al.*, 1989; Martin, 1987; Moller, 1987; Sugden & Beyersbergen, 1987; Seitz & Zegers, 1993; Dion *et al.*, 2000 ; Mezquida & Marone, 2002) at nest sites e.g. nest height (Martin, 1993b, b; Wada, 1994; Sloan *et al.*, 1998), vegetation characteristics (Dion *et al.*, 2000; Schneider, 2001; Stuart-Smith & Hayes, 2003; Bàtàry & Baldi, 2004) have also been quantified using the results from artificial nest studies. Identification of predator species through analysis of artificial nest remains has been used as a model to measure the impact of individual predator types on natural nest success within the predator community (Major, 1991; Major *et al.*, 1996; Marini & Melo, 1998). However, the aforementioned research has invoked the assumption that the success of artificial nests accurately reflects the success of natural nests, an assumption yet to be unanimously supported.

Artificial nests offer possibilities for nest predation studies because they are amenable to manipulation and can be used in designed experiments (Villard & Part, 2004). They can also be made available in large enough quantities to permit statistical inference (Major & Kendal, 1996). Identification of predators through natural egg remains is often unreliable (Lariviere, 1999). As predator identification is important in terms of conservation, the ability to identify predators using artificial eggs would also be highly advantageous. The successful application of this technique will avoid the invasive and time-consuming methods required to monitor natural nest success (Faaborg, 2004).

Natural nests that are detected by observers are often those that are slightly more exposed (Martin & Geupel, 1993) and regular monitoring may increase the probability of nest depredation (Tryjanowski & Kuzniak, 1999; Gutzwiller *et al.*, 2002) introducing biases when estimating natural nest success. Artificial nests may also provide an alternative and perhaps more accurate method than currently used techniques such as tracking tunnels and kill traps (Brown *et al.*, 1996b; Blackwell *et al.*, 2002), as they are more similar to real nests in terms of position and spacing, therefore the way predators will encounter them while hunting will also be similar. For example, one of the dominant predators of nests in the New Zealand forest is the ship rat (*Rattus rattus*) that nests predominantly in trees (Innes & Skipworth, 1983; Dowding & Murphy, 1994) therefore artificial nests, positioned in trees may reflect relative risk of nest predation more closely than tracking tunnels placed on the ground.

Artificial nests are yet to be accepted and used as a monitoring technique within local and governmental bodies. Reviews by Major and Kendal (1996) and Moore and Robinson (2004) highlight a disparity in the results of selected publications that both support and reject the use of artificial nests for predicting natural nest success. It is suggested that the effect of variation in the methodology used between researchers conducting artificial nest experiments is responsible for these conflicting results. Variation in the methods used in the construction, placement and exposure period of artificial nests can directly influence the probability of detection and hence success of nests. For example, using nests made from tennis balls or commercially supplied wicker nests, as opposed to nests constructed from natural materials, can affect artificial nest success by attracting or deterring predators (Martin, 1987, 1988; Moller, 1987; Reitsma *et al.*, 1990; Gibbs, 1991; Major & Kendal, 1996; Rangen *et al.*, 2000; Rodewald & Yahner, 2001). The placement and concealment of these nests can also affect nest detection by different predator types (Janzen, 1978; Martin, 1987; Yahner & Cypher, 1987; Yahner & Scott, 1988; Yahner *et al.*, 1989; Sieving, 1992) resulting in overestimation of the role of particular predators (Storaas, 1988; Willebrand & Marcstrom, 1988). Using nests baited with Japanese Quail (*Coturnix japonica*) eggs has been found to limit predation by smaller mouthed predators (Boag *et al.*, 1984; Roper, 1992; Haskell, 1995; DeGraaf & Maier, 1996) and influence nest detection through olfactory cues associated with egg decay (Henry, 1969). In addition, inadequate sample size and an increase in the likelihood of pseudo replication, resulting from the use of several study plots within single study sites, may reduce the measure upon which statistical inference can be made from the results obtained (McKone & Lively, 1993). The inclusion or combination of the aforementioned factors may be responsible for the disparity in results and lack of confidence in this method as an accepted and widely practised monitoring technique. However, an alternative explanation is that artificial nest success may not be closely correlated with natural nest success (Loiselle & Hoppes, 1983; Wilcove, 1985; Willebrand & Marcstrom, 1988; Paton, 1994; Reitsma & Whelan, 2000).

The intention of this research was primarily to determine the extent to which artificial nests can be used to predict natural nest success within forest fragments. Artificial nest experiments were conducted concurrently in nine reserves, with estimates of both natural and artificial nest successes calculated for each reserve. Reserves used vary in topography, habitat structure and management with a range in the success of natural nests. The spatial separation of the reserves ensure independence between sample sites, meeting the assumptions of the statistical methods used and increasing the confidence in the results obtained by introducing a variety of natural nest success estimates. The variety in size, location, vegetation and land-use surrounding the reserves chosen for this research introduced many confounding factors, which ultimately weaken the relationship between the success of artificial and natural nests. The purpose of this was to be able to assess which factors affect the accuracy of artificial nest success when establishing a relationship with natural nest success, as well as highlighting those factors, which need to be taken into account to promote successful application of this technique. The research was also designed to examine further the extent to which artificial nests can be used to discriminate between different predators, their subsequent influence on nest success and the importance of being able to identify predators when using artificial nests as a monitoring technique.

A particular focus of this study was to determine whether artificial nests may be used to assess habitat suitability before re-introductions of avian species to unoccupied areas of bush. Species re-introductions are a popular conservation technique in New Zealand, used to increase the distribution and abundance of protected species (Armstrong, 2000; Armstrong et al 2002a; Armstrong & Ewen, 2001, 2002b). Before species are reintroduced, predator control programmes are often carried out to reduce the threat from mammalian predators from the proposed introduction areas. Following eradication, tracking tunnels and kill traps are often used as an index to monitor the success of the poisoning operations by estimating prevailing numbers of mammalian predators in the bush areas (Brown *et al.*, 1996b; Blackwell *et al.*, 2002). This research aims to provide a more accurate method for predicting nest success in forest fragments to assess their suitability regarding natural nest success before re-introductions of avian species are carried out. In doing so, the research assesses whether artificial nests will be effective as an ongoing monitoring method to detect fluctuating levels of predation in areas with reintroduced and established populations, aiding future management decisions.

METHODS

Study Species

The species chosen as a model for natural nest success was the North Island Robin (*Petroica longipes*) (Holdaway *et al.*, 2001). This species is a predominantly ground-feeding insectivorous passerine that is especially vulnerable to predation from both terrestrial and arboreal predators. Classed as regionally threatened, robins have been closely monitored in many reserves in New Zealand resulting in data that can be used to estimate nest success (Armstrong & Ewen, 2002b).

Study sites

This study involved 9 sites located around the North Island of New Zealand (Table 1). Each of these sites is a scientific or scenic reserve managed by the New Zealand Department of Conservation (Boundary Stream, Paengaroa, Tiritiri Matangi, Waimanoa and Waipapa), a local trust (Bushy Park and Karori) or the local community (Waotu). Robins were reintroduced to seven of the sites following extirpation and have remnant populations at the other two sites (Table 1). These sites were known to vary in nest success due to different levels of introduced mammalian predators (Table 1), and nest success data were available from all sites.

Mammalian predators inhabiting these reserves include the Ship rat (*Rattus rattus*), Norway rat (*Rattus norvegicus*), Brush-tailed possum (*Trichosurus vulpecula*) and Stoat (*Mustela erminea*). These introduced species all prey on bird nests, and have caused the decline of many bird species including robins (Moors, 1975; Diamond & Veitch, 1981; Atkinson, 1985; Clout & Craig, 1995; Brown *et al.*, 1998; Innes *et al* 1999; Clout, 2002; Nugent *et al.* 2002; Innes *et al.* 2004). These reserves also have native avian predators including the Morepork (*Ninox novaeseelandiae*) (Brown *et al.*, 1998), Harrier Hawk (*Circus approximans*) and New Zealand Falcon (*Falco novaeseelandiae*).

The abundance and variety of these avian and mammalian predators depends on the frequency and intensity of predator control, together with the size of the reserve. Following eradication of mammalian predators and installation of a predator control fence (Karori), Tiritiri Matangi Island and Karori reserves are free of mammalian predators.

Table 1. Sites used to compare success of artificial nests and New Zealand robin nests, showing the location, area (of island or forest block), presence of mammalian predators, predator control, and history of robin population.

Site	Location	Size (ha)	Predators	Predator control	Robins
Boundary Stream	39°06′S 176°48′E	800	Yes	Yes	28 reintroduced in 1998
Bushy Park	39°55′S 175°00′E	90	Yes	Yes	21 reintroduced in 2001
Karori	41°40'S 174°8'E	252	No*	N/A	40 reintroduced in 2001 and 36 in 2002
Paengaroa	39°39′S 175°43′E	117	Yes	No	40 reintroduced in 1999
Tiritiri Matangi Island	36°36'S 174°53'E	240	No	N/A	44 reintroduced in 1992 and 14 in 1993
Waimanoa	38°33'S 175°42′E	300	Yes	No	Remnant population
Waipapa	38°24'S 174°38′E	4000	Yes	No	Remnant population
Waotu	38°10S 175°42E	35	Yes	During breeding season	30 reintroduced in 1993
Wenderholm	36°30'S 174°45E	80	Yes	During breeding season	21 reintroduced in 1999

*Mice (*Mus musculus*) present for duration of experiment

Natural nests

Data used for estimating natural nest success were collected from all nine reserves through the breeding season (August – February) both by the Department of Conservation and as part of other research projects (see acknowledgements). When sample sizes were small and there was no difference in nest success detected between years, the nest success was estimated using the data collected over several years to decrease the standard error associated with each estimate of nest success (this included Boundary Stream, Bushy Park and Wenderholm reserves). Data were collected during the breeding season from Tiritiri Matangi 2002 – 2003, Karori 2002 - 2003, Boundary Stream 1998 – 1999 and 1999 - 2000, Bushy Park 2001-2002 and 2002- 2003, Paengaroa 2002 – 2003, Waimanoa 1996 – 1997, Waipapa 1997 – 1998, Waotu 2002-2003, Wenderholm 1999 – 2000, 2000-2001, 2001-2002 and 2002-2003. Reserves were searched early in the breeding season (late August) to locate individuals and breeding pairs of robins. Robin call tapes and subsequent feeding (using mealworms) were used to aid in both robin and nest detection. Nests were found by throwing mealworms (*Tenebrio molitor*) to the robins, resulting in the male calling the incubating female off the nest or either parent taking the mealworm to the nest to feed the chicks. This behaviour was used to determine developmental stage of clutch for analysis of nest success. Chicks were counted as fledged when adults were observed feeding them off the nest. A nest was counted as successful if one or more chicks fledged and failed if the eggs failed to hatch or the chicks died.

Artificial nests

Artificial nests were constructed using materials (leaf litter, moss, fern scales) collected from each reserve where they were deployed. Leaf litter was bound together using garden mesh and twine and a cup formed using a plastic tumbler (with the bottom removed to avoid flooding) lined with moss and fern scales. Abandoned North Island robin nests were used as an aid to help with both the materials chosen and the method of nest construction.

To account for the influence of egg type on nest success each artificial nest contained either two clay eggs (CC) or one clay egg and one quail egg (CQ). Artificial eggs were made using Sculpy brand odour-free polymer modelling clay and a silicon mould, producing eggs measuring 19 by 22 mm (the same dimensions as robin eggs). Two colours of clay, grey and white, were blended together to create an off-white mottled effect similar to the colour of robin eggs. The eggs were attached to the nest by tying a length of nylon to a small piece of wood that was inserted into the centre of each clay egg. The nylon was threaded down through the cup of the nests and tied to the mesh binding the nest. This allowed the eggs to be moved around the nest but not removed completely. Quail eggs were chosen for their similarity in colour to the robin eggs and because they were the smallest eggs available from a commercial supplier (ranging from 19 by 20 to 22 by 26 mm). The slightly larger size of these eggs was compensated for by burying them deeper into the nest cup, thus, decreasing the visible surface area. This accounts for the foraging strategy of the more visually orientated avian predators. All quail eggs were washed using surgical soap (Virkon™) to avoid the transmission of egg borne disease.

The majority of nest predators in the reserves are nocturnal mammals that probably rely on olfactory rather than visual cues when foraging. Human odour is known to attract or deter predators (Whelan *et al.*, 1994; Olson & Rohwer, 1998; Skagen *et al.*, 1999; Duncan *et al.*, 2002). To avoid the transfer of human odour all material collection and nest and egg construction was carried out using surgical gloves.

Nest placement

Each of the nine reserves received 30 artificial nests. Nests were placed at 75 meter intervals, based on the average robin territories on Tiritiri Matangi (Armstrong & Ewen, 2002b), along transects in the larger reserves and grids for the smaller reserves. Nests were placed 1.5 meters from the ground in tree forks, crowns of tree ferns and crevices in tree stumps. This height restriction was constrained to assist volunteers checking nests and to minimise contact through the shortened time period required to check each nest. Nests were placed at a point that could support the nest in a horizontal position and secured in place using twine. To ensure relocation of each nest flagging tape was placed at each nest site. The tape was placed at least 5 metres from the nest site to avoid attracting predators to the nest (Bowman & Harris, 1980; Hein & Hein, 1996).

Checking routine

Artificial nests were exposed for 3 sets of 4-week periods, separated by 3-week intervals. The 4-week exposure period was slightly longer than the incubation period of the robin, which is 21 days. The nests were checked once a week during each 4-week period and these data used to estimate nest success. Nests were classed as depredated when one or more of the eggs were found marked or missing and the eggs were then collected. Man-made tracks in areas of bush are known to be used by mammalian predators (Olson & Rohwer, 1998; Skagen *et al.*, 1999). To avoid the creation of tracks leading directly to the artificial nest sites the nest was approached from a different direction each weekly check.

After every 3-week interval, the nests were moved 10 m to a similar location. Robins re-nest after nest predation, and as nest predation events can affect site fidelity and re-nesting location (Haas, 1998; Sieving & Willson, 1998, pers. obs.) the change in location after each exposure period took this behaviour into account. Changing the nest location was also done to minimise the impact of trap-lining and re-visitation or avoidance from previous predators (Yahner & Mahan, 1999; Buler & Hamilton, 2000). Once in their new locations the inner lining of each nest was replaced with fresh moss and fern scales to avoid any odour from previously depredated eggs attracting predators to the nests (Bayne & Hobson, 1999; Rangen *et al.*, 2000). Two new eggs were then placed in each nest, with an alternative egg combination than that from the previous exposure block i.e. Clay-Clay became Clay-Quail and vice-versa. Alternating the egg combination was done to account for the effect of egg type (clay versus quail) on nest success, independent of nest location.

A protocol was drawn up outlining the procedure to be used when checking nests. I checked the nests at two of the reserves (Paengaroa and Bushy Park) and the protocol was distributed to 'nest checkers' in each remaining reserve. The protocol included (1) changing the approach to each nest every week; (2) allocating 5 minutes only to searching for missing eggs (to minimize any bias in locating missing eggs between reserves); and (3) minimising contact with nests and eggs unless depredated. Following depredation, the eggs were collected and disturbance at the nest, nest destruction, and presence of faeces in or around the nests were noted. On collection, a brief description of damage to each egg was made including percentage damage to surface area and determination between teeth or beak marks.

Predator identification

Clay and quail eggs collected through the breeding season were stored in a freezer to preserve the imprints in the clay and real egg remains. Once the collection was complete, each egg was assigned a random number and its origin hidden. This 'blind identification' system avoided any bias in predator determination through knowledge of the predator community in the reserve of origin.

Predators were classed into six groups: rat, possum, bird, mice, insect, missing and unknown. The predator of each nest was assessed by examining any marks left on the clay and quail eggs and comparing them with sample imprints from both live animals and skulls. First-hand observation of an attack on an artificial egg in- situ provided the sample beak imprints for robins while skulls provided the imprints for larger species (e.g. Morepork or Harrier). Mouse (*Mus musculus*) imprints were obtained by placing clay and quail eggs in an artificial nest inside an enclosure with live wild mice overnight. To aid with identification of imprints belonging to the insect group, the dissected mandibles of a weta (*Hemideina species.*) were used to make imprints in the clay egg.

Weta depredation was determined through personal observations of their presence at nest sites, often hiding underneath nests, so were included in the insect group. Rat and possum imprints were obtained using skulls.

To distinguish between rats and mice, measurements of the width of the tip and base of both the top and bottom incisors and gape were taken using callipers from 25 mice (*Mus musculus*) and 25 rat skulls (*Rattus rattus* and *Rattus norvegicus*). Each measurement was taken three times and the average result used to reduce sampling variance. These measurements provided the maximum and minimum size of tooth marks possible for both mice and rats. Measurements of maximum gape and incisor width were then taken from the indentations in the depredated clay eggs. These were then separated into rat and mouse using criteria produced by discriminant analysis (see below). All measurements and identification was done using callipers and a magnification screen.

Statistical Analysis

Natural Nest Success

Estimates of natural nest success were calculated using Stanley (2000) stage-specific daily survival probabilities. This method is an adaptation of Mayfield (1975) method extended so that it is unnecessary to know the dates of egg failure or exact hatching dates. The program for Stanley's (2000) method can be down loaded from Ecological Archives (appendix) and is run using NLIN procedure in SAS (SAS institute, 1997). The basic input for the Stanley method requires knowledge of the duration of each exposure interval, the fate of the nest during the interval and the nestling stage at the beginning and end of each interval. Each interval between nest checks is coded according to its duration (number of days), the stage of the nesting cycle at the two checks (A= both checks during laying; B=checked during laying then at incubation; C= both checks during incubation; D= checked during incubation and then at nestling; E= both checks during nestling); and whether the nest survived the time between checks (coded as 1 0 for survived or 0 1 for failed).

For the purpose of this experiment the five categories for stage (A, B, C, D and E) given in Stanley's original model were reduced to three (C, D and E), leaving out the two that focus on survival rates during the laying stage. This adaptation is designed to suit robins, which lay only 2-3 eggs sequentially per clutch leaving little time for nest location during this period. Allocation of failed nests into categories C or D required knowledge of the stage a nest failed or succeeded. Estimates of this stage were based on a19-day incubation and 21-day nestling period (combined with the earliest and latest dates that eggs could have been laid (Powlesland, 1997) determined using behavioural cues.

Nest success was modelled, as a function of two factors (stage and season) believed to be biologically relevant (for season refer to Armstrong *et al.*, 2002c). A total of 5 models (Table 2) were compared to test the effect of stage (incubating or nestling) and season (early or late in breeding season). Stage was categorized as incubation or nestling by monitoring adult behaviour (described previously). To categorize early and late nests the median laying date for each reserve was found and clutches laid before this date were classed as early and those laid after were classed as late. Interaction terms were included in all candidate models including two factors or more.

Table 2. Set of 5 candidate models for estimating natural nest success.

Model [1]	k [2]	**Explanation** [3]	**Code** [4]
Constant	1	Constant daily survival probability across season and stage	1 for all intervals
Stage	3	Stage specific daily survival probability across season.	C = found and rechecked during incubation D = found during incubation and rechecked during nestling E = found and rechecked during nestling
Season	2	Group specific daily survival probability across stage.	1 = early 2 = late
Season*Stage	6	Daily survival probability varies with both season and stage	Combining stage and season to get C1, D1, E1, C2, D2, E2

[1] Candidate models for factors affecting daily survival probabilities.

[2] Number of parameters

[3] Explanation for parameter in model

[4] Code used to define model parameters used to estimate nest success using Stanley (2000) method in SAS.

The SAS output from these models included the ‘Objective’ or ‘Weighted loss’ which is equal to the negative log-likelihood of the model (-ln(L)) (Stanley, 2000). The output from all four models were compared using Akaike’s Information Criterion (AIC) (Burnham & Anderson, 2002) corrected for effective sample size (AIC_c), which is given by:

$$AIC_c = -2\ln(L) + 2k + 2k(k + 1)/(n - k - 1)$$

where k is the number of parameters and n is the effective sample size.

The model with the lowest AIC$_c$ is the most parsimonious model because it achieves the best compromise between model fit and parameter precision. The relative weights (w_i) of the alternative models were calculated from their delta AIC$_c$ values, i.e., the difference between their AIC$_c$ and that of the best model. The ratio of w_i between any two models indicates the relative (proportional) support between those two models and was used to select the best model (high w_i = strong support, low w_i = weak support).

The selected model output generated estimates of the daily survival probabilities, p associated standard errors, se($\hat{p}$) and the estimated correlation between survival probabilities at the incubation and nestling stages, r. The season model generated estimates for early (p_e) and late (p_l) in the season. The stage model generated estimates for the incubation (p_1) and nestling (p_2) stages. The probability of surviving from egg laying to fledging was estimated assuming the incubation period (^{t1}) was 19 days and the nestling period (^{t2}) was 21 days. To calculate the overall estimate of nest success for each reserve when the model selected had more than one parameter the following equations were used following Armstrong and Raeburn *et al* (2002c).

Season Model

$$\hat{S}_n = \frac{(\hat{p}_e^{\,t1+t2})(\hat{p}_l^{\,t1+t2})(s_e + s_l)}{s_e(\hat{p}_l^{\,t1+t2}) + s_l(\hat{p}_e^{\,t1+t2})}$$

Stage Model

$$\hat{S}_n = \hat{p}_1^{\,t1}\,\hat{p}_2^{\,t2}$$

Season*Stage Model

$$\hat{S}_n = \frac{(\hat{p}_{e1}{}^{t1}\hat{p}_{e2}{}^{t2})(\hat{p}_{l1}{}^{t1}\hat{p}_{l2}{}^{t2})(s_e + s_l)}{s_e(\hat{p}_{l1}{}^{t1}\hat{p}_{l2}{}^{t2}) + s_l(\hat{p}_{e1}{}^{t1})(\hat{p}_{e2}{}^{t2})}$$

* s = number of successful nests (assumed to be known accurately)

The standard error for each estimate of daily survival probability for natural nests success, resulting from the AIC$_c$ selected model with more than one parameter, was approximated using the delta method (Seber, 1982: pp 7-9), also following Armstrong *et al.* (2002c).

Season Model

$$se(\hat{S}_n)\sqrt{\left(\frac{se(\hat{p}_e)(t1+t2)(\hat{p}_e{}^{t1+t2-1})(\hat{p}_l{}^{t1+t2})^2 s_e(s_e+s_l)}{\left(s_e\hat{p}_l{}^{t1+t2}+s_l\hat{p}_e{}^{t1+t2}\right)^2}\right)^2 + \left(\frac{se(\hat{p}_l)(t1+t2)(p_l{}^{t1+t2-1})(p_e{}^{t1+t2})^2 s_l(s_e+s_l)}{\left(s_e\hat{p}_l{}^{t1+t2}+s_l\hat{p}_e{}^{t1+t2}\right)^2}\right)$$

Stage Model

$$se(\hat{S}_n)\sqrt{se(\hat{p}_1)t1(\hat{p}_1{}^{t1-1})(\hat{p}_2{}^{t2})^2 + se(\hat{p}_2)t2(\hat{p}_2{}^{t2-1})(\hat{p}_1{}^{t1})^2 + 2\operatorname{cov}(\hat{p}_1,\hat{p}_2)t1(\hat{p}_1{}^{t1-1})(\hat{p}_2{}^{t2})t2(\hat{p}_2{}^{t2-1})(\hat{p}_1}$$

where,

$$\operatorname{cov}(\hat{p}_1,\hat{p}_2) = r(\hat{p}_1,\hat{p}_2)se(\hat{p}_1)se(\hat{p}_2)$$

For the Season*Stage model the equation for stage model was used to obtain the standard error for each season. The overall standard error was then calculated by taking the square root of the average of the squares of the standard errors.

The confidence intervals given with the SAS output are based on a t-distribution, which is not sensible for survival rates, and should not be used (Stanley, 2000). Confidence intervals were obtained using a log-odds transformation on $\hat{p}$ (see Armstrong *et al.* [2002b]).

Artificial Nests

Distinguishing rat and mouse imprints

Discriminant function analysis (DFA) is an eigenanalysis technique that maximally separates a fixed number of groups (Manly, 2005). In this instance, it was used to separate mice from rats (SAS Institute, 1997). Measurements taken from the rat and mouse skulls were used to find a discriminant function to allocate unknown depredated clay eggs into predator groups. As a measure of the accuracy of the DFA, leave-one-out cross validation was used.

Estimating artificial nest success

The known fate model was used to calculate nest survival probability using program MARK (White & Burnham, 1999). This model estimates the probability of surviving an interval between sampling occasions. As the fate of the nest is 'known' it is assumed that the detection probability is 1. The basic input to program MARK is the encounter history for each animal (each "animal" is an artificial nest in this experiment). The program used this information to estimate survival probability via numerical maximum likelihood techniques. The model assumptions are that the encounter histories are mutually exclusive, the nests are independent, and all nests of the same type have the same underlying survival probability during intervals (homogeneity across individuals). This allows parameter estimation to be assessed across all individuals without bias.

The data consisted of encounter histories over four weeks pooled into three groups corresponding to the beginning, middle and end of the breeding season. The data were coded as follows; "10" the nest succeeded through the interval, "11" the nest failed during the interval and "00" the nest had failed before the start of the interval. To facilitate estimation of nest success resulting from predation by different predators the code was modified, replacing "11" with "00" in the interval where nest loss was the result of non-target predators. Using this technique ensured that the program only used nest loss from the predator of interest to estimate survival while ignoring others. The data for each reserve were coded accordingly to allow estimation of nest success resulting from predation by different predators within each reserve.

Nest success was modelled, as a function of two temporal factors (season and week) considered biologically relevant. A total of 5 models were compared (Table 3). The season model estimated nest success separately for the three exposure periods (beginning, middle and end of the breeding season). This was used to assess the sensitivity of artificial nests at detecting changes in predation throughout the breeding season. The week model estimated nest success separately for each week over a 4-week period within each exposure period. This allowed for assessment of the effect of stage (weeks 1-4) on nest success within exposure periods, which was then used to determine the amount of monitoring required for this technique to produce a correlation with natural nest success (see chapter 2). The interaction model enabled assessment of the combined effect of season and week on nest success. The additive model allowed for assessment of the additional effect of season when week effect is the same for each season, including both effects while reducing the number of parameters and hence increasing precision. Models were run using both sine and logit link functions, used to link the linear model specified in the design matrix with the survival parameters. The variance estimation option '2ndpart' was used to estimate the variance-covariance matrix of the estimates.

Table 3. Candidate models run for estimation of artificial nest success.

Model[1]	k[2]	**Explanation**[3]
(.)	1	Survival constant
(s)	3	Survival varies among seasons
(w)	4	Survival varies among weeks within a season
(s+w)	6	Survival varies temporally in parallel (week effect is the same for each season, with the groups effect additive to the time effect)
(s*w)	12	Survival varies with both season and week

[1] Candidate models for factors affecting daily survival probabilities.

[2] Number of parameters

[3] Explanation for parameter in model

As for natural nests, model selection was done using Akaike's Information Criterion corrected for effective sample size and ranked using AIC_c weights. Model output for each reserve and predator group included an estimate of weekly survival probability, $\hat{p}$ and associated standard error, se($\hat{p}$). Output for the season model produced survival estimates for early (p_e), middle (p_m) and late (p_l) in the season with associated standard error. The stage model produced estimates for weeks 1 ($\hat{p}_1$), 2 ($\hat{p}_2$), 3 ($\hat{p}_3$) and 4 ($\hat{p}_4$) with associated standard errors. Overall estimates for the probability of an artificial nest surviving all four weeks were calculated using the following equations:

Week Model

$$\hat{S}_a = \hat{p}_1 \hat{p}_2 \hat{p}_3 \hat{p}_4$$

Season Model

$$\hat{S}_a = \frac{p_e^{\,4} + p_m^{\,4} + p_l^{\,4}}{3}$$

Season*Week (or Season+Week)

$$\hat{S}_a = \frac{(\hat{p}_{e1}\hat{p}_{e2}\hat{p}_{e3}\hat{p}_{e4}) + (\hat{p}_{m1}\hat{p}_{m2}\hat{p}_{m3}\hat{p}_{m4}) + (\hat{p}_{l2}\hat{p}_{l2}\hat{p}_{l3}\hat{p}_{l4})}{3}$$

As for natural nests estimates the appropriate standard errors were approximated using the delta method (Seber, 1982: 7-9) as follows:

Week Model

$$se(\hat{S}_a) = \sqrt{\left[se(\hat{p}_1)\hat{p}_2\hat{p}_3\hat{p}_4\right]^2 + \left[se(\hat{p}_2)\hat{p}_1\hat{p}_3\hat{p}_4\right]^2 + \left[se(\hat{p}_3)\hat{p}_1\hat{p}_2\hat{p}_4\right]^2 + \left[se(\hat{p}_4)\hat{p}_1\hat{p}_2\hat{p}_3\right]^2}$$

Season Model

$$se(\hat{S}_a) = \sqrt{\frac{\left[se(\hat{p}_e)4\hat{p}_e^{\,3}\right]^2 + \left[se(\hat{p}_m)4\hat{p}_m^{\,3}\right]^2 + \left[se(\hat{p}_l)4\hat{p}_l^{\,3}\right]^2}{3}}$$

For the 'season*week' and 'season+week' models the equation for week model was used to obtain standard error for each season,

$$se(\hat{S}_{ia}) = \sqrt{\left[se(\hat{p}_{i1})\hat{p}_{i2}\hat{p}_{i3}\hat{p}_{i4}\right]^2 + \left[se(\hat{p}_{i2})\hat{p}_{i1}\hat{p}_{i3}\hat{p}_{i4}\right]^2 + \left[se(\hat{p}_{i3})\hat{p}_{i1}\hat{p}_{i2}\hat{p}_{i4}\right]^2 + \left[se(\hat{p}_{i4})\hat{p}_{i1}\hat{p}_{i2}\hat{p}_{i3}\right]^2}$$

with $_i$ being the season.

The overall standard error was then calculated by taking the square root of the average of the squares of the standard errors.

$$se(\hat{S}_a) = \sqrt{\frac{\left[se(\hat{S}_{ea})\right]^2 + \left[se(\hat{S}_{ma})\right]^2 + \left[se(\hat{S}_{la})\right]^2}{3}}$$

Fitting the relationship between artificial and natural nest success

General linear modelling was used to fit a relationship between survival of natural nests (S_n) and artificial nests (S_a). The relationship between these two probabilities was expected to take the form:

$S_n = \alpha S_a^{\beta}$

The parameter α is the probability of a nest surviving when there are no predators, and accounts for failure of natural nests due to factors such as starvation or disease. The parameter β reflects the relative survival probabilities for natural and artificial nests, and this accounts for the different exposure period of natural (40 days) and artificial (28 days) nests as well as potential differences in predation rate.

Taking the logarithms of both sides of the equation gives the linear model

$$\log S_n = \log \alpha + \beta \log S_a$$

This relationship was fitted by taking the logarithms of the estimates for S_n and S_a for all sites, and the residual sum of squares (RSS) calculated. This was repeated with S_a calculated for five different predator groups to assess which model gave the best prediction of S_n (Table 4). The models were compared using AIC, with the likelihood calculated from the following equation (Burnham & Anderson, 2002):

$$\ln(L) = \frac{1}{2} n \ln(\frac{RSS}{n})$$

Artificial and natural nest success, were both estimated with error. To account for this, confidence intervals for the relationship between natural and artificial nest success were obtained using a parametric bootstrap, a technique for generating data simulations based on the estimates and standard errors from the original data. Ten thousand data sets were sampled from Log-odds transformed nest success estimates (to allow for sampling within a normal distribution), and the data were then back transformed for interpretation from real figures.

Table 4. Models run for each predator group for assessing their effect on the relationship between natural and artificial nest success.

Model[1]	k[2]	Explanation[3]
$S_n = \alpha$	1	No relationship between natural and artificial nest success
$S_n = \alpha S_{all}^{\beta}$	3	Relationship exists between natural nest success and artificial nest success as a result of predation by all predators.
$S_n = \alpha S_{rpb}^{\beta}$	3	Relationship exists between natural nest success and artificial nest success as a result of predation by rats, possums and birds.
$S_n = \alpha S_{rpm}^{\beta}$	3	Relationship exists between natural nest success and artificial nest success as a result of predation by rats, possums and mice.
$S_n = \alpha S_{rp}^{\beta}$	3	Relationship exists between natural nest success and artificial nest success as a result of predation by rats and possums.
$S_n = \alpha S_b^{\beta}$	3	Relationship exists between natural and artificial nest success as a result of predation by birds.

[1] Candidate models for fitting relationship between artificial and natural nest success.

[2] Number of parameters

[3] Explanation for parameters in model

RESULTS

Natural Nests

Nest success estimates for each reserve

The reserves with the highest natural nest success were Karori at 83% and Wenderholm at 73%. Nest success for Boundary Stream was significantly lower at 47% and the lowest values for nest success were found at Waimanoa (14%) and Bushy Park (13%) reserves. Nest success did not vary much between Paengaroa (32%), Tiritiri Matangi (33%), Waipapa (29%) and Waotu (35%) reserves (Figure 1).

Nest success was generally higher at the reserves with predator control. The exception to this was the low success at Tiritiri Matangi, which is a predator free offshore island reserve and Waotu which at 35ha (25, 6 and 4 ha bush patches) is significantly smaller than the other reserves.

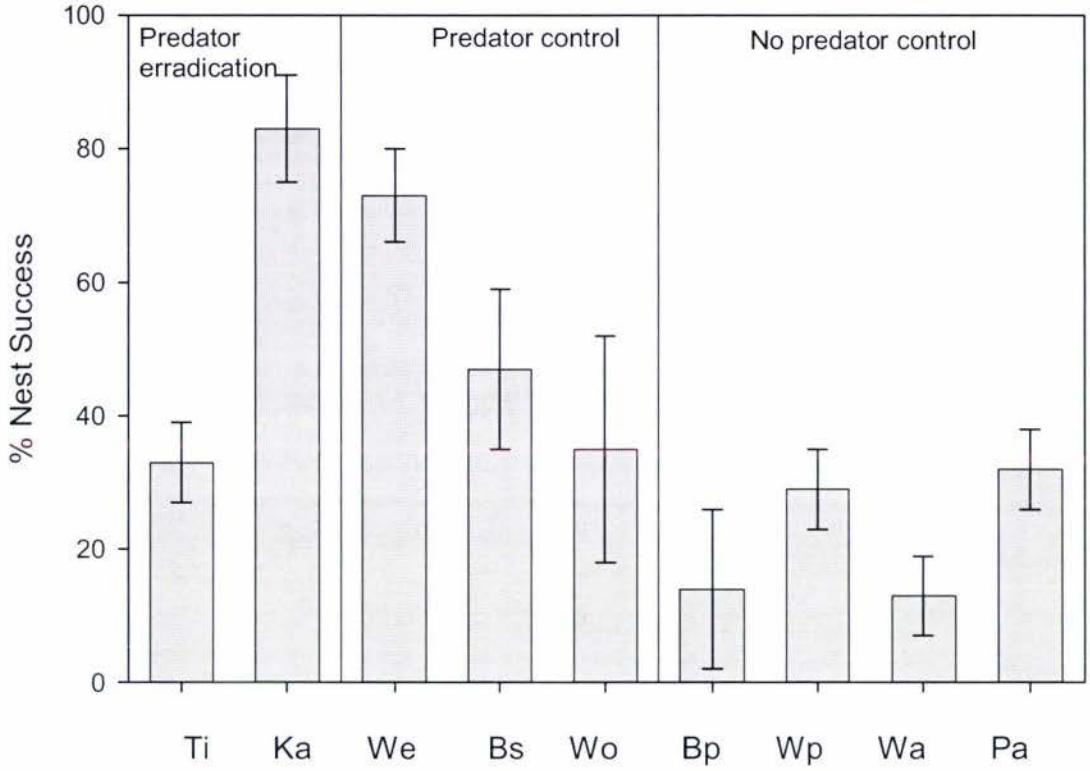


Figure 1. Natural nest success estimates, generated from the best model, with associated standard error for each of the 9 reserves. Dividing lines separate reserves with mammalian predator control, no mammalian predator control and mammalian predator eradication. (Ti = Tiritiri Matangi; Ka = Karori; We = Wenderholm; Bs = Boundary Stream; Wo = Waotu; Bp = Bushy Park; Wp = Waipapa; Wa = Waimanoa; Pa = Paengaroa)

Model selection for each reserve

There was a range of factors included in the models selected to represent natural nest success, revealing variation in the patterns of predation across individual reserves. Models chosen for reserves with predator control included factors *'season' and 'stage'* as well as the selection of the constant model, revealing no similarity in the pattern of nest depredation across these reserves. However, in the reserves without predator control, models that included the factors season and stage were always included in the selection, indicative of an overriding similarity in the pattern of predation between these reserves.

The strength of support for the selected model, indicated by the AIC$_c$ weight (w_i) was strong for Karori, Waimanoa, Bushy Park, Tiritiri Matangi, Waipapa and Waotu reserves, indicated that the factors included in the model choice had a strong influence on nest success. For Boundary Stream, Paengaroa and Wenderholm the model choice had only a marginal lead over the other model options, indicated by lower values for AIC$_c$ weight. This then suggests that the factors included in the chosen model were only marginally better at explaining the variation in the data than the factors included in the other model options and therefore had a relatively weak influence on nest success.

Boundary Stream, Bushy Park and Waotu had large values for standard error, 0.12, 0.12 and 0.17 respectively. The small sample size at these reserves contributed to these large values.

No clear pattern was found between small and large reserves for predator control and no control reserves, with regards to both nest success (Figure 1) and model choice (Table 5).

Table 5. Model selected, parameters and AIC_c weight representing natural nest success in nine reserves. AIC_c weight (proportion from 100% for each reserve) calculated from four models run for each individual reserve.

Reserve[1]	Model[2]	k[3]	AIC_c weight[4]
Boundary Stream	Season	2	0.37
Bushy Park	Stage	1	1.00
Karori	Stage*Season	5	1.00
Paengaroa	Season	2	0.34
Tiritiri Matangi	Constant	1	0.44
Waimanoa	Stage	3	0.50
Waipapa	Stage*Season	5	0.48
Waotu	Stage*Season	5	0.51
Wenderholm	Constant	1	0.41

[1] Reserve from which nest success was estimated

[2] Model selected via AIC model selection, used to estimate nest success.

[3] Number of parameters in model

[4] AIC weight attributed to the model selected

Artificial Nests

Predator Identification

From the entire sample of 810 nests, 443 (54.7%) were depredated. From these, 174 (39.3%) were preyed upon by rats, 6 (1.4%) by possums, 41(9.25%) by mice, 127 (28.7%) by birds, 23 (5.2%) by insects and 18 (4.1%) were unknown.

The results of the skull measurements revealed a clear difference between the teeth and gape of rats and mice, allowing easy separation of the two groups. The model produced from discriminant analysis using skull measurements correctly predicted group membership in 89% of cases. Rats were accurately classed 95% of the time and mice were accurately classed 83% of the time (Table 6).

Table 6. Discriminant analysis results for separation of rat and mouse teeth measurements showing the number of observations (percent classified in brackets) into rat and mouse.

From ⇨ **To** ⇩	**Rat**	**Mouse**	**Total**
Rat	20(95.24)	1(4.76)	21(100.00)
Mouse	4(16.67)	20(83.33)	24(100.00)
Total	24(53.33)	21(46.67)	45(100.00)

A characteristic of the mouse imprint included a crescent shaped nature to the indentation, further aiding the separation from rats. Rats and possums were deemed 'high-risk predators' as it was assumed that depredation of nests by these predators would result in nest failure. As the number of depredation events by possums was very small, they were grouped together with the rats for analysis of nest success. The majority of imprints that were found in the clay eggs allocated to the bird group were similar to those made by robins. The remaining imprints resembled marks made by larger predatory birds such as morepork, harrier, and falcon.

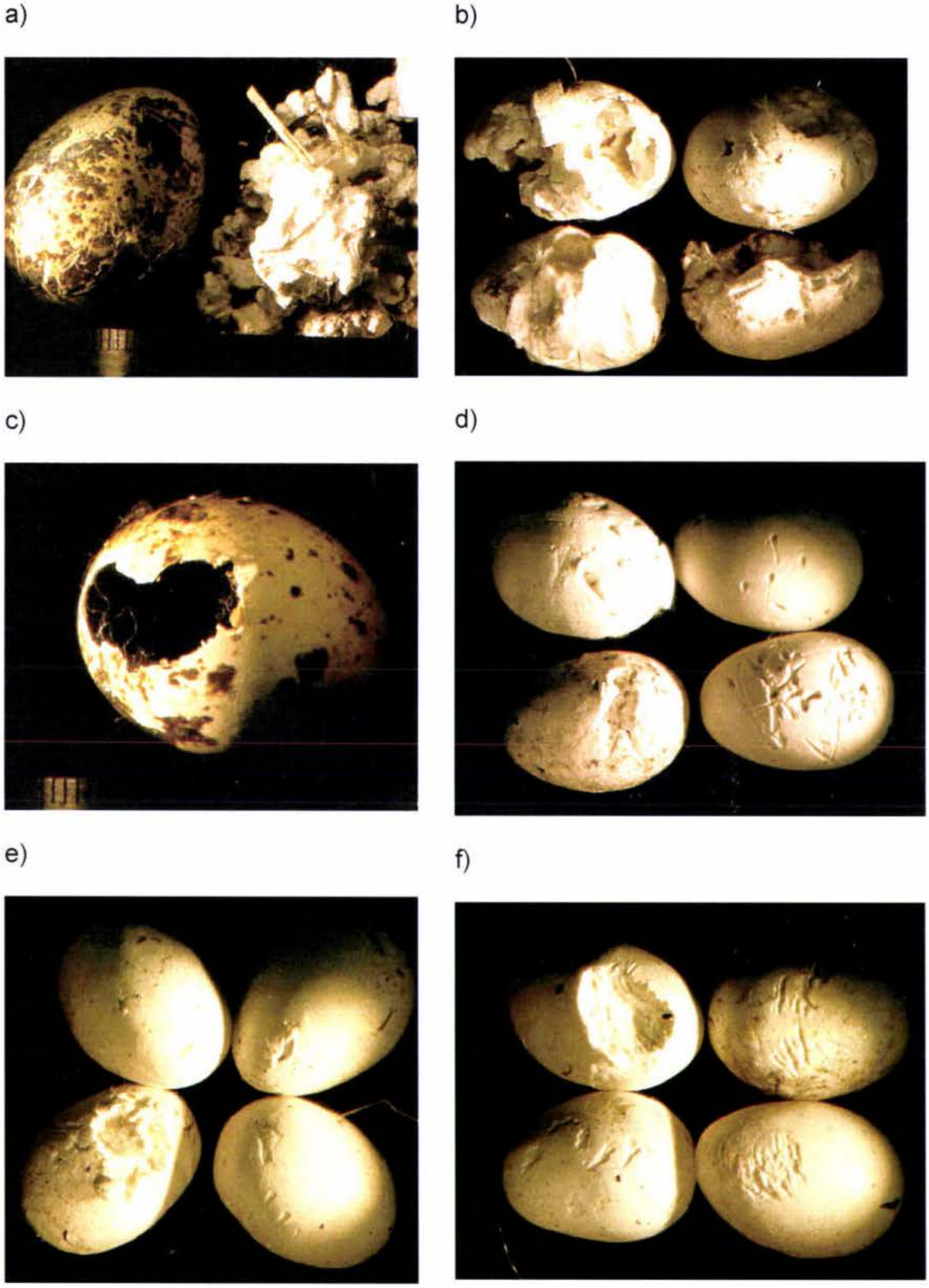


Figure 2. Imprints on clay and quail eggs depredated by each predator (a) rat; (b) possum; (c and d) bird; (e) mouse; (f) insect.

Photography by Rebecca Lewis

Nest success estimates for each reserve and predator group

The estimates for artificial nest success fluctuated between reserves and predator groups (Figure 3). Reserves with no predator control (Waimanoa, Waipapa, Paengaroa and Bushy Park) produced lower estimates of nest success in all four reserves for all of the predator groups (rat and possum ($_{rp}$), rat, possum and mice ($_{rpm}$), rat, possum and bird ($_{rpb}$) and all predators ($_{all}$)) than the three reserves with predator control (Boundary Stream, Wenderholm and Waotu). Reserves where rats and possums were eradicated (Karori and Tiritiri Matangi) had surprisingly low nest success resulting from two (S_{all} and S_{rpb}) of the four (S_{all}, S_{rpb}, S_{rpm}, S_{rp}) models. However, both of the models that produced low nest success estimates include birds (S_{all} and S_{rpb}) suggesting that predation in these reserves was attributable to birds.

In the reserves with predator control (with the exception of Waotu), the addition of mice to the S_{rp} model lowered estimates of nest success more than the addition of birds. This pattern was reversed in the reserves with no predator control. Hence, mice had a greater impact on artificial nest success in reserves with predator control and birds in reserves without predator control showing sensitivity of the artificial nests to changes in predator community resulting from predator control.

Nest success resulting from bird predation only, remained relatively high in all three reserves with predator control and one without predator control (Waimanoa). For the remaining three reserves with no predator control, nest success resulting from bird predation was low compared to nest success in reserves with predator control. Both Tiritiri Matangi and Karori reserves are free of rats and possums, mice are also absent from Tiritiri Matangi. The estimates of nest success in these reserves, resulting from bird predation only, produced much lower estimates of nest success when compared to the other 7 reserves, with Tiritiri Matangi producing the lowest success of all 9 reserves. Hence, artificial nest depredation by birds increased when mammalian predators were absent.

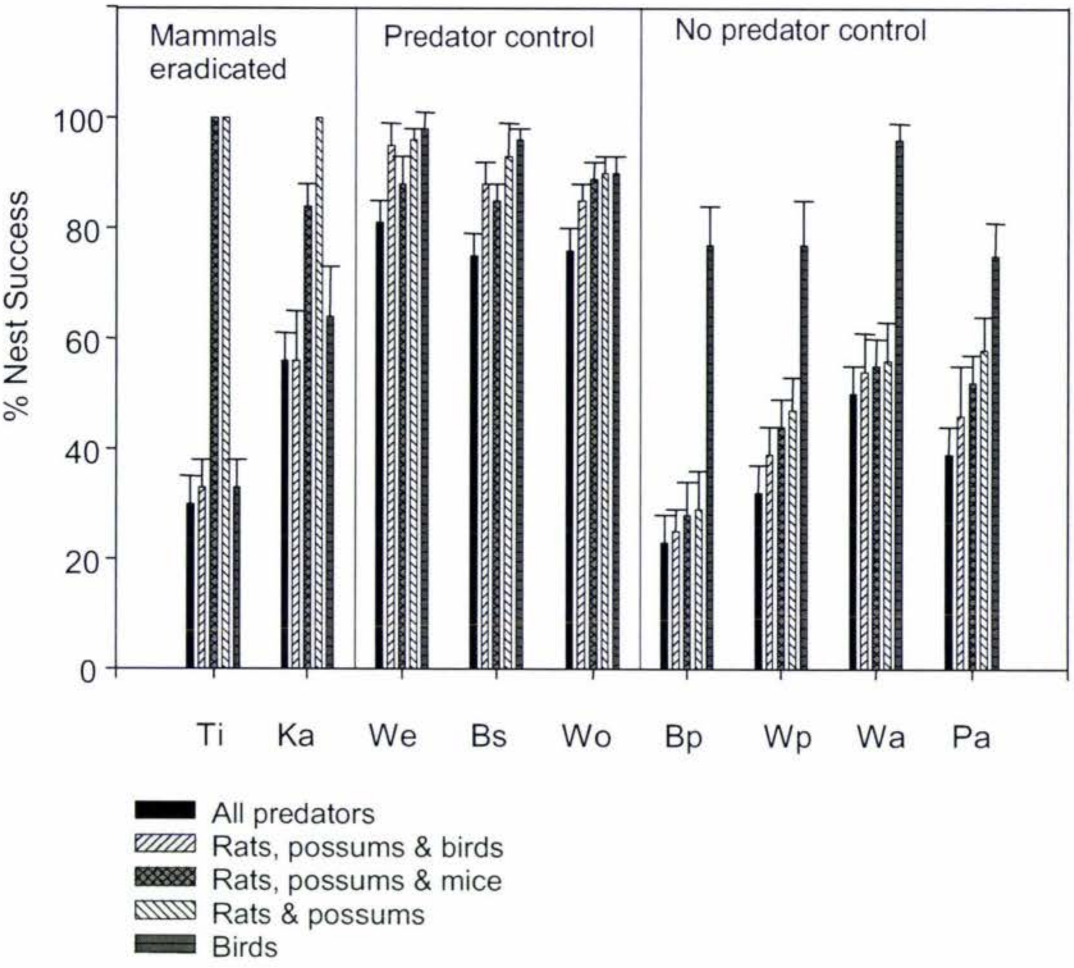


Figure 3. Artificial nest success estimates and standard error for each predator group in each of the 9 reserves (Ti = Tiritiri Matangi; Ka = Karori; We = Wenderholm; Bs = Boundary Stream; Wo = Waotu; Bp = Bushy Park; Wp = Waipapa; Wa = Waimanoa; Pa = Paengaroa).

Model Selection for each reserve and predator group

Separate analysis of the different predator groups revealed different model choices and nest success estimates (see appendix). The results that show the strongest correlation with natural nest success were the estimates of nest success resulting from predation by rats and possums revealed by the selection of the S_{rp} model (Table 8 & 9). Results from the model selection procedure (Table 7) show that AIC_c weight supporting each of the models chosen in reserves with rat and possum predation was high ($w_i = 41 - 82$). This then provides strong support for the model selected, which is indicative of a strong pattern of predation.

For reserves without predator control, the factor 'week' was always included in model choice (Table 7). This implies that the greatest variation in nest success for each of these reserves occurred across the 4 weekly nest checks, whereas in reserves with predator control, the influential factor selected in the model choice varied between factors. A similar pattern was reflected in the values for AIC_c weights supporting the model selected. Reserves without predator control have relatively high AIC_c weights, 58 – 82%, compared with reserves with predator control where AIC_c weights lay between 41 – 46%.

The three reserves that did not include the factor time in the model choice, Boundary stream, Wenderholm and Waotu, also had the lowest rates of nest depredation by rats and possums (Figure 3). No clear pattern was found between small and large reserves with regards to both nest success (Figure 3) and model choice (Table 7).

Table 7. Model selection, number of parameters and AIC$_c$ weight (1-100%) calculated from four models run for each individual reserve.

Reserve[1]	Predator group[2]	Model[3]	k[4]	W_i[5]
Tiritiri Matangi	rats & possums	NO PREDATION		
Karori	rats & possums	NO PREDATION		
Wenderholm	rats	S(.)	1	0.46
Boundary Stream	rats & possums	S(s)	3	0.41
Waotu	rats & possums	S(.)	4	0.46
Bushy Park	rats & possums	S(w)	4	0.65
Waipapa	rats	S(w)	4	0.66
Waimanoa	rats & possums	S(s+w)	6	0.82
Paengaroa	rats	S(w)	4	0.58

[1] Reserve from which nest success was estimated

[2] Predator group responsible for nest depredation

[3] Model selected via AIC model selection, used to estimate nest success.

[4] Number of parameters in model

[5] AIC weight attributed to the model selected

Fitting the relationship between artificial and natural nest success

Results from the model selection procedure (Table 8 and 9) show the model with the lowest AIC$_c$ and therefore the most parsimonious, resulted from predation by rats and possums only (model $S_n=\alpha S_{rp}{}^{\beta}$). The AIC$_c$ weight attributed to this model is significantly higher, ~50%, than the w_i for the second ranking model ($S_n=\alpha S_{rpm}{}^{\beta}$) showing strong support for this model. The sum of the remaining three models is only 0.373 consequently providing further strong support for the best model, with fairly limited support for the second best model.

Thus, the data supports one model as convincingly best dispelling the need for model averaging and providing relative certainty for the predator group chosen. The results from the bootstrap generated data set (Table 9) provided further support for the results produced by the original estimates, with the $S_n=\alpha S_{rp}^{\beta}$ model again producing the lowest AIC_c (based on the mean residual sum of squares from the bootstrapped data sets). A decrease in the value for the parameter slope (β) from 1.106 for the original data set to 1.096 for the bootstrap data set (approaching a value of 1), and the value for the parameter intercept (α) decreasing from 0.50 for the original data set to 0.49 for the bootstrap data set (approaching a value of 0), demonstrates a slight increase in the predictive accuracy of the model.

The reduction of the all predator group (S_{all}) to the rats and possums predator group (S_{rp}) increased the value for slope (β) from 0.84 to 1.106. The value of the intercept (α) decreased from -0.45 to -0.69 as a direct result of the reduction of the all predator group to the rat and possum only group, increasing the success values of artificial nests only and consequently the difference between natural and artificial nest success. The ΔAIC_c value between these two models was > 2 for both the original and bootstrap data set corresponding to a significant difference and credibility to the chosen models application (Burnham & Anderson, 2002).

The addition of mice to the S_{rp} model did not lower the model ΔAIC_c value although this value allocated to the S_{rpm} model remained relatively low when compared with the other model options. The $S_n = \alpha S_{all}^{\beta}$ and $S_n = \alpha S_{rpb}^{\beta}$ models had a weak relationship with natural nest success, revealed by ΔAIC_c values which exceeded that produced by the $S_n = \alpha$ model. Therefore the inclusion of birds or mice in the model, hence predation by birds on artificial nests, did not improve the fit of data to the model, hence did not strengthen the correlation with natural nest success.

Table 8. Model selection for each predator group from the original estimates of nest success

Model selection from original estimates				
Model[1]	k[2]	**AIC$_c$**[3]	Δ_i[4]	**w$_i$**[5]
$S_n = \alpha S_{all}^{\beta}$	3	-2.54	3.95	0.07
$S_n = \alpha S_{rpb}^{\beta}$	3	-2.92	3.57	0.09
$S_n = \alpha S_{rpm}^{\beta}$	3	-4.72	1.76	0.22
$S_n = \alpha S_{rp}^{\beta}$	3	-6.49	0	0.52
$S_n = \alpha$	2	-3.23	3.26	0.10

Table 9. Model selection for each predator group from bootstrap estimates sampled from 10,000 data sets.

Model selection from 10,000 bootstrap estimates				
Model[1]	k[2]	**AIC$_c$**[3]	Δ_i[4]	w_i[5]
$S_n = \alpha S_{all}^{\beta}$	3	1.12	3.07	0.09
$S_n = \alpha S_{rpb}^{\beta}$	3	0.94	2.88	0.10
$S_n = \alpha S_{rpm}^{\beta}$	3	-0.60	1.35	0.21
$S_n = \alpha S_{rp}^{\beta}$	3	-1.94	0	0.42
$S_n = \alpha$	2	-0.34	1.61	0.19

[1] Choice of models used to fit relationship between artificial and natural nest success

[2] Number of parameters in model

[3] Aikaike's Information Criterion value

[4] Delta AIC, indicating the difference in AIC value from the best model

[5] AIC weight, calculated from the 5 models run

The graph in Figure 4a shows that prior to the separation of the predator groups, there is a recognisable relationship between artificial and natural nest success ($r = 0.37$). However, for a strong relationship to be found (see Figure 5) it was necessary to separate the predator groups.

The results of the S_{rp} model (Figure 4b) show 6 of the 9 estimates of nest success lying within the 95% confidence interval generated by the bootstrap simulated data sets (denoted by the central broken line). Two of the other nest success estimates, with associated standard errors, (Karori and Wenderholm) sit outside the upper 95% confidence limit while one (Tiritiri Matangi) sits just outside the lower 95% confidence limit. Nest success estimates for 5 of these reserves also sit relatively close to both the bootstrap generated mean and the mean from the original data set providing further support for the predictive ability of the S_{rp} model. The results of the aforementioned model are expressed by the relatively high r-squared (r^2=0.61) value, hence relatively good fit of data to this model and consequently reasonably precise predictive ability.

Figure 4c illustrates the marginal difference in the position of point estimates of nest success for artificial nests when mice were added to the predator group. The main difference from the aforementioned model is the change in position of the point estimate for Karori reserve further to the left hand side on the x-axis. The result was a decrease in support for this model when compared with the S_{rp} model brought about by a decrease in the fit of the data to the model ($r = 0.50$) (as the number of parameters stays the same) and slight widening of the confidence limits required to account for the 95% certainty.

Figure 4d illustrates why the addition of birds to the S_{rp} model decreased the level of support. When estimates of nest success generated by bird predation alone are used to fit a relationship with natural nest success nine of the data points sit outside the 95% confidence limits on the plot ($r = 0$). As a result, the addition of birds to the S_{rp} model decreases the overall fit of data to the model reducing the amount of support allocated during the model selection procedure.

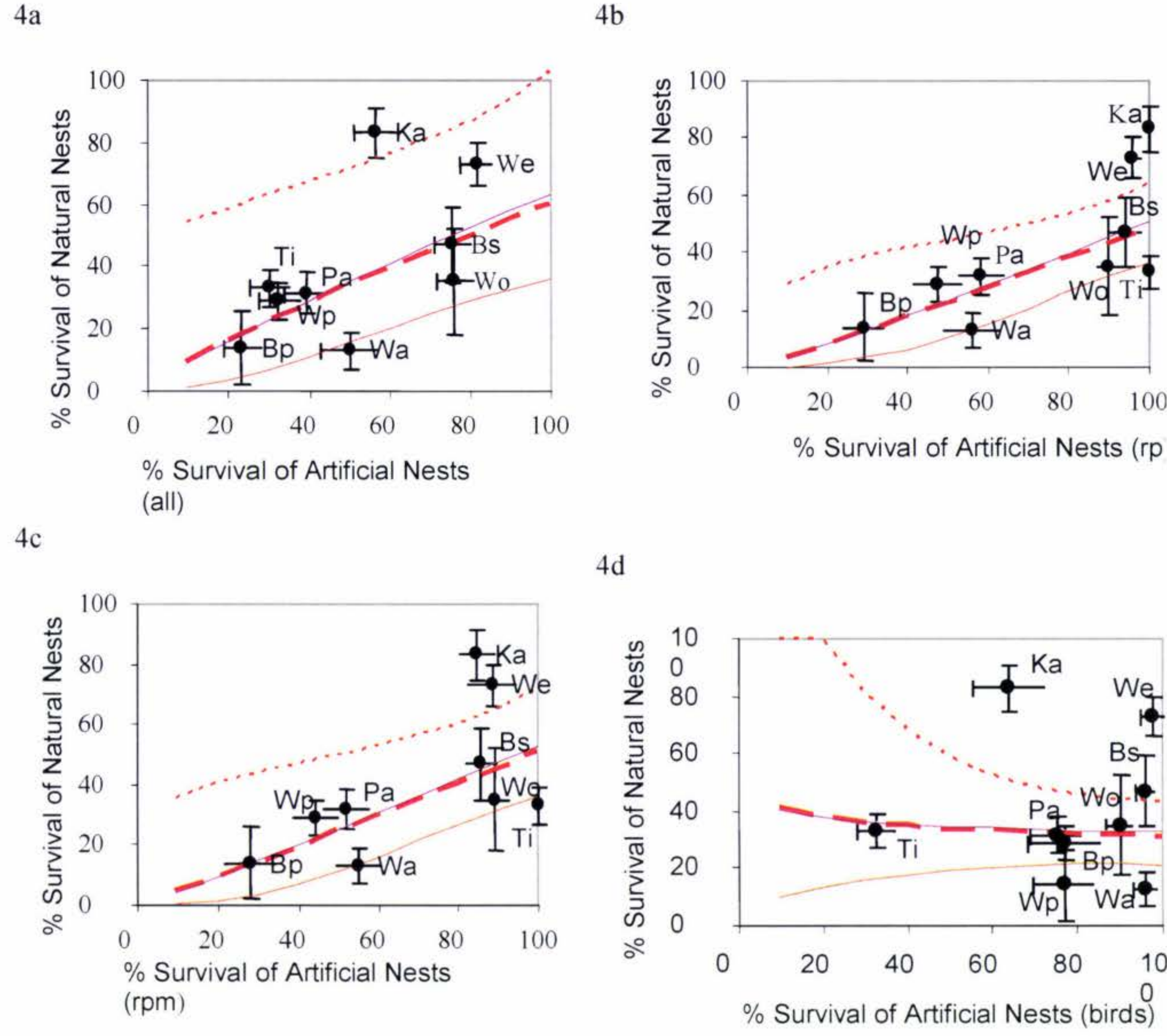

4a
4b
4c
4d

Figure 4a, b, c and d. Relationship between natural and artificial nest success estimates for each predator group (a = all predators; b = rats and possums; c = rats, possums and mice; d = birds. Each point represents the estimate with associated error for each of the nine reserves. The mean value from the original data set is represented by the central broken line and the mean value from the simulated, bootstrap data set by the solid central line. The 95% confidence limit is represented by the upper and lower broken line (Ti = Tiritiri Matangi; Ka = Karori; We = Wenderholm; Bs = Boundary Stream; Wo = Waotu; Bp = Bushy Park; Wp = Waipapa; Wa = Waimanoa; Pa = Paengaroa)

DISCUSSION

Using artificial nests to predict the success of natural nests is supported by the results of this study. Although the estimates of nest success for natural and artificial nests were different from each other within each reserve, the overall pattern for all nine reserves was relatively consistent, that is to say, a rise or fall in natural nest success was mirrored by a rise or fall in artificial nest success. The existence of this relationship between artificial and natural nest success was established first through the model selection procedure, the selected model providing relatively good representation of the data. Due to the discrepancy in the results of previous research (Major & Kendal, 1996; Moore & Robinson, 2004) it was important to test the validity of the results obtained. Confidence in the results was achieved by using the bootstrap procedure, employing a large number of data sets to test the limits of the error produced. Ultimately, this provided further support for the result as the model selected from the bootstrap data set via AIC model selection was the same as that chosen using the original estimates, with similar patterns in AIC_c weights attributed to the chosen model.

A relationship existed between artificial and natural nest success despite the variety of confounds introduced through the diverse range in habitat structure, area and location of the nine reserves, providing further confidence in the results. Additionally, the array of natural nest success estimates between reserves also ensured that the relationship between artificial and natural nest success did not arise simply from similarities in nest success between reserves. The spatial separation between individual reserves chosen for this study also ensured that the nest success results from each reserve were independent of each other. Factors responsible for weakening the relationship between natural and artificial nest success may therefore be explained by differences within each reserve, not as the result of aversion/attraction of mutual predators between reserves (e.g. increased probability that a small number of predators were responsible for all predation events (Laurence & Yensen, 1991; Buler & Hamilton, 2000) or repercussions resulting from poisoning regimes conducted in adjoining reserves. One of the limitations of previous research using artificial nests is that the number of sites has frequently been constrained to only a few, often closely situated sites, resulting in many more replicates within sites than there are sites. Consequently, little statistical power can be obtained from the results to support the biological inferences made. The fact that ecological phenomena are often spatially variable made it more desirable to conduct experiments simultaneously at multiple sites (McKone & Lively, 1993; Pfister & Stevens, 2003). Increasing the scope of the study to maximize the distance between reserves accounted for this variability and avoided the risk of the results being confounded by pseudo-replication (McKone & Lively, 1993). As an additional benefit, this variety in the habitat structure highlighted the factors (discussed later) that differentially affect the success of artificial and natural nests. Consequently, the results also show that artificial nests have the ability to predict natural nest success in a range of bio-geographical situations. This plasticity is an important consideration for the successful application of artificial nests as a widespread monitoring technique.

Predator identification and significance using artificial nests

Crucial to achieving this strong relationship between artificial and natural nest success was the separate analysis of the different predator groups, which depended on the ability to identify predator group. The preservation of prints in the clay enabled reasonably clear identification of each predator except a small percentage of unknown marks (the majority of which were suspected to be the result of debris falling into the nest). Once eggs with such markings, and others presumed to be non-predators, were removed from the analysis, the predictive power of this technique improved substantially. In New Zealand, the introduction of rats and possums has had a detrimental effect on the survival of many native species (Aitkinson and Bell, 1973; Diamond & Veitch, 1981; Moors, 1983, 1985; Bell, 1991; Innes & Hay, 1991; Clout & Craig, 1995; Lovegrove, 1992,1996; Brown *et al.*, 1998; Duncan *et al.*, 1999; Craig *et al.*, 2000; Atkinson, 2001). The fact that nest depredation by rats produced the strongest relationship with natural nest success provided both support for the previously mentioned research and further validation for the ability of this technique to accurately represent the predator-prey dynamic in the current system. Possums, although known to depredate nest and eggs (Brown *et al.*, 1996a) constituted a very small proportion of depredation events. The effect of possums on nest success may partially result as a secondary consequence of their effect on the structure of the habitat, e.g. canopy collapse resulting in habitat loss, the results of which would not be detected using artificial nests. It is therefore possible that the inclusion of possums in this sample may not have improved the predictive ability of the technique. However, nests depredated by possums were included with the rats as it is assumed that any attack on a nest by a possum would result in nest failure (Brown *et al.*, 1996a; James & Clout, 1996).

Birds depredated a large proportion of the eggs collected. Previous studies have also documented bird predation as contributing to a large proportion of artificial nest failure (Martin, 1987; Major *et al.*, 1996; Matthews *et al.*, 1999; Buler & Hamilton, 2000; Bàtàry *et al.*, 2004), often accounting for the majority of nest depredation events. The previously mentioned research identified corvidae as the main avian predators. It was assumed from the size of the marks and through personal observations of robins at artificial nests, that most of the imprints made by birds in this research were the result of robins or other similar sized species. Unlike artificial nests, adult birds are present to defend natural nests against intrusions from other similar and smaller sized species of bird, and this may provide an explanation for the fact that nest depredation from avian predators in the reserves used in this research had no relationship with natural nest success. Only 16 out of the 127 artificial nests depredated by birds across all of the reserves were the result of larger avian predators. Of this 16, the majority occurred in Tiritiri Matangi and Karori reserves where depredation of nests by avian predators was the most prevalent. The absence of high-risk mammalian predators may have encouraged an increase in the survival rates of these larger birds, increasing the likelihood of nest depredation for smaller avian species. However, with such a small sample of nest depredation by large avian predators it was not possible to assess the relationship with natural nest success. Although, the infrequent occurrence of such depredation events from the entire sample suggests that the influence that these larger predators had on overall nest success was very small.

The inclusion of mice, previously recorded as predators on both real (Maxson & Oring, 1978; Guillory, 1987) and artificial nests (Leimgruber *et al.*, 1994; Picman & Schriml, 1994; Reitsma & Whelan, 2000), did not improve the predictive ability of the model in this study, suggesting that mice do not threaten the success of natural robin nests. However, this does not mean that they do not pose a threat to nest survival for smaller species of birds (Guillory, 1987). Mice did depredate artificial nests in all but one of the reserves, although nest depredation by mice constituted only a small proportion of depredation events. It has been suggested that mice may pose a threat to nest success for species such as the black robin by taking eggs from nests (Don Merton pers. comm.) It is interesting to note that in reserves with predator control, estimated nest success experienced a greater decline when depredation by mice was included in the S_{rp} model, compared to the decline in estimated nest success experienced in the majority of reserves with no predator control. This pattern may reflect a subsequent rise in the number of mice as rat numbers decrease following predator control, increasing mice depredation in reserves with no predator control. Such an effect may be of greater importance when considering the effect of mouse predation on the survival of nest of smaller species of passerine, especially when considering predator control measures. With this in mind, collection and production of the clay eggs should depend on the model species for which the monitoring is purposed and mice viewed as a potential threat to nest success.

Differences between artificial and natural nest success

Nest success estimates resulting from predation by 'rats and possums' was selected as the best model when fitting the relationship with natural nest success. However, the fit of the data to this model was not perfect. The higher overall rates of nest success for artificial nests compared to natural nests across all of the reserves may be accounted for by the difference in exposure time between artificial (28 days) and natural (40 days) nests. However, the difference between natural and artificial nest success values within individual reserves was not consistent across all reserves. This inconsistency weakens the relationship between artificial and natural nest success by reducing the strength of the correlation. Reasons for this inconsistency could be linked to the confounding factors introduced by the variability within individual reserves, e.g. different habitat structure, reserve size, predator community and control regime. Extenuating circumstances specific to each reserve i.e. influences from surrounding land use may also exacerbate the effect of these confounding factors. In addition, this difference could also be accounted for by the use of data collected from previous years, which would not account for any changes in nest mortality during the year of artificial nest data collection.

The difference between artificial and natural nest success for the 'rats and possums' predator group in Tiritiri Matangi, Waotu, Boundary Stream and Waimanoa reserves was much larger compared to the other reserves. Despite the lack of mammalian predators, natural nests on Tiritiri Matangi did experience high levels of failure. As previously discussed, nest predation by birds detected using artificial nests, had no relationship with natural nest success. This could imply that natural nest failure on Tiritiri Matangi is largely due to factors other than predation (as there are no mammalian predators). This reserve stands out from all the others because it is the only island reserve. A consequence of this isolation and hence area restriction is the captive exposure of its inhabitants to factors such as severe weather conditions, starvation, drought and disease. The fragmentation of the forest decreases the amount of suitable habitat available by increasing the edge to area ratio. As a result, birds may be forced to build nests nearer to the edge, increasing exposure, which may exacerbate the effects of severe weather and decrease food availability. The lack of mammalian predators has allowed an increase in the number and diversity of small birds in this reserve. It is possible that such high abundance of passerines may not be directly responsible for natural nest failure, i.e. nest depredation, but instead have an indirect consequence. For example, high passerine abundance may increase adult mortality due to higher energy expenditure on territorial disputes and nest defence, consequently decreasing the time available for foraging to feed themselves and their young (affecting both incubation and nestling stages). High densities also result in increased competition for space and resources, birds may be forced to build their nests in poorer quality habitats and food abundance may be limited, potentially reducing adult and nest survival.

Waotu is the smallest reserve and is composed of three fragments, two small and one larger. The increased edge due to fragmentation and small area may increase the exposure to avian predators that are more common in open areas and edges, such as starlings, mynahs and harriers. This may reduce the natural nest success of robins as a direct result of increased energy expenditure due to increased vigilance, territorial behaviour and nest defence as well as predation. The small area and fragmentation may also leave the bush more exposed to extreme weather conditions resulting in a high nest failure rate (discussed previously for Tiritiri Matangi). The effect of this may be exacerbated by the fact that the edges of the smaller fragments are clear-cut reducing the buffer effect of a successional growth gradient. The reserve's close proximity to farmland may also increase the risk of nest failure due to higher numbers of predators such as domestic cats that are known to prey on nestlings and are not targeted by predator control (Gordon Stephenson, pers. comm.) Support for increased nest mortality due to high levels of nest depredation at the nestling stage may be reflected by the inclusion of the 'stage' factor in the model choice for this reserve. The predator control programme used in Waotu is targeted at reducing the numbers of rats. As a consequence of this, together with invasions from surrounding farmland, numbers of mice may be high. High numbers of mice together with the small area could reduce the food supply available for the robins, increasing the incidence of nest failure due to starvation of both adults and nestlings competing for invertebrates.

Waimanoa and Boundary Stream reserves, being larger continuous sections of bush, may not be so affected by the effects of fragmentation and edge effect. However, larger areas of bush may support larger numbers of larger predators like mustelids and feral cats that prey on nestlings (Moors, 1983; King 1984). This effect may be more prevalent in Waimanoa (also reflected by the inclusion of 'stage' in model selection for natural nest success), where predator control is not carried out. The data used for estimating natural nest success was collected from previous years for Waotu, Boundary Stream and Waimanoa, which may not accurately reflect the patterns shown in the same year that artificial nests were run. For Waotu and Boundary Stream the sample size used to estimate natural nest success was very small, decreasing model precision hence predictive capability.

Advantages and limitations of the statistical technique

Previously used analytical techniques have categorized nest fate as survived or failed over entire exposure period assigned by the researcher ignoring much of the variation in the data. The methods used in this experiment (known fate model MARK and Stanley 2000) make it possible to look at the patterns of predation that occur on a daily, weekly, monthly basis for different stages within the exposure period, capturing the main structure and variability underlining nest depredation (Burnham & Anderson, 2002).

Of the set of candidate models used in the models compared for analysis of natural nest success, particularly useful was the inclusion of the factor stage. Survival probability has been found to remain constant throughout the incubation and nestling stages (Drachmann *et al.*, 2002), however, other studies have found that predation varies according to time of the nesting cycle, e.g. nests may experience higher predation after chicks are hatched than when eggs are present (Schaub *et al.*, 1992; Morton *et al.*, 1993; Small *et al.*, 1993). In this research, rats were found to be the main predators of artificial nests and these predators are known to depredate nests at both the egg and chick stage (Atkinson, 1985; Brown *et al.*, 1998). The fact that artificial nests only represent the egg stage limits the extent to which they can accurately predict absolute natural nest success at the nestling stage. In an attempt to account for nest predation at both stages of development the exposure period for artificial nests was extended past the incubation stage, assuming that this would increase the probability of predation, decreasing the difference between nests success estimates for artificial and natural nests. Mustelids are also known nest predators, taking eggs, nestlings and adult robins, especially during incubation and nestling stages when the adults are on the nest (Murphy *et al.*, 1998). No depredation event on an artificial nest was identified as mustelid through marking on the clay eggs, hence the extended exposure period may not be enough to account for such predators as the stimulus provided by chicks may be what promotes predation by these predators.

The results for artificial nests suggest that model choice may reflect predator type and relative abundance between and within each reserve. In reserves where rats were responsible for the majority of nest depredation, model selection favoured the factor 'week' (which represented weekly nest success). In reserves where rats are targeted for poisoning, the 'week' factor is selected far less frequently and the strength of support when this factor is included is reduced. This suggests that the weekly patterns of nest depredation produced in the presence of high numbers of rats may be less distinguishable for model selection when rat numbers are low. Predator control regimes may also differ between reserves, disrupting any established pattern of nest depredation by the targeted predators (namely rats). As a result, a variety of factors is included in the models chosen for the reserves with predator control. Therefore, it may be feasible to infer predator type and relative abundance through the factors included in the model selection and the strength extrapolated via AIC model selection weight. However, in reserves where nest failure is the result of a diverse predator assemblage, consisting of species that exhibit similar patterns of predation, the aforementioned conclusions may be applicable but only with caution.

Other factors affecting the difference in the nest success estimate of artificial and natural nests, which cannot be accounted for in the design of artificial nests, are nest failure due to starvation, weather, infertility and disease. The statistical technique used to fit the relationship between artificial and natural nest success accounted for the difference by fitting the parameters α and β (page 31) to account for confounding factors introduced through reserve variability. Any differences within individual reserves could then be related to confounding factors introduced by the circumstances within that reserve, and the consequences for using artificial nests in that given situation highlighted. An additional benefit of this technique is that it is extremely conservative, treating all the data collected at each site as a single observation. The advantage of this is that the focus is not on individual relationships at specific reserves that may be predominantly due to factors other than predation, but on the general trend between reserves. This reduces the chance of over fitting the model constraining the predictive ability of artificial nests to the patterns observed between one particular set of circumstances, i.e. the confounding factors relevant to the reserves in this study only. As a beneficial consequence, the results of this study are transferable i.e. can be used to assess predation in reserves outside those used in this research.

Limitations of artificial nests

While artificial nests have been shown to provide a relatively accurate method of representing the relative risk of predation for natural nests there are some features of natural nests that remain extremely difficult to account for in the design of artificial nests. For this research, all foreseeable precautions were taken to account for factors previously recorded to influence the success of artificial nests e.g. materials used in nest and egg construction and odour control. However, physical factors such as parent guarding (Martin *et al.*, 2000; Ghalambor & Martin, 2001), presence of chicks and their sensory cues such as smell (Schaub *et al.*, 1992), warmth and noise (Haskell, 1994 ; Roulin, 2001a, b Leonard *et al.*, 2005) associated with natural nests are not easy to replicate hence were absent from this artificial nest design. Begging calls (Haskell, 1994; Roulin, 2001a, b) and olfactory cues associated with the presence of chicks during the nestling stage have also been highlighted as important factors contributing to the risk of nest failure in natural nests. The presence of the adults during the incubation and nestling stages has been reported to attract predators, through both olfactory cues and the movement of adults to and from the nest (MacIvor *et al.*, 1990; Sloan *et al.*, 1998; Martin & Ghalambor, 1999; Martin *et al.*, 2000).

The implications associated with such differences, i.e. different absolute values for artificial and natural nest success, may be difficult if not impossible to avoid. Attempting to replicate such features may only increase the confounding factors introduced as a result of excessive manipulation of the nests. For example, attempting to mimic olfactory cues by spraying odours (e.g. diluted mixture of faeces may inadvertently attract more predators to the nest site (Part & Wretenberg, 2002). Likewise attaching artificial robins to the nests, although presumed to mimic depredation risk associated with adult presence at nests, inaccurately reflects adult presence at the nest site because in natural nests adults are not present 100% of the time. The addition of cameras may also affect nest survival due to the increased human presence at nest sites (MacIvor *et al.*, 1990; Gutzwiller *et al.*, 2002). Cameras used to identify predators have been found to increase and decrease predator activity as some species are attracted and others deterred by the presence of cameras (i.e. 'novelty factor') (Angelstam, 1986; Hernandez *et al.*, 1997; Yahner & Wright, 1985). In addition to this, over complication of methods and increased financial input through the use of additional sophisticated equipment i.e. cameras and artificial robins (Brown *et al.*, 1998; King *et al.*, 2001) may make the artificial nests too time consuming and less affordable for those wishing to use them as a monitoring technique.

A common criticism of artificial nest experiments is the sudden introduction of nests, dramatically increasing the number of nests available for depredation during the first week of exposure. The effect of such an introduction is an increase in nest encounter rate by potential nest predators and therefore possible decrease in the initial success rate of artificial nests (resulting in the observed weekly pattern of predation). Of this sample, those more amenable to predation will be depredated quickly resulting in a high initial rate in nest failure. Nests that survive the first week will be present in lower numbers, hence reduced encounter rate, and be those less amenable to depredation. However, a similar pattern can be found in natural populations as the onset of the breeding season is also signified by a similar, but maybe a less dramatic appearance of nests and those more exposed to predation will be taken first, resulting in high rate of nest failure during the initial stages. One of the features missing with the artificial nest technique is a representative nest building stage. Predators may use cues such as parents carrying materials to and from the nest site to locate nests. Predators that use such cues may take longer to locate artificial nests.

Recommendations

The design of this experiment aimed at representing the natural breeding season of robins as closely as possible. However, the exposure time for artificial nests did not cover the entire incubation and nestling stages. This decision was made for practical reasons given the large number and spatial separation of reserves. Whilst it cannot account for the aforementioned stimulus created by the presence of nestlings, it would be interesting to see if extending the exposure period to cover the entire incubation and nestling stages improves the predictive capabilities of artificial nests. The sample size used for artificial nests was based on the territory size of robins; therefore it was assumed that the proportion of artificial nests depredated would accurately represent potential natural nest loss. If nest predation rate was positively correlated with nest density, the addition of 30 artificial nests to all of the reserves would have decreased the chances of nest success in the smaller reserves more than larger reserves. However, previous research has also found that increasing the density of inactive nests reduces the predators harvest rates or serves as a predator deterrent (Collias & Collias, 1978; Robinson, 1985; Leonard & Picman, 1987; Watts, 1987; Martin & Roper, 1988). Without any parental activity artificial nests may be looked upon by predators as inactive. It may be interesting to explore further the effect of nest density on nest success (Reitsma, 1992; Schmidt & Whelan, 1998) using artificial nests in order to refine the technique, increasing its efficiency as a predictor of overall nest success.

The data used to estimate natural nest success in this research were collected over a number of years, and the year used to fit the relationship sometimes changed (i.e., current data for natural nest success were not available for all sites). Robin populations have been shown to fluctuate in number between years (Powlesland, 1983). Although I detected no apparent change between the years through the data sets I combined, to develop this technique further I would recommend collecting nest success data for both artificial and natural nests over the same year to see if this improves the predictive ability. However, it is assumed that for the population within each reserve to have survived long enough to become established, dramatic fluctuations in population size between years must be infrequent in order to sustain the population.

The AIC model selection procedure was used in this study primarily to obtain the best models for deriving estimates of nest success. However, it was also used to allow me to look for any strong patterns of predation by different predator types. For this reason model averaging was not used. In this instance, all of the models selected were supported by a high AIC weight so model averaging may not have had a significant effect on the estimates. However, as a consideration for future analysis of artificial nest success, rather than basing decisions on the single model most strongly supported by the data, model uncertainty should perhaps be acknowledged by considering the entire set of models, each weighted by its own strength of evidence (Buckland *et al.*, 1997).

Preliminary classification of predator type into subsequent groupings, through examination of prints on the eggs during weekly nest checks, was problematic due to the differences in interpretation amongst nest checkers in each reserve. I therefore decided to request that volunteers remove all eggs that were marked. The result of this was an inflated all predator group which included marks made by 'non-predators' such as insects and falling debris. It is feasible that implementation of this monitoring procedure in individual reserves, monitored by fewer people, (reducing variety in the interpretation of marks), could produce a less inflated all predator group by avoiding collection of 'non-predator' marked eggs. Analysis and fieldwork would thus be less time consuming.

The results of this study have established that there is a relationship between artificial and natural nest success, although the strength of this relationship was weakened by confounding factors. The benefit of including these factors was that it allowed me to test how well artificial nests can predict natural nest success given a variety of realistic scenarios. However, it would also be useful to test the accuracy of artificial nests as an index in the absence of those confounding factors. This may be done by using several sample plots in replicate areas within one large forest block allowing for control of confounding factors. However, maintaining an adequate distance between plots within the large forest block may be essential to maintain independence. As tracking tunnels are an accepted and commonly used method of monitoring predator abundance in New Zealand it would also be useful to test the strength of the relationship with natural nest success to compare with artificial nest success. Unfortunately, tracking tunnel data were not available from all the reserves in this study.

Management implications

An important consideration for future artificial nest use is the predator community involved. Nest predation is a predator-prey system and complete understanding of what is happening to the prey is strongly dependent on the behavioural ecology of nest predators (Lariviere, 1999). Not only can predator type affect the stage, pattern and scale of nest depredation events but the effect of such factors can also be influenced by the predator's use of habitat structure and area. This is highlighted both by model selection and through the influence of confounding factors within and between reserves. While artificial nests are extremely useful for identification of predators that visit and depredate eggs, it cannot predict the effect of those that do not. Predators that preferentially prey on nestlings, resulting in high nest mortality rates during this stage, cannot be accounted for using artificial nests. The result may result in overestimation of nest success.

Also important to consider is the species for which the monitoring is aimed. The nest structure and height, clutch size, egg size, incubation and nestling period, breeding season, response to nest depredation, adult size and defence strategy are just some of the things that have to be taken into consideration when designing an artificial nest experiment and analysing the results. However, it may be possible to design this method to cover a range of species, providing some similarities exist in their life histories.

In situations where factors influencing nest success do not include nest predation, or predation events occur mainly at the chick stage only, artificial nests become ineffective. However, when predation is the primary cause of nest success and failure at the egg stage has a strong influence on overall nest success artificial nests become a powerful tool for monitoring potential natural nest success.

APPENDIX

Table 1. Results of model selection procedure, showing model selection used for estimating nest success for each predator group in each reserve.

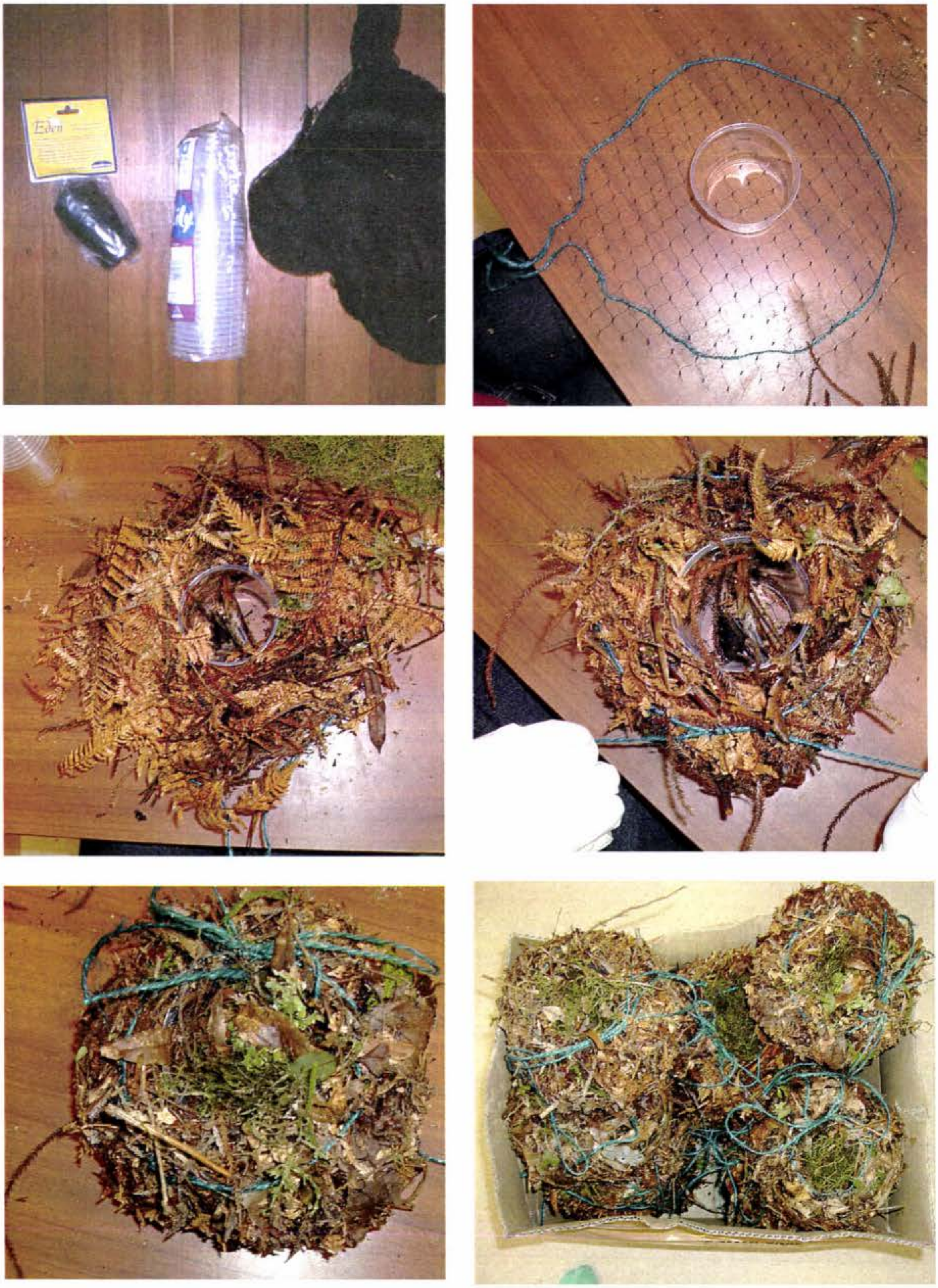
Reserve	Predators	Model	k	AIC weight	Estimate	Standard Error
Boundary Stream	all predators	S(.)	1	0.75	0.76	0.05
	rats, possums & birds	S(.)	1	0.57	0.89	0.04
	rats & possums	S(g)	3	0.41	0.94	0.05
	birds	S(.)	1	0.44	0.96	0.02
Bushy Park	all predators	S(t)	4	0.998	0.23	0.05
	rats, possums & birds	S(t)	4	0.72	0.25	0.05
	rats & possums	S(t)	4	0.65	0.29	0.05
	birds	S(.)	1	0.75	0.77	0.07
Karori	all predators	S(.)	1	0.63	0.56	0.05
	rats, possums & birds	S(g)	3	0.48	0.64	0.09
	rats & possums	N/A	-	N/A	1	0
	birds	S(g)	3	0.48	0.64	0.09
Paengaroa	all predators	S(t)	4	0.39	0.39	0.05
	rats, possums & birds	S(g*t)	7	0.62	0.47	0.09
	rats & possums	S(t)	4	0.58	0.58	0.06
	birds	S(.)	1	0.39	0.75	0.06
Tiritiri Matangi	all Predators	S(.)	1	0.73	0.30	0.05
	rats, possums & birds	S(.)	1	0.77	0.33	0.05
	rats & possums	N/A	-	N/A	1	0
	birds	S(.)	1	0.77	0.33	0.05
Waimanoa	all predators	S(t)	4	0.72	0.5	0.05
	rats, possums & birds	S(g+t)	6	0.90	0.55	0.07
	rats & possums	S(g+t)	6	0.82	0.56	0.08
	birds	S(.)	1	0.42	0.96	0.03
Waipapa	all predators	S(t)	4	0.75	0.32	0.05
	rats, possums & birds	S(t)	4	0.67	0.40	0.06
	rats & possums	S(t)	4	0.66	0.47	0.06
	birds	S(g+t)	6	0.74	0.77	0.09
Waotu	all predators	S(.)	1	0.77	0.76	0.05
	rats, possums & birds	S(.)	1	0.78	0.91	0.03
	rats & possums	S(t)	4	0.39	0.91	0.03
	birds	S(t)	4	0.83	0.90	0.03
Wenderholm	all Predators	S(.)	1	0.73	0.81	0.04
	rats, possums & birds	S(g)	3	0.30	0.95	0.04
	rats & possums	S(.)	1	0.46	0.96	0.02
	birds	S(g)	3	0.47	0.98	0.03

GALLERY

Material collection and artificial nest construction

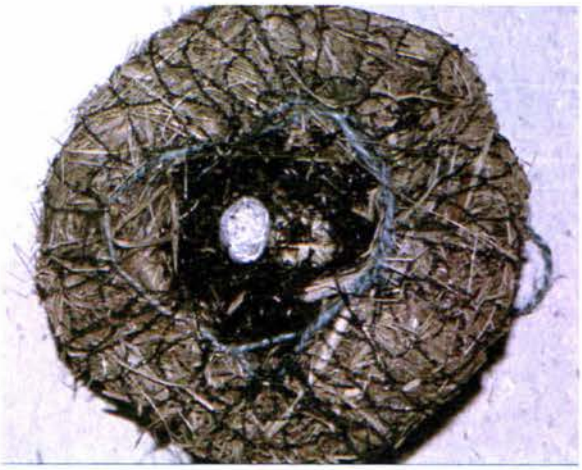
Photographs taken by Doug Armstrong

Artificial nest construction



Photographs taken by Doug
Armstrong and Rebecca Lewis

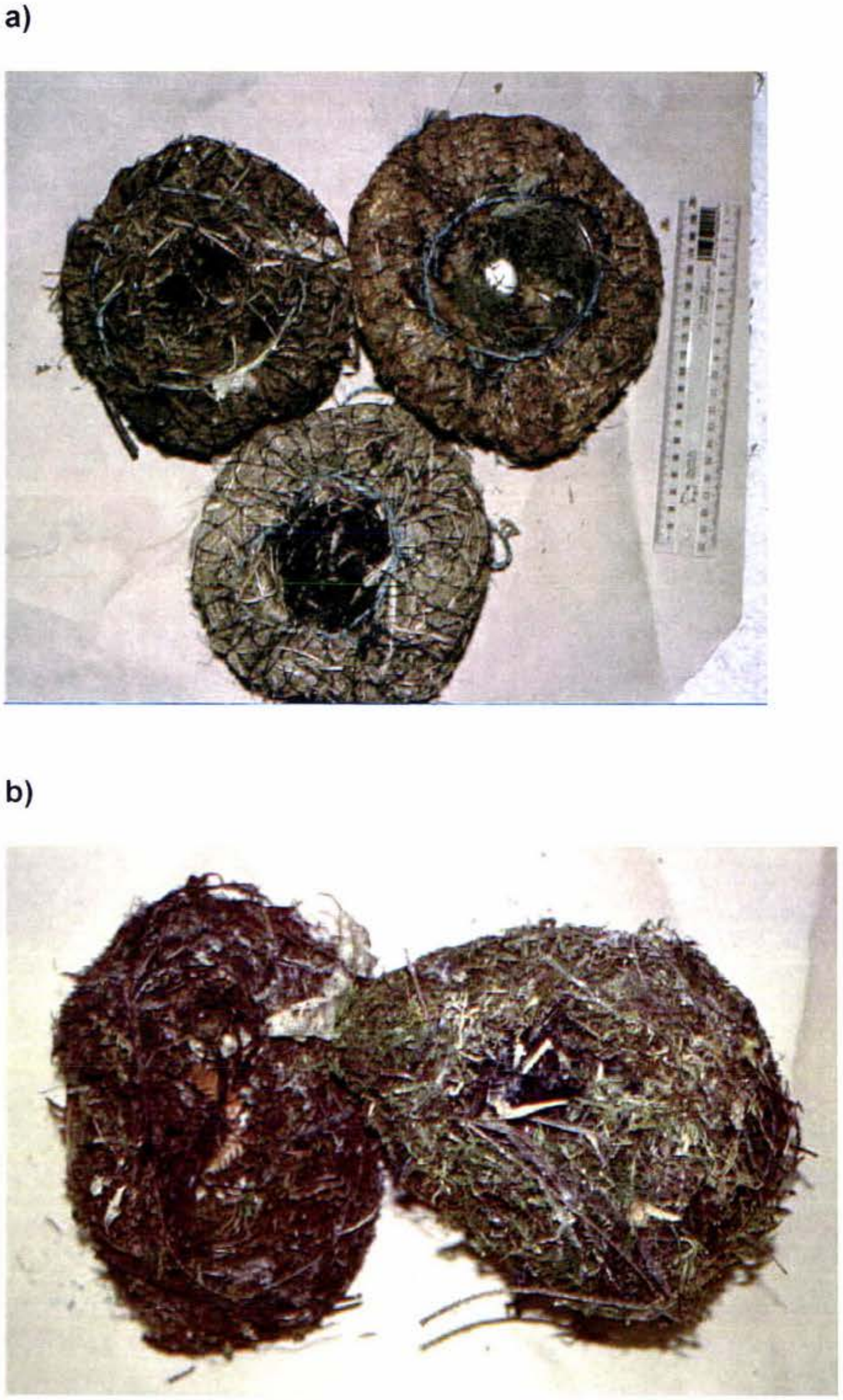
Artificial nests with Clay: Clay and Clay: Quail egg combinations



Artificial nests in location

Photographs taken by Rebecca Lewis

Artificial nests (a) and natural North Island Robin nests (b), illustrating the difference in colour and texture using material collected, and natural nests constructed from each reserve.



Photographs taken by Rebecca Lewis

Chapter Three

Methodology for obtaining meaningful results using artificial nests in New Zealand forest fragments

ABSTRACT

Artificial nests have been proposed as a monitoring technique for predicting the success of natural nests. Whilst artificial nests have been found to be successful in a range of experimental conditions, dispute over the methodology to be used, their design and application has hindered their acceptance as a viable monitoring technique. The aim of this research was to examine the method of using artificial nests and eggs to increase their predictive ability and facilitate their use as a technique for monitoring natural nest success in New Zealand forest fragments. Four areas were examined; 1) the level of monitoring required to facilitate an accurate prediction of natural nest success using artificial nest success; 2) the influence of length of exposure period on the ability to accurately record predation events using egg remains; 3) the effect of using quail eggs versus clay eggs alone on the probability of artificial nest success; 4) the ability to identify predator type following depredation events by using real and artificial eggs and nest remains.

The results of this research suggest that; (1) predation rates on artificial nests over one week gave a better prediction of nest success than estimates from monitoring over 4 consecutive weeks. However, nests should be monitored at regular intervals over the whole breeding season since predation rates change during the season; (2) leaving nests out longer than one week before checking increases the chance of the marks becoming obscured, hampering predator identification; (3) adding a quail egg has little effect on predation rate, particularly on the rate of predation by mammals; and (4) it is necessary to include clay eggs in artificial nests as marks left on quail eggs and damage done to artificial nests were not reliable indicators of predator type. Additionally, egg size has a limited effect on the ability of the predator to cause detrimental damage to the eggs in artificial nests, as each predator group was able to penetrate the shell of the larger quail eggs.

INTRODUCTION

The value of any monitoring technique may be measured by the frequency of its application in circumstances applicable to its design. This may come as a direct result of its plasticity and the degree of simplicity of its application. Artificial nests have been proposed as a monitoring technique for predicting the success of natural nests. Whilst this technique has been found to be successful in a range of experimental conditions, dispute over the methodology to be used in its application has hindered its acceptance as a monitoring technique by local and central governmental bodies (Major & Kendal, 1996; Moore & Robinson, 2004).

Factors affecting the decision to apply and the effectiveness of any monitoring technique may be dependant on the individual circumstances i.e. environmental and social factors, influencing the proposed monitoring site. Environmental factors such as the habitat structure, predator assemblage and the climatic conditions can provide a unique set of circumstances which need to be factored into the design of any monitoring technique. Social factors such as financial restrictions and human resources may restrict the materials available and time allocated for the application of the technique. Facilitation of any monitoring technique may therefore require a certain level of manipulation of the methods used to suit each individual situation. However, this manipulation must be done without hampering the predictive ability of the technique itself.

Artificial nests have a relatively high level of plasticity as a monitoring technique as they are amenable to manipulation at all stages of their design. The type of nests used in previous research has ranged from natural e.g. using abandoned natural nests or building artificial nests using a frame (e.g. wire mesh) camouflaged with sticks and mosses (King *et al.*, 1999; Part & Wretenberg, 2002), to artificial e.g. commercially supplied woven nests or un-camouflaged constructions (Loiselle & Hoppes, 1983; Wilcove, 1985; Ortega *et al.*, 1998; Davidson & Bollinger, 2000). The type of eggs used also ranges from natural e.g. quail, chicken, Zebra Finch, sparrow and Budgerigars (Ortega *et al.*, 1998; King *et al.*, 1999; Buler & Hamilton, 2000; Lindell, 2000), to artificial, e.g. modelling clay, ceramic, wax or hard plastic (Weidinger, 2001; Zanette, 2002; Burke *et al.*, 2004) or both natural and artificial eggs (Davidson & Bollinger, 2000; Part & Wretenberg, 2002; Thompson & Burhans, 2004). Exposure time, frequency of monitoring and nest placement can also be designed to suit the prevailing circumstances. Exposure of nests has ranged from 2 hours (Gotmark & Ahlund, 1984) to 8 months (Slagsvold, 1980) in previous research. Monitoring frequency ranges from daily (Thompson & Burhans, 2004) to weekly (Burke *et al.*, 2004). Nests have been placed to estimate the success of both ground nesting (Yahner & Wright, 1985; Opermanis, 2004) and canopy nesting avian species (Boulton & Clarke, 2003; Gregoire *et al.*, 2003) and to answer questions concerning the influence of different habitat characteristics (Hartley & Hunter, 1998; Soderstrom, 1999; Mezquida & Marone, 2002; Chalfoun *et al.*, 2002a, b;).

However, the ability of artificial nests to predict natural nest success has been found to depend on the variability of such factors, along with their ability to identify predators and predator community assemblage For example, nests that are more natural in appearance have been found to provide a more accurate prediction of nest success than those that are not (Martin, 1987; Davidson & Bollinger, 2000), although, research by Davidson *et al* (2000) found the contrary. Likewise, predation rates have been found to be significantly influenced by egg type (Lindell, 2000) and the addition of real eggs has been shown to be important for accurate prediction of nest success (Part & Wretenberg, 2002). Obtaining an accurate estimate of the risk of predation from each predator type, within the predator community, has also been linked to the size of eggs used and visual and olfactory attributes of nests and eggs (DeGraaf & Maier, 1996; Ettel *et al.*, 1998; Rangen *et al.*, 2000; Blanco & Bertellotti, 2002; Fulton & Ford, 2003).

Artificial nests differ from natural nests in a number of important ways that may influence the rates of nest depredation (Wilson *et al.*, 1998). The way in which these differences are accounted for may depend on the modelled species, the habitat within the study sites and the predator community involved. Such differences may in turn be dependant on the country in which the technique is carried out, so it is important first to establish the effect of these differences prior to use.

The aim of this research was to examine the method of using artificial nests and eggs to increase their predictive ability and facilitate their use as a technique for monitoring natural nest success in New Zealand forest fragments. Four areas were examined; 1) the level of monitoring required to facilitate an accurate prediction of natural nest success using artificial nest success; 2) the influence of length of exposure period on the ability to accurately record predation events using egg remains; 3) the effect of using real eggs versus clay eggs alone on the probability of artificial nest success; 4) the ability to identify predator type following depredation events by using real and artificial eggs and nest remains.

METHODS

Study Sites and Field Methods

The experimental procedure using artificial nests, on which this chapter is based, is outlined in chapter one. Additional techniques relevant to each of the aims in this chapter only are detailed below.

Aim 1: - ***The level of monitoring required to facilitate an accurate prediction of natural nest success using artificial nest success***.

To illustrate patterns of predation resulting from depredation by rats and possums that occur across weeks (1-4) and season (early, middle and late in the breeding season) estimates of artificial nest success were calculated for all reserves with rats and possums, i.e. Bushy Park, Boundary Stream, Waimanoa, Waipapa, Waotu, Wenderholm and Paengaroa reserves.

To assess the amount of monitoring required within each seasonal period (early, middle and late) to maintain a strong relationship between artificial and natural nest success, two monitoring regimes of low and high intensity were compared using all nine reserves. For the low intensity regime, nest success was estimated from data collected from the first week of nest checks for all of the three seasonal periods (denoted as $\alpha\ S_{aw1}{}^{\beta}$ in table 2). For the high intensity regime, nest success was estimated from data collected from all 4 weeks for all of the seasonal periods (denoted as $\alpha\ S_{aw4}{}^{\beta}$ in table 2).

General linear modelling was used to fit a relationship between survival of natural nests (S_n) and artificial nests ($S_{a1wk,}\ S_{a4wk}$). The relationship between these two probabilities was expected to take the form

$$S_n = \alpha S_a{}^{\beta}$$

The parameter α is the probability of a nest surviving when there are no predators, and accounts for failure of natural nests due to factors such as starvation or disease. The parameter β reflects the relative survival probabilities for natural and artificial nests, and this accounts for the different exposure period of natural (40 days) and artificial (7 or 28 days) nests as well as potential differences in predation rate.

Taking the logarithms of both sides of the equation gives the linear model

$$\log S_n = \log \alpha + \beta \log S_a$$

This relationship was fitted by taking the logarithms of the estimates for natural nests (S_n) and artificial nests (S_{a1wk} and $S_{a4wk)}$ for all sites, and the residual sum of squares (RSS) calculated. This was repeated with S_a calculated for five different predator groups to assess which model gave the best prediction of S_n (Table 4). The models were compared using AIC, with the likelihood calculated from the following equation (Burnham & Anderson, 2002).

$$\ln(L) = \frac{1}{2} n \ln(\frac{RSS}{n})$$

Artificial and natural nest success, were both estimated with error. To account for this, confidence intervals for the relationship between natural and artificial nest success were obtained using a parametric bootstrap, a technique for generating data simulations based on the estimates and standard errors from the original data. Ten thousand data sets were sampled from Log-odds transformed nest success estimates (to allow for sampling within a normal distribution), and the data were then back transformed for interpretation from real figures. The confidence limit was set to 95%. AIC method of model selection was then used to compare the 2 linear models (Table 1).

Table 1. Set of candidate models for estimating artificial nest success for low and high monitoring intensity regimes.

Model[1]	**k**[2]	**Explanation**[3]
$S_n = \alpha S_{aw1}^{\beta}$	3	Correlation exists between artificial nest success (estimated from the first week of every exposure period (S_{aw1}) and natural nest success (S_n).
$S_n = \alpha S_{aw1-4}^{\beta}$	3	Correlation exists between artificial nest success (estimated from all 4 weeks of every exposure period (S_{aw1-4})) and natural nest success (S_n).

[1] Candidate models used to fit relationship between artificial and natural nest success.

[2] Number of parameters in model

[3] Explanation for parameter in model

Aim 2: - ***The influence of length of exposure period on the ability to identify predators using egg remains***

Two-hundred and seventy artificial nests were exposed for 3 sets of 4-week periods, separated by 3-week intervals. After each 7 week period (4-week period plus the 3 week interval) the position of each artificial nest was changed and the eggs replaced ready for the next 4 week exposure period. During the 4 week periods the nests were checked once a week, during the 3-week interval nests were checked only once at the end of the three weeks. To compare the effect of exposure time on the ability to discriminate between predator types using imprints on artificial eggs, the numbers of clay and quail eggs that were missing and clay eggs that received unknown or multiple marking were recorded for both exposure periods (weekly and three weekly). The frequency of occurrence of each of the three types (missing, unknown and multiple marked eggs) was then compared between exposure periods (corrected for effective sample size).

Aim 3*: - The effect of using real eggs versus clay eggs alone on the probability of artificial nest success*

To assess the effect of using real and artificial eggs in each reserve, AIC model selection procedure was used to see if the addition of the egg factor to the previously selected 'temporal model' (see chapter one) explained more of the variation in the data whilst retaining precision capability. For example if the model S(w) (Survival varies among weeks) was selected for a reserve, to test for any influence of egg factor, both the S(w) and S(w+egg) (survival varies among weeks and egg type) models were compared. This procedure was carried out for each reserve and predator group.

Estimates of nest success, with associated standard error, were calculated using the S(egg) model for each egg combination separately (i.e. two clay eggs or one clay, one quail egg), for each reserve using the known fate model in MARK. This procedure was carried out for both mammalian and avian predator groups. The results were displayed using a bar graph to illustrate any similarities in the pattern of predation resulting from each egg combination between reserves.

Aim 4: - *The ability to identify predators using artificial nest and egg remains*

During each weekly check, nest checkers were asked to collect descriptive evidence from the depredated eggs and nests. For quail eggs the percentage of times the egg was damaged during a depredation event and percentage of times each type of damage was done (i.e. scratches, holes and bites) for each predator type, were calculated. For clay eggs, the percentage of times the egg was damaged during a depredation event and the percentage of the surface area damaged by each predator type were calculated. Identifying the predator of quail eggs was aided by examination of marks on the accompanying clay egg in each nest.

For nests, the percentage of times a nest was damaged (i.e. disruption or removal of the lining or structural damage) and faeces found on the nest following a depredation event were calculated.

RESULTS

Aim 1: - *The level of monitoring required to produce an accurate prediction of natural nest success using artificial nest success.*

Seasonal nest success estimates (Figure 1) resulting from depredation by rats and possums fluctuated between early, middle and late in the breeding season. Reserves with predator control implemented throughout the breeding season exhibited a similar within -seasonal trend in predation as reserves without predator control. The notable exception was the early success in Paengaroa reserve where nest success was higher than Waotu reserve which had predator control. Although overall, nest success is higher during each period (early, middle and late) in reserves with predator control. For all seven reserves, there was an increase in nest success from the early period to the middle period of the season. This pattern of increase continued into the late period for three of the reserves, Bushy Park, Waimanoa and Wenderholm, with nest success at its highest in the late period of the season. For the remaining reserves nest success decreased from the middle to late period of the season, with nest success at it's highest in the middle period of the season.

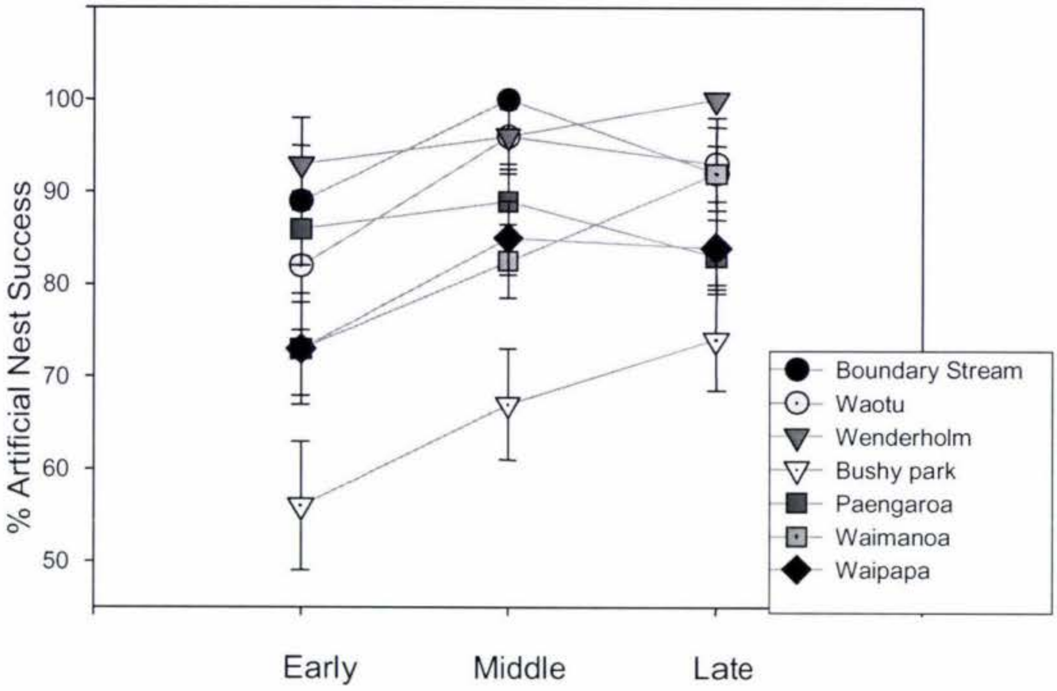


Figure 1. Seasonal trends in survival probabilities (% nest success with standard error) for artificial nests, as a result of predation by rats and possums early middle and late in the breeding season at 7 reserves with and without predator control.

Weekly nest success (Figure 2) resulting from depredation by rats and possums varied between weeks one to four in all reserves. A clear difference can be seen between the reserves with and without predator control. The four reserves without predator control have a larger difference in nest success between week 1 (ranging between 45 and 77% success) and the remaining 3 weeks (ranging between 83 and 98% success). Although the aforementioned trend in weekly nest success is stronger in two of these 4 reserves (e.g., Bushy Park and Waimanoa) an increase in nest success after week one is apparent in all four reserves. This pattern means that the majority of depredation events by rats and possums occurred during the first week of exposure. In reserves where predator control was conducted throughout the breeding season there was a similar pattern in nest success, although the difference in nest success between week1 (ranging from 96 to 98 % nest success) and the remaining 3 weeks (ranging from 96 to 100 % nest success) was significantly smaller than in reserves without predator control. In Waotu reserve nest success shows the opposite trend, decreasing from week 1 to 2 and 3, then rising to its highest during week 4. Overall, nest success was significantly higher during each weekly check for all 3 reserves with predator control than in those without predator control (Figure 2).

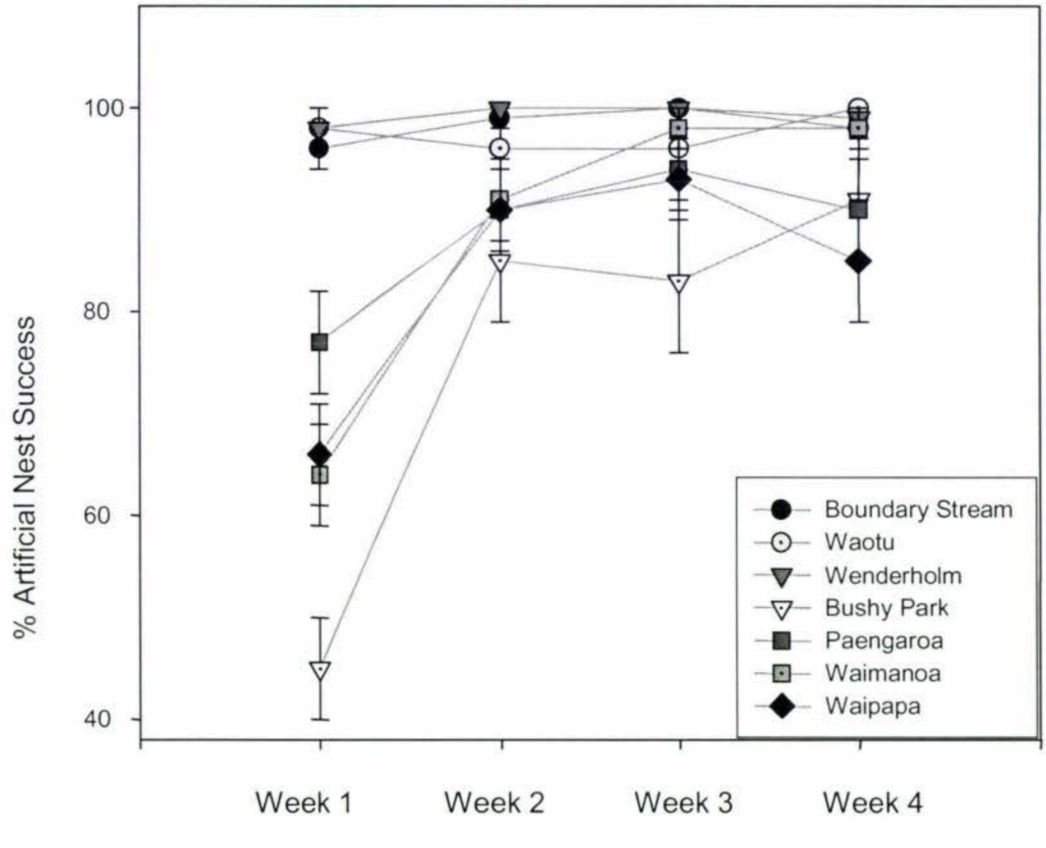


Figure 2. Weekly trends in survival probabilities (% nest success with standard error) for artificial nests, as a result of predation by rats and possums during weeks 1-4 in 7 reserves with and without predator control.

The results from the model selection procedure (Table 2) show the model with the lowest AIC$_c$ resulted from low intensity monitoring i.e. over a 1-week period ($S_n = S_{a1wk}$), indicating an improvement in model fit. The AIC$_c$ weight for this model was 28% higher than that for the $\{S_n=S_{awk4}\}$ model showing strong support for this model. The results from the bootstrap generated data sets provided further support for this result with the $\{S_n=S_{a1wk}\}$ model producing the lowest AIC$_c$ and highest AIC$_c$ weight. The value of the parameter β, 1.134, for the 4 week model increased to 1.87 for the 1 week model, while the value of the parameter intercept 0.510 for the 4 week model was very similar to, 0.509 for the 1 week model (Table 2). These changes in parameter values account for the larger difference between the estimates of natural and artificial nest success for the 1 week versus the 4 week model.

Table 2. Results from AIC$_c$ model selection procedure for 4 week and 1 week monitoring regimes.

Model[1]	***k***[2]	α[3]	β[4]	**AIC$_c$**[5]	**Δ_I**[6]	***w_I***[7]
$S_n=\alpha\, S_{aw4}{}^{\beta}$	3	0.510	1.134	-1.95	1.15	0.36
$S_n=\alpha\, S_{aw1}{}^{\beta}$	3	0.509	1.87	-3.10	0	0.64

[1] Models used to fit relationship between artificial and natural nest success

[2] Number of parameters in model

[3] Model value for intercept

[4] Model value for slope

[5] Aikaike's Information Criterion corrected for effective sample size.

[6] Delta AIC, indicating the difference in AIC value from the best model

[7] AIC weight, calculated from the 5 models run

The results for both the $\alpha\, S_{aw1}{}^{\beta}$ (Figure 3) and $S_n=\alpha\, S_{aw4}{}^{\beta}$ (Figure 4) model show 6 of the 9 estimates of nest success lying within the 95%

confidence interval generated by the bootstrap simulated data sets (denoted by the central dashed line). The nest success estimates with associated standard errors for Karori and Wenderholm sit outside the 95% confidence limit in both models. Nest success estimate for Tiritiri Matangi sits just outside, while the upper error bar sits just inside the confidence limit. Nest success estimates for three (Bs, Wp and Bp) of these reserves are intersected by the original (and bootstrap generated) mean for the 1 week model, for the 4 week model nest success estimates for two (Bp and Bs) of the reserves are intersected. The result is a slight improvement in the fit of the data in the 1-week model resulting in an increase in AIC weight and predictive ability of this model. The aforementioned results are expressed by an increase in correlation co-efficient from 0.61 to 0.67.

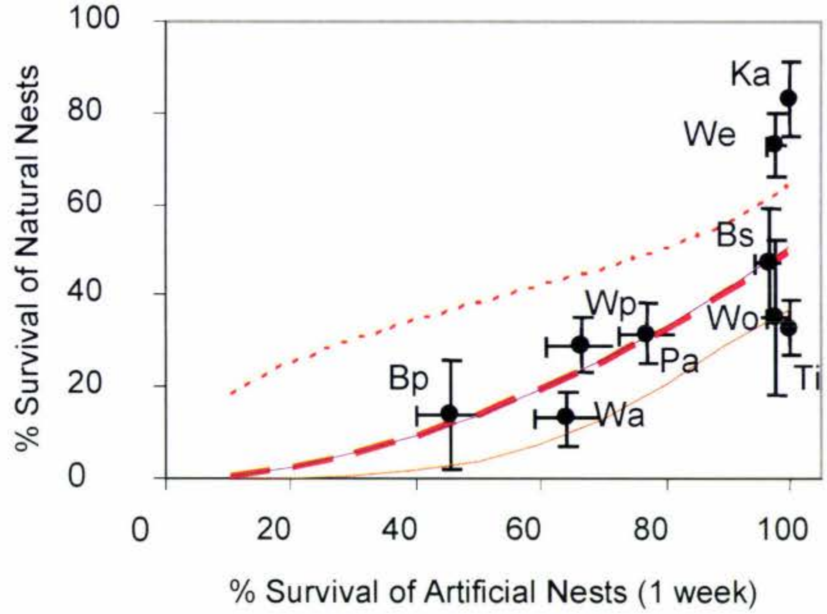


Figure 3. Correlation of one week estimates of nest success (± standard error) for artificial and natural nests resulting from predation by rats and possums. The mean value from the original data set is represented by the central broken line and the mean value from the simulated, bootstrap data set by the solid central line. The 95% confidence limit is represented by the upper and lower broken line (Bs = Boundary Stream, Bp = Bushy Park, Ka = Karori, Pa = Paengaroa, Ti = Tiritiri Matangi, Wa = Waimanoa, Wp = Waipapa, Wo = Waotu and We = Wenderholm).

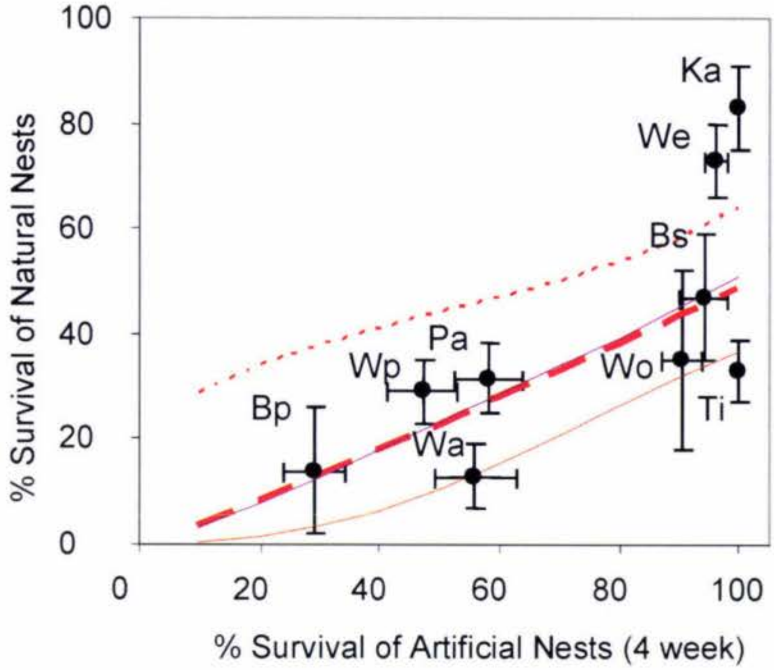


Figure 4. Correlation of four week estimates of nest success (± standard error) for artificial and natural nest resulting from predation by rats and possums. The mean value from the original data set is represented by the central broken line and the mean value from the simulated, bootstrap data set by the solid central line. The 95% confidence limit is represented by the upper and lower broken lineBs = Boundary Stream, Bp = Bushy Park, Ka = Karori, Pa = Paengaroa, Ti = Tiritiri Matangi, Wa = Waimanoa, Wp = Waipapa, Wo = Waotu and We = Wenderholm.

Aim 2: - *The influence of length of exposure period on the ability to identify predators using egg remains*

Overall, from a sample size of 810 nests, 44 received multiple markings, 22 received unknown markings on the clay eggs and 6 nests had missing eggs. The results illustrated in Figure 5 show that the percentage of clay eggs that sustained multiple marks was much lower for eggs exposed for one week (5.9%) than those exposed for three weeks (13.6%). Likewise, the number of eggs with unknown marks was much lower for nests exposed for 1 week (4.4%) than those exposed for three weeks (9%). However, the incidence of missing eggs from nests was higher during the first week of exposure (1.5%) than from nests exposed for three weeks (0.9%).

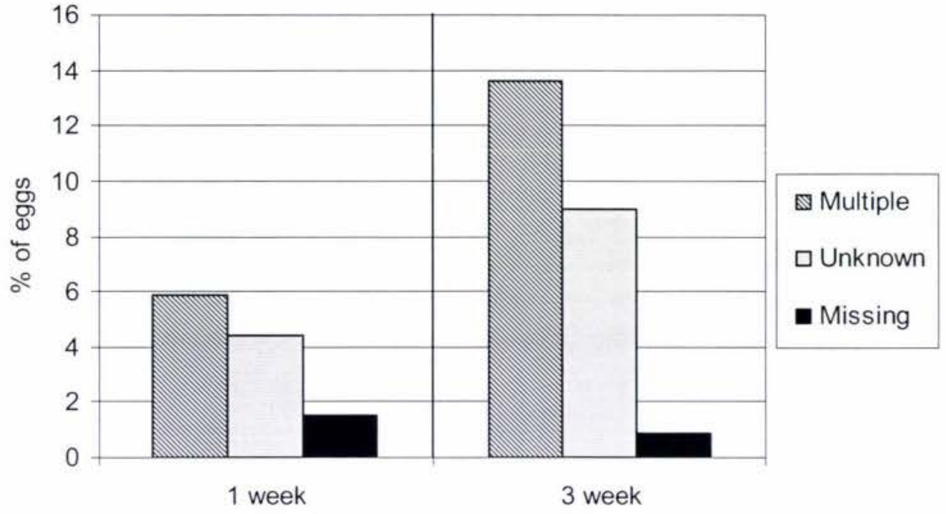


Figure 5. The percentage of clay eggs missing or having received multiple or unknown markings collected weekly and once every three weeks for 9 reserves.

Aim 3: - *The effect of using real eggs versus clay eggs alone on the probability of artificial nest success*

When given the choice of 2 models (previously selected temporal model or egg model) for 'rat and possum', 'rat possum and mice' and avian predator groups for each of the 9 reserves (except Tiritiri Matangi that only has avian predators) the egg combination came out as a significant factor in the model selection 4 times from a possible 25 pairs of models (i.e. 16%).

The egg factor was significant for both the rat and possum and avian predator groups in one of the reserves and for the avian predator group in 3 reserves (Table 3). The AIC_c weight supporting models including egg factor in 3 out of 4 reserves for avian and mammalian predator groups was high (w_i = 89% – 97%), providing strong support for the model selected. This result indicates that egg combination has a significant effect on the likelihood of nest success in these reserves. The AIC weight supporting the inclusion of the egg factor in model selection just held the majority at 59% for Karori reserve suggesting that the inclusion of the egg factor in the chosen model was only marginally better at explaining the variation in the data than the week factor included in the original model selection (see chapter one for original selection).

Table 3. Reserves (and predator groups) where model selection selected egg as an important factor.

Reserve [1]	**Predator group** [2]	**Model** [3]	**No. models run** [4]	**AIC (weight)** [5]
Boundary Stream	rat and possums	(egg+s)	2	0.97
	bird	(egg)	2	0.89
Karori	bird	(egg+s)	2	0.59
Waotu	bird	(egg+w)	2	0.89
Wenderholm	bird	(egg+s)	2	0.97

[1] Reserve from which nest success was estimated

[2] Predator group responsible for nest depredation

[3] Model selected via AIC model selection, used to estimate nest success.

[4] Number of model run for designated reserve and predator group.

[5] AIC weight attributed to the model selected, derived from the comparison of two models.

The egg combination that resulted in the highest nest depredation rate by avian predators was two clay eggs per nest, (in 3 out of 4 cases) and one clay and one quail egg per nest (in 1 out of 4 cases). With the rat and possum predator group the egg factor was included only once in the model selection, with the clay / quail egg combination producing the lowest nest success rate.

There was only a small reduction in nest success for nests with quail eggs compared to nests with two clay eggs in 6 out of 7 reserves (Figure 6). However, the overlap of error bars associated with these estimates, with the exception of Boundary Stream (nest success for the CC egg combination was 100%), illustrates the lack of a significant difference in success estimates resulting from the two egg combinations (i.e. hence there is no large effect undetected via the model selection procedure due to lack of power). For Boundary Stream, the absence of any overlap illustrates that the difference between egg combinations is significant, hence its selection as a significant factor in the model selection results (Table 3). Tiritiri Matangi and Karori were not included because they have no rats or possums.

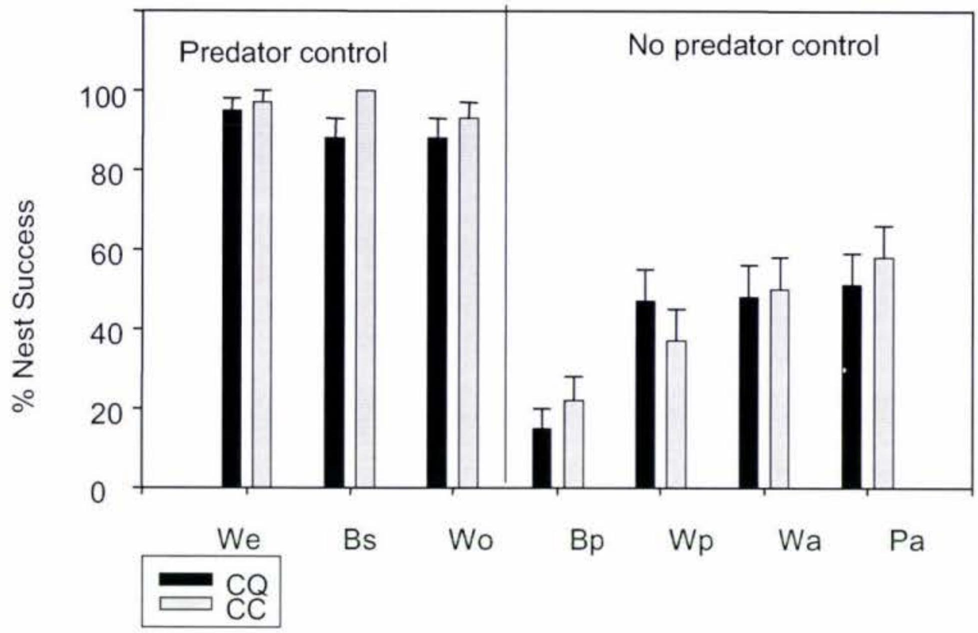


Figure 6. Estimates of nest success for nests containing two clay (CC) and one clay, one quail egg (CQ) resulting from predation by rats and possums. We = Wenderholm, Bs = Boundary Stream, Wo = Waotu, Bp = Bushy Park, Wp = Waipapa, Wa = Waimanoa, and Pa = Paengaroa. Bars show means ± standard error.

The estimates of nest success for nests with quail eggs have a marginally lower success rate resulting from rat, possum and mice predation than nests with two clay eggs (Figure 7) in 6 out of 8 reserves. The overlap of error bars associated with these estimates illustrates the lack of a significant difference in success rates of the two egg combinations. Interestingly, the results from Waimanoa reserve show the reverse pattern to the results for rat and possum depredation, with CQ egg combination now having a higher mean estimate of nest success than the CC egg combination. Tiritiri Matangi was not included because it has no rats, possums or mice.

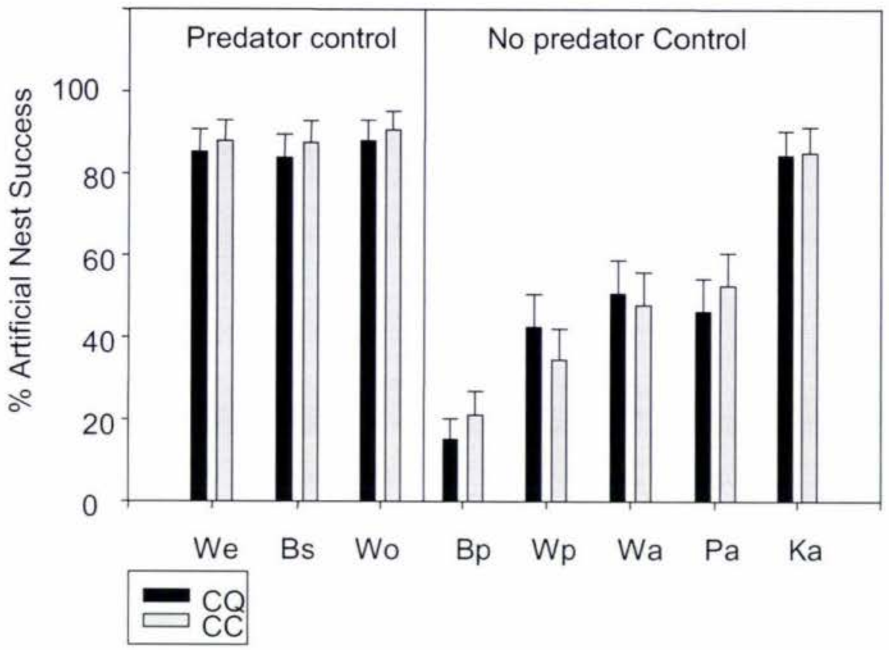


Figure 7. Estimates of nest success for nests containing two clay (CC) and one clay, one quail egg (CQ) resulting from predation by rats, possums and mice. We = Wenderholm, Bs = Boundary Stream, Wo = Waotu, Bp = Bushy Park, Wp = Waipapa, Wa = Waimanoa, Pa = Paengaroa, and Ka = Karori. Bars show means ± standard error.

The estimates of nest success for each egg combination in all the reserves shows that nest success resulting from avian predation is not strongly influenced by any one particular egg combination (Figure 8). While 4 of the reserves show a decrease, the other 5 show an increase in nest success associated with the addition of a quail egg. The overlap of the error bars associated with the estimates from 5 of the 9 reserves illustrates the lack of a significant difference in success estimates of the two egg combinations, hence there is no large effect undetected in the model selection procedure due to lack of power. For Boundary Stream, Karori, Waotu and Wenderholm the estimates with error show no overlapping illustrating that the addition of a quail egg significantly reduced the likelihood of nest survival.

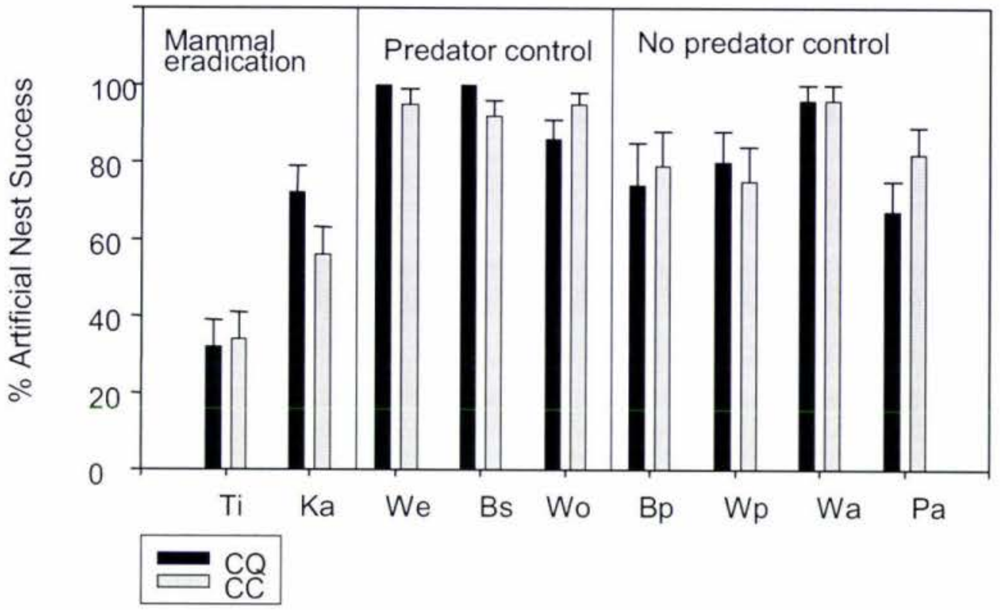


Figure 8. Estimates of nest success for nests containing two clay (CC) and one clay, one quail egg (CQ) resulting from predation by avian predators. Ti = Tiritiri Matangi, Ka = Karori, We = Wenderholm, Bs = Boundary Stream, Wo = Waotu, Bp = Bushy Park, Wa = Waimanoa, Wp = Waipapa and Pa = Paengaroa. Bars show means ± standard error.

Aim 4: - *The ability to identify predator type by using artificial nest and egg and real egg remains.*

Predators were identified through examination of the imprints left on clay eggs in each nest. The percentage of damage done to these clay eggs was not always consistent within and between predator types (Table 4). Rats and possums show potential to inflict a range of damage to clay eggs. The majority of eggs depredated by rats only received damage to 1-10% of the surface area. However, a large number received 71% -100% damage to the surface area.

For mice and birds, the damage done was mainly in the lower ranges where damage was done to 1-30% of the surface area of the clay egg.

Table 4. Percentage of the surface area of clay eggs damaged by rats, possums, mice and birds on visiting an artificial nest.

Predator type	Number. of nests visited.	Damage done to clay eggs (%)				
		71-100%	51-70%	31-50%	11-30%	1-10%
Rat	176	18	15	20	41	82
Possum	5	1	2	2	0	0
Mouse	39	0	0	1	2	36
Bird	129	0	1	9	24	95

A high percentage of rats damaged the quail eggs when they visited an artificial nest (Table 5). The damage they did, in 70% of cases, was only to the surface of the shell, which may not increase egg mortality. However, in 30% of cases, the rat broke the eggshell, which would result in increased egg mortality.

The results obtained from possum nest depredation (Table 5), although through a very low sample size, do suggest that possums are capable of causing significant damage to quail eggs. From this sample of eggs 1 was eaten and 1 was missing. Where the egg was missing possum identification was possible through examination of prints on clay eggs. This outcome can also be seen from the sample of nests depredated by mice as they also show capability (breaking the eggshell) and therefore potential to cause irreparable damage to the quail eggs.

From the sample of quail eggs damaged by birds (Table 4) 44% of the damage was superficial, (scratches on the surface of the eggshell). However, 56% of the damage inflicted was irreparable i.e. breaking the eggshell.

Although the percentage of damage done to the quail eggs differs between predator types, each predator displays the ability to cause irreparable damage to the quail egg (Table 5). The type of damage done is unreliable as an indicator of predator type, as the marks left by both avian and mammalian (rats, possums and mice) predators are similar.

Table 5. Damage done to quail eggs by rats, possums, mice and birds

Predator type	**No. of nests visited with quail egg**	**% times quail egg damaged**	**% damage done**	
Rat	91	75	Scratches	70
			Eaten	30
Possum	2	100	Eaten	100
			Missing	100
Mouse	18	17	Scratches	33
			Hole	67
Bird	57	32	Scratches	44
			Hole	56

A higher percentage of nests depredated by rats were damaged and contained faeces than those depredated by possums, mice and birds (Table 6). All of the nests that contained faecal remains from mice and birds were also damaged. All of the nests that contained faecal remains from rats were not always damaged.

Table 6. Level of destruction to nests and presence/absence of faeces.

Predator	Number of nests depredated	% of nests damaged	% of nests with faeces
Rat	176	7.4	13
Possum	5	0	0
Mouse	39	2.6	2.6
Bird	129	2.3	2.3

Discussion

Aim 1: - *The level of monitoring required to facilitate an accurate prediction of natural nest success using artificial nest success.*

The results of this analysis suggest that it is not necessary to conduct an intense monitoring regime to increase the accuracy of artificial nests when using them to predict natural nest success in New Zealand forest fragments. Support for this conclusion was provided by the significant advantage in AIC weight resulting from an improvement in model fit for the low-intensity monitoring regime, with further support provided by the results of the bootstrap evaluation. This implies that the collection of nest success data following the first week simply added noise to the data set, decreasing the fit of the data to the model. The low success of nests experienced in the first week of exposure may be a consequence of an increased encounter rate resulting from this initial distribution of nests. Also, nests that were more vulnerable to predators would have been taken first. The result is an increase in nest success from week one onwards. The method used to estimate nest success was corrected for effective sample size. However, it was not able to account for this reduction in vulnerability of the nests following the initial losses in the first week of exposure. It is possible that distributing a new sample of nests each week may reduce the difference in absolute values between artificial and natural nest success. However, these results suggest that weekly monitoring provided adequate data to predict natural nest success. These results are consistent with Ortega *et al* (1998) who found that the duration of monitoring intensity was critical, as opposite results were obtained between 5 and 15 -day visits, and predation of artificial nests most closely approximated predation on natural nests at the ten-day visit.

The results of my research also highlight an increase in nest success in all the reserves following the first week of exposure. The weekly pattern of nest success was similar in all reserves but was much less pronounced in reserves with predator control. The reverse pattern observed for Waotu reserve, where nest success was lower during weeks 2 and 3 than in week 1. However the overlap in error bars suggest that this difference was not significant and therefore may be due to random differences, possibly resulting from sampling variation. Although, it is worth considering that the reverse pattern seen for Waotu may be explained by the fact that it is by far the smallest reserve, and its location amidst farmland may make it more vulnerable to sporadic changes in nest success resulting from eruptive populations of rats in surrounding areas invading the reserve.

Changes in nest success over the course of the breeding season were found in this research. Seasonal fluctuations in nest success have also been documented for natural robin nests (Armstrong *et al.*, 2002c) and in previous research using both artificial (Weidinger, 2001; Roos, 2002;) and natural nests (Palomino *et al.*, 1999; Clausen *et al.*, 2001; Drachmann *et al.*, 2002). Not all of the reserves in this research showed the same pattern of seasonal fluctuation in nest success. Nest success in Paengaroa reserve was at its lowest during the late stage of the breeding season. The reason for this may be due to the fact that predator control in Paengaroa reserve was discontinued earlier in the same year that this research was carried out. As a result, rat numbers may have been lower during the early stages of the breeding season, contributing to a higher nest success, and gradually climbing in numbers towards the end of the season (without the restraints of predator control) resulting in lower nest success. Without continued monitoring over the breeding season this inconsistency would not have been detected, hence the importance for monitoring procedure to include periods throughout the season. When monitoring indicates seasonal changes in nest success, predator control can then be adjusted accordingly. Reserves with predator control implemented throughout the breeding season exhibited a similar within-season trend in predation. However, nest success was higher during each period (early middle and late) than in reserves with no predator control, resulting in a higher overall nest success. It is therefore sensible to commence a predator control regime before the beginning of the breeding season to reduce predator numbers before the bird's start nest building.

Variations in the rate of nest success found throughout the breeding season may be dependant on a combination of changes in activities, diets, numbers, or species of predators (Nolan, 1963). For example, different patterns of threat throughout the season may be predicted depending on whether the prey species is primary prey or secondary prey (Jones, 2003; Salek *et al.*, 2004). Rats are the main predators in all of the reserves with mammalian predators and their diet is composed mainly of invertebrates and fruits, the proportions of which vary seasonally (King, 1990). Sudden environmental changes e.g. extended periods of frost or flooding resulting in fruiting failure and an impoverished invertebrate community, may lead to a dramatic increase in nest depredation rate as species relying on these sources turn to their secondary food supply (e.g. eggs and nestlings) to subsidise their food intake. Crabtree and Wolfe (1988) attributed a seasonal decline in artificial nest success to increased incidental nest predation resulting from an increased effort in foraging by skunks for invertebrates. Conversely, an abundant primary food supply can lead to an increase in fecundity of nest predators which may inevitably lead to an increase in the probability of incidental nest predation. Rats are known to be particularly receptive to marked increases in food supply, responding with eruptive population growth (Alterio *et al.*, 1999; Blackwell *et al.*, 2003).

Landscape composition surrounding reserve areas may also be important to consider when deciding the monitoring intensity required. Rodewald and Yahner (2001) found nest success of songbirds to be lower within forested landscapes disturbed by agriculture, and suggested that landscape composition within forested landscapes significantly influences avian nest success by altering interactions between nest predators and nesting birds. When forest fragments are surrounded by agricultural land an increased yield may dramatically increase food availability and predator numbers in these surrounding landscapes. When food supply begins to fall these predators may then move into the forest to forage (Rodewald, 2003). The seasonal fluctuations in nest success resulting may then depend on the timing of certain types of crop grown in the surrounding farmland.

The beginning and duration of a species' nesting season are important to overall reproductive performance. It determines the climatic conditions, or range of conditions, the young must cope with, and whether sufficient time is available to the adults for raising more than one brood or re-nesting after nest failure (Roseberry, 1970). It is therefore important to be able to detect the factors that may affect levels of nest success throughout this period. Implementation of a programme of monitoring that will detect such changes is an integral part of population conservation. Artificial nests used to monitor nest success at the beginning, middle and end of the breeding season (whilst maintaining consistency between years) may account for the variability.

The amount of time, effort and financial input required to use artificial nests as a monitoring technique is also important. The results of this research suggest that monitoring once a week three times during the season was enough to facilitate sufficient monitoring while providing a low intensity and financially viable monitoring technique.

Aim 2: - *The influence of exposure period on the ability to identify predators using egg remains*

The results of this analysis show that the amount of time artificial eggs are exposed for has important consequences for artificial nest use as a reliable monitoring technique. These results also provide further support for the low intensity monitoring regime discussed previously. Extending the exposure period from one to three weeks increased the number of incidences where eggs were found with multiple and unidentifiable markings. The most significant consequence of these findings is the inability to link particular predators to depredation events.

Eggs with multiple markings made by more than one species made positive identification of predator type difficult due to an increased level of destruction and obscured and overlapping prints. The result is an inability to implicate a particular species of predator to the initial depredation event, making it impossible to identify which predator poses the highest threat. Artificial nests are more susceptible to depredation from a whole host of opportunistic predators that may not pose a threat to natural nests protected by parents (Maxson & Oring, 1978; Major & Kendal, 1996). Many of these predators may be able to cause significant damage to artificial eggs, and when the predator community is relatively unknown, this may result in the inclusion of such depredation events in the estimation of nest success. Therefore, while some of the marks may be from high-risk predators, others may be from opportunists taking advantage of an undefended nest (although the benefits of parental defence have been questioned by Guillory (1987) and Pietz & Granfors (2000). Increasing the exposure time increased the risk of such predators visiting the nest and obscuring marks made by high-risk predators. The result would be an underestimation of nest success by high-risk predators and result in confusion when assigning a particular type of predator control. Weidinger (2001) reported that uncertainty in identification of predators and multiple markings on artificial eggs precluded statistical testing of the data. However, the majority of previous studies fail to report on the number of multiple marked eggs, preventing comparison between studies.

The results also show that the number of unknown marks on clay eggs increased with an extended period of exposure. Unknown markings are often the result of debris falling into the nest or weather damage (e.g. disintegration of the clay). The longer the eggs are exposed for, the more chance that they will be marked in such a manner. Collection of such eggs whilst monitoring is being carried out can substantially reduce the sample size, leaving less power for statistical inference and the possibility of inaccurately estimating nests success through misidentification of such markings. Additionally, unknown marking from high-risk predators may have worn down due to weathering of marks during the increased exposure time, making them less recognizable and more likely to be classed as unknown. The result may be an underestimation of nest success resulting from nest depredation by high-risk predators, a mistake that could have grave consequences for the mortality of the species under protection. Mathews *et al.* (1999) recorded the incidence of unknown markings accounting for 29.1% of predation events following a 15 day exposure period. However, in the majority of studies the number of unknown markings is unreported.

Contrary to the above findings, the percentage of nests found with missing eggs decreased with an increase in exposure time. It may be possible that the extended exposure may have resulted in egg decay, deterring predators from removing eggs from nests visited. The sample used for the three-week exposure period encompassed those that remained after each seasonal period trial (i.e. each 4-week block early, middle and late in the season). It is therefore possible that eggs that were easy to remove (e.g. slightly smaller quail eggs or less efficiently secured clay) were removed during the seasonal period trials, whereas those that remained for the 3-week exposure trial were more of a challenge to remove and as a result remained in the nest. The likelihood of an egg going missing at each site may depend on the capability of the predator defending the territory containing an artificial nest site. If the resident predators, unable to remove eggs from the artificial nest, retained their territories throughout the three-week trial, the number of missing eggs would potentially remain constant. In situations where the resident predator is displaced by a larger mammal the percentage of eggs missing could potentially have been greater. It may be that, as the number of eggs in this sample marked by previous nest visits increased, the appeal of the eggs decreased. It is interesting to note that the percentage of eggs missing within each exposure period was relatively low, thus suggesting the effort required to remove the eggs often outweighed the gain. Gardner (1998) reported 16 cases when both eggs were missing from the nest, preventing predator identification, resulting from nest checks and collection of depredated eggs occurring every 3 to 7 days.

The amount of time available to any monitoring body will guide its decision as to which monitoring technique it uses. It is apparent from these results that the amount of time that artificial nest are exposed for is crucial to the identification and analysis of risk by predator types. It is therefore important that artificial nests are checked at least weekly to reduce the amount of bias introduced through the misidentification and accumulation of unknown markings. The type of clay used to make artificial eggs may influence their longevity in the field, affecting the clarity of marks (Fulton & Ford, 2003). However, it cannot change the amount of eggs marked by falling debris. Replacing quail eggs with clay eggs may eliminate the problem of egg decay, but may also introduce a bias in the type of predator that is attracted to the nest. With regards to missing eggs, this may depend on the predator community involved, e.g., larger predators may cause more damage and be capable of removing more eggs with an increased exposure time. With this in mind it is advisable to attach at least one of the eggs to the nest to enable identification of the predator. Additionally, when predator numbers are high, the incidence of multiple marked and missing eggs may occur over a shorter period of time.

Aim 3: - *The effect of using real eggs versus clay eggs alone on the probability of artificial nest success.*

Real eggs are frequently used in artificial nest experiments in an attempt to mimic the cues such as smell and appearance that may influence predation in natural nests. The results of this analysis suggest that the type of egg used in artificial nests does not bias the probability of nest success resulting from predation by mammalian or avian predators. Although the model selection procedure found egg type to be an important factor contributing to the probability of nest success in one reserve (Boundary Stream) in the mammalian predator group (MPG) and in 4 of the reserves (Boundary Stream, Karori, Waotu and Wenderholm) in the avian predator group (APG) the number of times 'egg' was selected as a significant factor overall was low, and the direction of difference was not consistent within predator groups.

Boundary Stream reserve has a low incidence of nest depredation by rats, so it is possible that the significance of the egg factor, selected via the model selection procedure, may have been a chance occurrence as this result was not supported by reserves with a higher incidence of nest depredation by rats. For example, in Waipapa, Waimanoa, Paengaroa and Bushy Park reserves, nest depredation by rats was high but the egg factor was not a significant contributing factor influencing nest success. This result was surprising for the mammalian predator group as they are assumed to detect food sources using olfactory cues, which in this experiment would have been supplied by the addition of the quail egg. Higher predation rates of nests containing quail eggs only have been reported in previous studies (Small & Hunter, 1988; Wilcove, 1985). However, support for the result in this research is provided by Major *et al.* (1994) who found that artificial nests containing clay eggs suffered very similar rates of predation as natural nests of the New Holland honeyeater (*Phylidonyris novaehollandiae*). Previous research has also suggested that the odour from clay eggs may be responsible for preferential depredation of nests containing clay eggs (Rangen *et al.*, 2000).

However, evidence to the contrary was found by Bayne and Hobson (1999), supporting the lack of a bias in nest depredation in artificial nests containing only clay eggs.

Despite all attempts to avoid the transfer of human scent during the research it is possible that human smell may have contaminated the real eggs. Human odour may have masked the natural odour or human scent may have influenced predators' attraction to each of the nest sites indiscriminate of the nest egg-combination (MacIvor *et al.*, 1990; Reitsma *et al.*, 1990). Whelan *et al.* (1994) found that olfactory searching predators can cue on human odours left in the area of artificial nests suggesting that scent does influence the probability of nest depredation. However, Skagen (1999) found no evidence to suggest that human scent trails or trails created by trampled vegetation lowered nest success, rejecting the suggestion that human scent may detract from any influence of egg type.

In Karori, Boundary Stream and Wenderholm, nest success resulting from depredation by birds was higher in nests containing both a quail and clay egg (CQ) than those with two clay eggs (CC). The significance of this preference in egg type for birds is further substantiated by the result from Karori, which has a dense population of birds. However, for Tiritiri Matangi which has an equally dense population of birds, the egg factor was not selected as significant and in Waotu reserve it was the CC egg combination that significantly increased nest success. Despite the fact that most of the marks made on the eggs were identified as being from robins and other similar sized species it was assumed that the less cryptic clay egg combination would be more attractive to all visually searching avian species. Therefore this sample would represent the risk from avian predators in general. The results would suggest that egg combination is an important factor influencing nest depredation by small avian species suggesting that differences between preferences for egg combination may be instead attributable to circumstances within each reserve.

Tiritiri Matangi has a very dense population of small avian species and numbers of some species are encouraged through supplementary feeding. High numbers may mean that in this reserve encounter rates of nest are very high, indiscriminate of egg combination. Waotu reserve is the smallest reserve and is composed of two small and one larger fragment. This small size and fragmentation may mean that it is subject to intrusions from avian species more common to open areas depredating nests. Andrén (1992) found that the density of corvids increases as forests become more fragmented and intermixed with agricultural land, causing an increase in nest predation. If different species of avian predators are attracted to different types of eggs, then preferences for egg combination may depend on the avian community within each reserve. However, due to the small proportion of depredated events attributed to large avian predators the answer to this question goes beyond the scope of this research. It is also possible that if the clay eggs are indeed more attractive to avian species the presence of one or two clay eggs makes the nest just as attractive. Alternatively, research has shown that certain avian species can remember nest sites and learn to use human cues for locating nests (Anderson, 1977; Gotmark *et al.*, 1990) hence the risk of nest predation may not be connected with a particular preference for egg type but on the level of disturbance near the nest.

The effect of confounding factors may have influenced the risk of nest depredation, concealing any effect of egg type. For example, although all efforts were made to conceal human scent from artificial nests there is still a possibility that it may have contaminated the nests, attracting or deterring mammalian predators equally to all nest sites. The effect of research activity, i.e. weekly nest checks, may also have inadvertently attracted or deterred predators from the nest site. However, the protocol used in this study was designed to avoid the creation of trails by approaching the nest from a different direction with each nest check.

When deciding whether to use real eggs it is also worth considering learning processes of predators and the way they search for prey. It is possible that predators will learn through reward. For example, if they are continually visiting nests with clay eggs they may learn that there is no reward. Long-term use of artificial nests with only clay eggs may become less efficient at predicting natural nest success over time as predators learn that there is no reward to be gained, so avoid such nests. The next logical step would be to run field trials to test the effect of predator learning under the 'reward hypothesis' to see if the depredation rate decreases over a number of trials.

Handling real eggs in any monitoring technique can be problematic due to their fragility and longevity (although see DeGraaf & Maier, 2001). Artificial eggs can be moulded to the required dimensions and can be produced in any colour, whereas finding real eggs of similar size, shape and colour is highly problematic. The results of this study, while providing a result that escapes the necessity for real eggs in artificial nests, is not free of confounds that may reduce the confidence in the result obtained (e.g. odour from clay eggs attracting predators).

Aim 4: - *The ability to identify predator type by using artificial nest and egg remains.*

The results of this analysis show that the large size of quail eggs does not prevent the smaller mammalian predators i.e. mice, from destroying them in artificial nests. Each of the predator groups (which included both small predators, i.e. mice, and large-mouthed predators i.e. rats) was able to perforate the eggshell hence destroying the egg. This result is supported by previous research indicating that size of eggs has little influence on predation (Craig 1998; Lewis & Montevecchi 1999).

The issue of egg size is a deemed as important among researchers, and as a result is developing its own body of research solely dedicated to answering this question. The question often raised is whether small-mouthed predators are able to damage larger, thicker shelled quail eggs often used in artificial nest experiments (Haskell 1995; Lewis, 1999; Maier & Degraff 2000). If they are unable to do so then using these larger eggs may drastically underestimate the role of small-mouthed predators as nest predators, therefore excluding a potentially major mortality factor. The disparity in size between quail and passerine eggs has recently been emphasised because potential predators such as mice have a mouth wide enough to open passerine eggs, but insufficient to break quail eggs (Roper, 1992; Haskell, 1995; DeGraaf & Maier, 1996; Bayne & Hobson, 1997; Ettel *et al.*, 1998; Lindell, 2000). Craig (1998) provided evidence to show that mammals destroyed larger eggs by using the cup of the nest as leverage to break open the eggshells. It has also been suggested that the shape of the egg was important rather than the overall size, as small-mouthed predators were found to break the shell by focusing on the small end of the egg (Craig, 1998).

The type of damage that was done, superficial or detrimental also varied little between the predator groups. As a result, identification of predator type using signs of damage done to both quail eggs and nests was ultimately unreliable. Research by Brown *et al.* (1996) demonstrated an ability to differentiate between predators by the remains left following nest depredation by rats and possums through analysis of video footage of nest depredation events. However, without the backup of video footage, allowing positive identification, this method remains unreliable (Marini & Melo, 1998; Lariviere, 1999). Clay eggs, however, were found to be a useful tool for identifying predator type and the amount of damage done may provide some information as to the predator type. It is therefore important that clay eggs are included as a component of this monitoring technique. It is equally important to secure clay eggs to the nest, as rodents often transport eggs for long distances and makes it difficult to recover the remains of the eggs (Maxson & Oring, 1978; Boag *et al.*, 1984).

The results, based on visits to artificial nests, show that rats and possums were more likely to damage the quail egg than birds and mice.

Although the results show that all groups are able to damage quail eggs, the effort required to break into a quail egg may be greater for mice and birds. Rangen *et al.* (2000) reported that handling times required by captive mice to break finch eggs were substantial (15 to 40 minutes). The amount of effort that they are willing to invest may depend on the availability of other food sources, how hungry they are (Bradley & Marzluff, 2003) and whether or not they are disturbed by other intruders while in the nest.

The results from the analysis of clay eggs suggest that the amount of damage done to the eggs may exhibit a moderate difference between predator types. While the damage done by rats and possums ranged from complete obliteration to small marks, damage done by mice and birds usually consisted of only a few small marks. An explanation for this pattern may be related to the amount of effort required for the predator to damage the egg. For example, a mouse may experience higher resistance from the clay than a rat, so the effort required to bite into it will be greater. Consequently, mice may leave fewer bite marks. Additionally, small-mouthed mammals did not always leave marks on eggs they attempted to consume. For clay eggs marked by birds, the explanation for the smaller amount of damage done may relate to the intention behind the depredation. Birds depredating the nests may not have been doing so for the purpose of gaining a meal but to destroy the competition, hence a simple hole in the surface would suffice. Simons and Simons (1990) observed that cactus wren (*Campylorhynchus brunneicapillus*) destroyed nests but did not consume egg contents, and suggested that nest attacks represented competitive behaviour rather than predation.

Alternatively, the amount of damage done may be a measure of the predators' own susceptibility to predation. Rats in New Zealand forests have only a small number of predators and are therefore unlikely to be chased from a nest site, leaving them longer to spend inflicting damage to the eggs. Mice and birds are both susceptible to predation by rats and may be more easily disturbed from the nest site, leaving them less time to inflict damage to the eggs (hence fewer marks left on eggs). Possums, being the largest predators to depredate the eggs, are less susceptible to predation and inflict damage on eggs without being disturbed.

Overall, the results from depredated nests show that only a small proportion of the nests visited were damaged or contained faeces for all of the predator groups. It is therefore impossible to connect a depredation event to the predator responsible simply by looking at the evidence at the nest site, as in the majority of instances, all predator groups' depredated nests without leaving any sign. The higher incidence of damage and deposition of faeces in nests depredated by rats may be representative of their status, as mentioned above. It is therefore important to consider the predator community you are dealing with when considering the amount of damage done to artificial nests.

In summary the results of this research suggest that; (1) it is not necessary to conduct an intense monitoring regime to increase the accuracy of artificial nests when using them to predict natural nest success in New Zealand forest fragments (leaving nests out for one week rather than four weeks increased the accuracy of the technique), but nests should be monitored at regular intervals over whole breeding season since predation rates change seasonally; (2) the amount of time artificial eggs are exposed for has important consequences for artificial nest use (leaving them out longer before checking increases the chance of the marks becoming obscured, hampering predator identification); (3) the type of eggs used (real or artificial) in artificial nests does not bias the probability of nest success resulting from predation by mammalian or avian predators (adding a quail egg has little effect on predation rate, particularly on the rate of predation by mammals). Implying that olfactory cues associated with egg type were not an influential factor affecting artificial nest success; and (4) It is necessary to include clay eggs in artificial nests as marks left on quail eggs and damage done to artificial nests were not reliable indicators of predator type. Additionally, egg size has a limited effect on the ability of the predator to cause detrimental damage to the eggs in artificial nests, as each predator group was able to penetrate the shell of the larger quail eggs.

APPENDIX

Table 1. Results showing estimates of nest success (and associated standard error) for each egg type.

Reserve	**Predators**	**[1]CQ**	**se**	**[2]CC**	**se**
Boundary Stream	rat and possum	88	0.03	1	0.03
	bird	1	0.00	92	0.04
Bushy Park	rat and possum	15	0.05	22	0.06
	bird	74	0.11	79	0.09
Karori	rat and possum	N/A	N/A	N/A	N/A
	bird	72	0.07	56	0.07
Paengaroa	rat and possum	51	0.08	58	0.08
	bird	67	0.08	82	0.07
Tiritiri Matangi	rat and possum	N/A	N/A	N/A	N/A
	bird	32	0.07	34	0.07
Waimanoa	rat and possum	48	0.08	50	0.08
	bird	96	0.04	96	0.04
Waipapa	rat and possum	47	0.08	37	0.08
	bird	80	0.08	75	0.09
Waotu	rat and possum	88	0.05	93	0.04
	bird	86	0.05	95	0.03
Wenderholm	rat and possum	95	0.03	97	0.03
	bird	1	0	95	0.04

[1] One clay and one quail egg in nest

[2] Two clay eggs in nest

Chapter Four

The influence of habitat structure on the probability of artificial nest depredation by avian and mammalian predators in New Zealand forest fragments: consequences for using artificial nests.

ABSTRACT

The aim of this research was to assess the effect of habitat structure on artificial nest predation. The experimental procedure was conducted as part of a larger project focusing on artificial nests as a technique of monitoring natural nest success. The focus of this chapter was to (1) highlight influences of habitat structure that may confound the use of artificial nests as an accurate predictor of natural nest success; (2) establish whether distance to bait station may influence nest success, confounding interpretation of habitat structure influences on nest success. The influence of habitat was quantified on both the macro- (individual reserves) and microhabitat (individual nest sites) scale and related to nest success from individual reserves and individual nest sites. Quantifying the influence of the structural composition of habitat at nest sites on nest survival has previously been analysed using linear statistics. For this research, a non-linear ordination technique, non-metric multidimensional scaling (nMDS), was used as an alternative method of analysis to visualize differences in habitat and relate them to differences in nest success.

The results of this research revealed: (1) no strong or consistent evidence to suggest that the fine-scale structural composition of habitat components at nest sites had a significant influence on the probability of nests being depredated by either mammals or birds; (2) reserve size may confound interpretation of the results of the microhabitat analysis by exerting an additional influence on nest success resulting from rat and possum predation but not bird predation, and; (3) the vicinity of individual nests to a bait station may influence the probability of nest success. The variability in nest success between reserves must therefore be due to factors other than those measured in this study, i.e. influence from surrounding landscape. The resulting implication for artificial nests as a technique for monitoring natural nests is that differences between estimates of success between the two nest types may be due to factors such as nest height, parental defence or nest failure resulting from depredation by different predator groups.

INTRODUCTION

Nest failure resulting from predation is recognised as one of the major causes of nest failure in birds (Skutch, 1947; Ricklefs, 1969; Rotenberry & Wiens, 1989; Martin, 1993b; Soderstrom, 1999). However, the severity of predation pressure may depend on the structure of the habitat. Habitat structure may influence nest survival directly, by providing suitable living space and food supply, or indirectly by providing an environment that either increases or reduces the risk of predation. Assessing the nature of the relationship between artificial nest success and habitat is important to consider when using artificial nests to assess the predation pressure on natural nests. If the fate of an artificial nest is dependant on the structure of the habitat in which it is placed, inferences concerning the risk for natural nests may then be confounded by differences between habitat characteristics surrounding artificial and natural nests.

The influence that habitat structure has on nest success may also depend on how each predator type i.e. mammalian or avian perceives and responds to habitat characteristics and how this links to its efficiency as a nest predator. Predators that use olfactory cues may be influenced in a different way by habitat structure than those that use visual cues and those that have an arboreal lifestyle may be influenced in a different way by habitat structure than those that have a terrestrial lifestyle. Birds have been recorded placing their nests under or in specific plants, suggesting that they were choosing specific vegetation that may directly influence nest survival (Martin, 1993c). Several investigators (Duebbert & Lokemoen, 1976; Livezey, 1981; Hines & Mitchell, 1983) posit that tall, dense vegetation establishes visual and scent barriers between predators and nests, and serves as an impediment to mammalian movement (Crabtree *et al.*, 1989). Determining relative risk therefore requires knowledge of both the predators involved and the structural attributes within the habitat that are influencing the risk of predation by each predator type.

Many studies have shown the importance of nest-site characteristics in determining nest predation in natural nests (Wray & Whitmore, 1979; Livezey & Humphrey, 1986; Nias, 1986; Moller, 1988, 1989; Wada, 1994) and artificial nests (Martin, 1987; Moller, 1987; Seitz & Zegers, 1993; Sugden & Beyersbergen, 1987). High nest success rates have been found to occur more frequently in a habitat with a high degree of structural diversity ((Bowman & Harris, 1980; Brown *et al.*, 1998; Crabtree *et al.*, 1989; Fleming & Giuliano, 2001; Ratti & Reese, 1988; Yahner & Wright, 1985). Topographical differences in aspect (McShea, 2000), incline (Elliott, 1992; McShea, 2000) and presence or absence of waterways (Saracco & Collazo, 1999), may, through their effect on plant growth (Elliott 1992) and stability of ground surface, create either suitable or unsuitable habitat for both predators and prey. Characteristics of the canopy, understorey, species richness, vegetative density, patch size and minimum distance to water and dyke width were found to be significant determinants of the fate of a nest (Yahner & Wright, 1985; Sugden & Beyersbergen, 1987; Yahner & Cypher, 1987; Crabtree & Wolfe, 1988; Martin & Roper, 1988; Leimgruber *et al.*, 1994; Delong *et al.*, 1995; Taylor & Ford, 1998). Fine-scale structural differences such as the texture of the tree trunk surface and girth of the tree may influence access to the nest by predators, hence nest survival by making the tree harder or easier to climb.

The aim of this research was to assess the effect of habitat structure on artificial nest survival resulting from predation by avian and mammalian predators. This experimental procedure was conducted as part of a larger project focusing on artificial nests as a technique for monitoring natural nest success. Artificial nests were positioned within each reserve in sites that resembled those chosen by the model species. Any variation in habitat structure surrounding these artificial nest sites (with the exception of nest height that was controlled to allow for efficiency of nest monitoring) was therefore influenced by its suitability as a nest site for the model species. The focus of this study was to; (1) establish whether distance to bait station influences the probability of nest success (confounding interpretation of habitat structure influences on nest success); (2) highlight external influences from habitat structure from within this sample, which may confound and therefore limit the use of artificial nests as an accurate predictor of natural nest success. The influence of habitat was quantified on both the macro- habitat (individual reserves) and microhabitat (individual nest sites) scale and was then related to nest success from individual reserves and individual nest sites respectively. Quantifying the influence of the structural composition of habitat at nest sites on nest survival has previously been analysed using linear statistics. For this research, a non-linear ordination technique, non-metric multidimensional scaling (nMDS), was used as an alternative method of analysis (McCune and Grace, 2002). This non-parametric technique enabled non-linear relationships to be revealed, and allowed for visual examination of structural similarities in the habitat found between both reserves and individual nest sites.

METHODS

The sampling procedure using artificial nests, for which this chapter is based, is outlined in Chapter 1. Reserves used in this chapter included all but one (Wenderholm) of those used in Chapter 1, as I was unable to collect habitat data from this site. Individual nests within reserves that failed throughout the entire period of artificial nest exposure as the result of depredation by predators other than the one of interest were excluded from the sample (e.g. eggs removed from artificial nests following depredation by mice in each exposure period were excluded from the analysis when looking at nest success resulting from rats and possums only). Additional techniques relevant to this chapter only are detailed below.

Habitat measurements

Measurements of habitat structure were taken from 229 nest sites within 8 reserves located around the North Island of New Zealand. Nine habitat components were scored from around each nest site. The percentage of leaf litter and undergrowth cover (up to 1 m tall) and the height of the canopy and nest tree (m) were assessed visually. Distances to nearest clearing, waterway and bait station were allocated into one of three categories, (1) 10 m from the nest site, (2) within 75m radius from the nest site and, (3) outside a 75m radius from each nest site (Table 1). The distance of each nest to the edge of the forest fragment was measured using a hip chain. Aspect and incline were measured using a compass and plumb line, with incline measured in degrees and aspect categorized according to its orientation and subsequent exposure to the sun (i.e., orientation of slopes resulting in maximum exposure to direct sunlight, categorised as dry and those with minimum categorized as wet) (Table 1). The trees in which the nests were placed were categorized as large (>10m), medium (6-10m) and small (<6m) with rough or smooth bark, or as Tree Ferns (Table 1).

Table 1. Categories used to classify 5 of the 9 microhabitat components scored from each nest site in all reserves.

Microhabitat Component	Category	Category description
Aspect	0	Flat
	1	Wet
	2	Dry
Distance to clearing, waterway, bait station (m)	0	<10
	1	<75
	2	>75
Tree Type	1	Small tree, rough bark
	1.5	Medium tree, rough bark
	2	Large tree, rough bark
	2.5	Small tree, smooth bark
	3	Medium tree, smooth bark
	3.5	Large tree, smooth bark
	4	Tree Fern.

Bait Stations

Mammalian predators were controlled in 5 of the 8 reserves; this control was done using poison bait stations. Bait stations contained brodifacoum cereal pellets or cyanide paste. Animals consuming a lethal dose of brodifacoum may take several days to die, whereas those consuming cyanide are killed immediately. As the vicinity of individual nests to bait stations was believed to have the potential to influence nest mortality, confounding any influence of habitat structure, the existence of any relationship was tested to eliminate potential bias in the results prior to the ordination analysis. Bait stations are not expected to attract or deter birds; however, in the event that they attracted mammals it is conceivable that the increased presence of mammals at the site may have acted as a secondary deterrent for birds. The influence of bait station was therefore tested for both mammalian and avian predator groups.

Statistical Methodology

The following analytical steps were carried out for mammalian (rats and possums) and avian predators separately.

The influence of distance to bait station on nest success

To determine the effect of distance to bait station on nest success, the average weekly survival probability was calculated for individual nests (Mayfield method, see below) located in three categories: > 75 m, 10-75 m, and < 10 m from the nearest bait station.

The influence of microhabitat on nest success

Non-metric multidimensional scaling (nMDS) was used to assess whether nest success was related to the overall structural composition of 9 habitat components measured at each nest site, and if so, which variables contributed the most to this relationship. General relativisation was used to transform all of the habitat measurements to a value between 0 and 1 to reduce the possibility of individual habitat components obscuring information from the bulk of the data. Habitat structure and nest success estimates were converted to similarity matrices using the Bray-curtis similarity coefficient, and then ordinated using nMDS. Determination of significant relationships between habitat structure and nest success was assessed using correlation analysis.

Outlier analysis was used to highlight individual outlying nest sites from the sample. All nests recognized as outliers were assumed to exhibit relatively unusual habitat structure, e.g., very low canopy or close proximity to the bush edge. When conditions within the habitat become less favourable (e.g., due to reduction in area resulting from habitat fragmentation) the number of preferred nest site locations may be reduced. As a result, birds may be forced to nest in areas with less favourable characteristics for example those found near canopy openings at forest edges (Latta, 1995). If a nest was recognised as an outlier, it was retained in the ordination but the association between such structurally unusual nest locations and nest success was determined to assess further the significance of placing nests in such locations. This was done by looking for any similarity between nest success estimates for these outlying nests and the remaining nests from the sample.

The influence of macrohabitat on nest success

Sizes of the reserves in the sample ranged from 35 to 4000 ha, adding a confounding factor to be considered when assessing the influence of the fine-scale habitat structure on nest success. To assess the possible influence of reserve size on nest success, the nest success calculated for each reserve (using MARK, see chapter one) was plotted against reserve size.

Variety in habitat structure between nest sites within reserves may reduce the possibility of predators developing a search image for a particular nest site, increasing their efficiency as nest predators. To test for this, the range in habitat structure surrounding nests found in each of the reserves was illustrated by plotting the scores generated from the ordination of habitat components. Any dissimilarity in the range of nest site structure between reserves was then related to nest success to check for any discontinuity between reserves.

Nest success

For analysis of the influence of habitat structure at individual nest sites, it was necessary to estimate nest success for each nest. Weekly nest success estimated for individual nests resulting from predation by mammalian (rats and possums) and avian predators was estimated separately for each predator group over a 12-week period using the Mayfield method (Mayfield, 1975). Using this method, daily survival probability is estimated from the total number of failures and the total number of days nests were exposed to predation, using the equation:

$$\hat{p} = 1 - (\text{losses}/\text{exposure days})$$

where p is the daily survival rate, losses is the number of failed nests, and exposure is the total number of days the nests were exposed. I used $\hat{p}^7$ to obtain an estimate of weekly rather than daily survival probability. The total number of days included only those where nest failure resulted from predation by the predator of interest. The likelihood of nest success was estimated using weekly nest checks conducted over 3 individual, 4-week periods (beginning, middle and end of the breeding season) separated by three week intervals.

To illustrate patterns in nest success in the ordination, nest success was treated in one case as a continuous variable (Mayfield estimates) for statistical assessment of relationship and in another as a categorical (category 1 >50%, 2 <50% nest success) variable for illustrative purposes.

RESULTS

Mammalian predators

Influence of distance to bait stations on nest success

Analysis of nest success resulting from predation by rats and possums in the three reserves with bait stations (Boundary Stream, Bushy Park and Waotu) found that average weekly survival probability 99% for nests > 75 m from a bait station, 81% for nests 10-75 m from the nearest bait station, and 72% for nests < 10 m from a bait station, and as a result may confound any observable effects that habitat structure has on nest success. Consequently, for the rat and possum predator group, no further habitat analysis was carried out on data from reserves with bait stations.

The influence of microhabitat on nest success

Outlier analysis using Sorensen distance measure, given a cut-off of 2.0 standard deviations from the grand mean, recognised no habitat components as outliers. This result removed the possibility of individual habitat components biasing the results of the ordination. The nMDS ordination plot produced a relatively low stress value of 12, indicating that the plot is relatively close to a three dimensional representation of the rank order of the similarity matrix. Of the structural components measured given an r^2 cut off 0.50, canopy height and tree type explained the greatest amount of variability, hence dissimilarity between nest sites. Coefficients of determination for the correlations between ordination distances and distances in the original space, using Sorensen (Bray-Curtis) distance measure, allocated the proportion of variance between three axes. Axis 1 = 0.24: axis 2 = 0.45: and axis 3 = 0.20, which accumulates to 0.89 for all axes. Axis 1 and 2 where used to illustrate nest sites in Figure 1 to illustrate the largest proportion of variance in the data possible in a two dimensional plot.

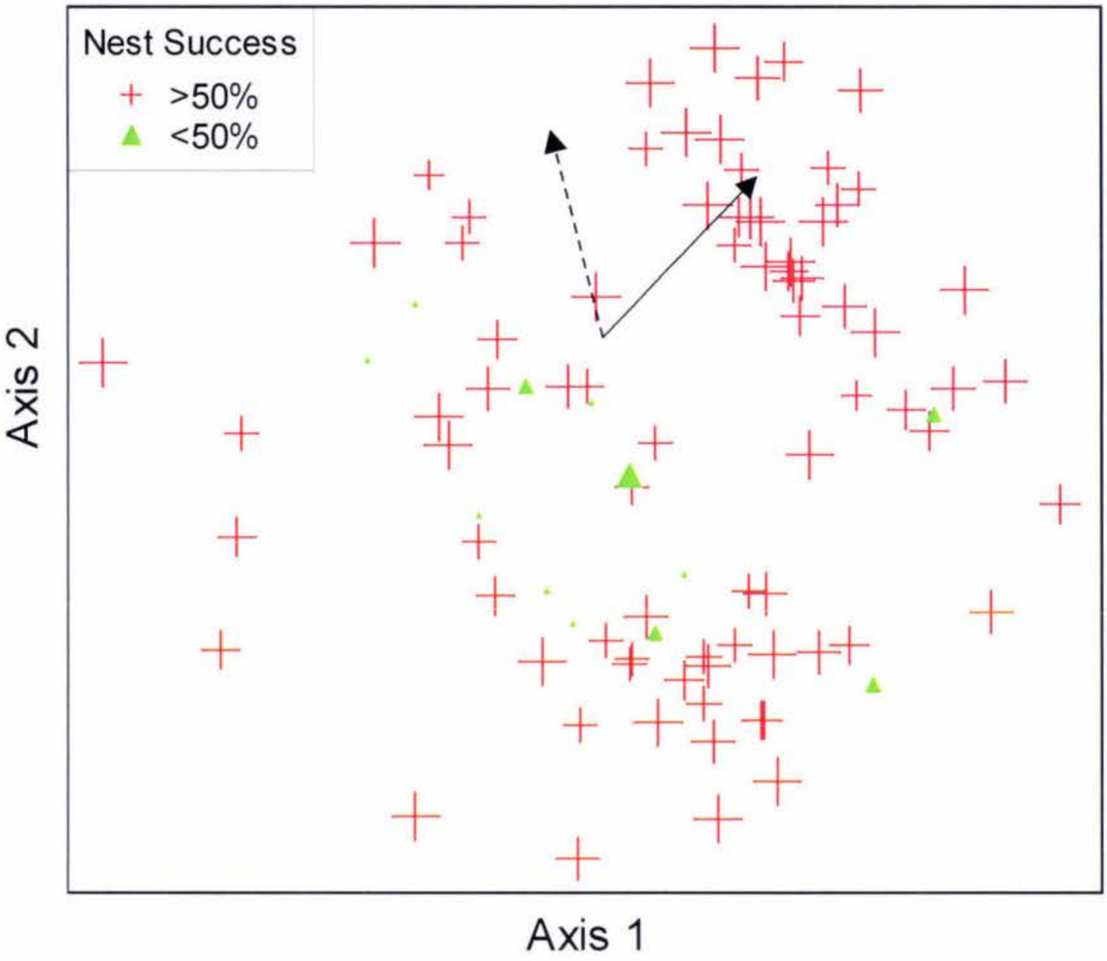


Figure 1. A two-dimensional nMDS ordination plot of nest sites. Ordination was based on 9 microhabitat components scored for 90 nests sites within three reserves (arrows indicate the direction of the 2 habitat components (broken arrow = canopy height, solid arrow = tree type) that explain the largest proportion of variation in the data (given a cut-off of 0.5). Individual nests are represented by symbols. Distance between symbols reflects level of dissimilarity in habitat structure between nest sites, the size of the symbol represents the value of nest success (larger the symbol the higher the success).

There is an even spread of symbols from each category of nest success spread throughout the ordination plot. The correlation between axis one (0.24 proportion of the ordination) and nest success (Mayfield estimates) was represented by *r* = 0.19, and axis two (0.45 proportion of the ordination) and nest success, represented by $r = 0.13$. This suggests that from the variety of differences in habitat structure found, no particular structural composition at nest sites had a significant influence on the probability of nest success.

Outlier analysis recognized nests W30, P30, W1 and P1 as outlying nests with standard deviations of 3.67, 2.59, 3.12 and 2.30 and percentage nest survival at 100, 89, 90 and 83 for each nest respectively. However, the nest success values for these sites lay within the range of values found for the remaining sites, revealing no relationship between outlying nests and nest success.

The influence of macrohabitat on nest success

The habitat structure surrounding nest sites only shows some similarity between Waipapa and Waimanoa reserves, as indicated by the slight overlap of error bars in Figure 2. Nests sites for Waipapa and Paengaroa show the greatest amount of dissimilarity in habitat structure at nest sites. The range in habitat structure at nest sites within reserves is greatest in Paengaroa, closely followed by Waimanoa, and smallest in Waipapa. Nest success estimates for each of these reserves was as follows: Paengaroa 58% (se 0.06), Waimanoa 56% (se 0.07) and Waipapa 47% (se 0.06). The results suggest therefore, that an increase in the level of dissimilarity of habitat structure between reserves is accompanied by an increase in the difference in nest success (i.e., as found for Paengaroa and Waipapa). Additionally, reserves with the larger range in habitat structure at nest sites produced higher nest success.

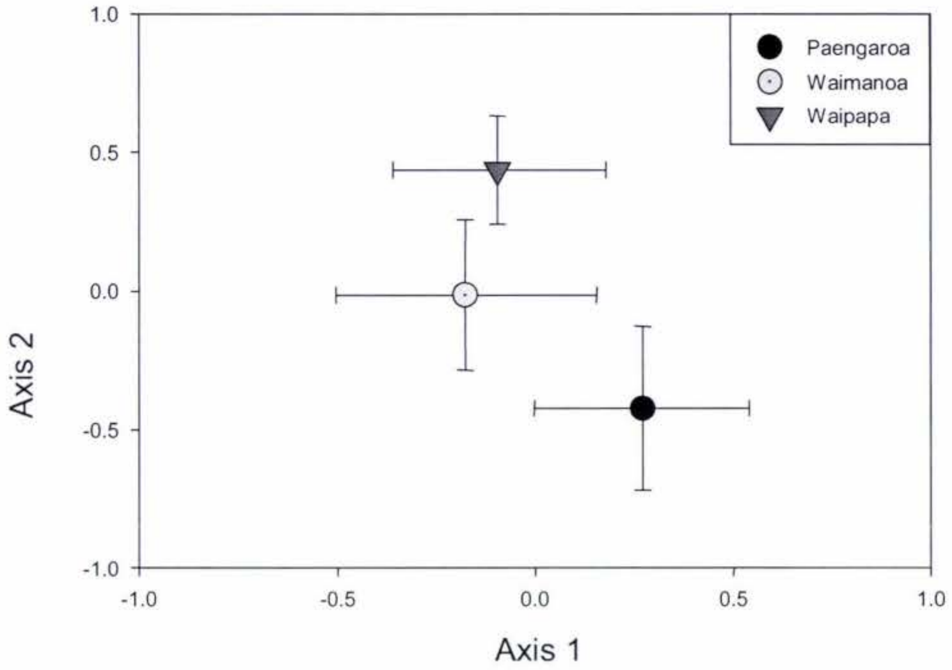


Figure 2. Representation of the scores generated from the ordination, with 95% confidence intervals, illustrating the differences in range of habitat structure, found at nest sites, between 3 reserves.

As reserve size increased, the mean estimate of nest success resulting from predation by rats and possums decreased. However, the large overlap of error bars between the error bars for Paengaroa and Waimanoa suggests that the increase in reserve size from 100 to 300ha does not have a significant influence on nest success. The overlap of error bars between Paengaroa and Waipapa however is much smaller, suggesting that an increase from 100ha to 4000ha may be associated with a decrease nest success (Figure 3).

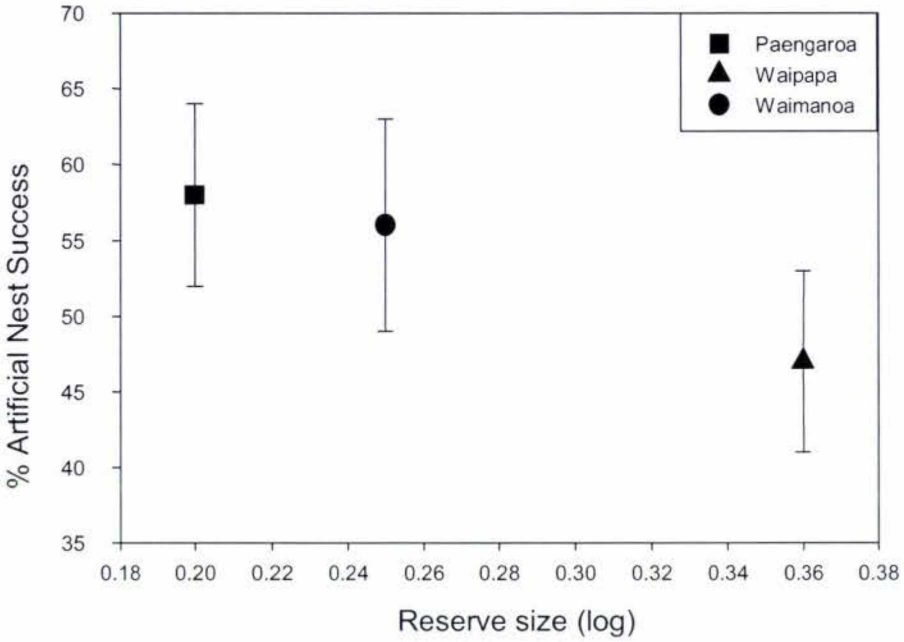


Figure 3. Estimates of nest success (with standard error) resulting from depredation by rats and possums for each reserve without predator control.

Avian predators

The influence of distance to bait stations on nest success

Analysis of nest success resulting from predation by birds in all of the 8 reserves found no observable effect of proximity to bait station, with weekly nest success remaining at 99% for all three distances from bait stations. All reserves were therefore included in analysis of the effect of habitat structure on the risk of nest depredation by birds.

The influence of microhabitat on nest success

Outlier analysis using Sorensen (Bray-Curtis) distance measure, given a cut-off of 2.0 standard deviations from the grand mean, recognised no habitat components as outliers. This result removed the possibility of individual habitat components biasing the results of the ordination. The nMDS ordination plot produced a moderate stress value of 15.54 indicating that the plot is relatively close to a three dimensional representation of the rank order of the similarity matrix. Of the structural components measured, given an r^2 cut off of 0.50, distance to clearing (0.75 axis 2, 0.63 axis 3) and aspect (-0.71 axis 3) explained the greatest amount of variability, hence dissimilarity between nest sites. Coefficients of determination for the correlations between ordination distances and distances in the original space (using Sorensen distance measure) allocated the proportion of variance between three axes. Axis 1 = 0.16, axis 2 = 0.29 and axis 3 = 0.43, accumulating to 0.88 for all three axes. Axis 2 and 3 were used for ordination as they explained the majority of the results (Figure 4).

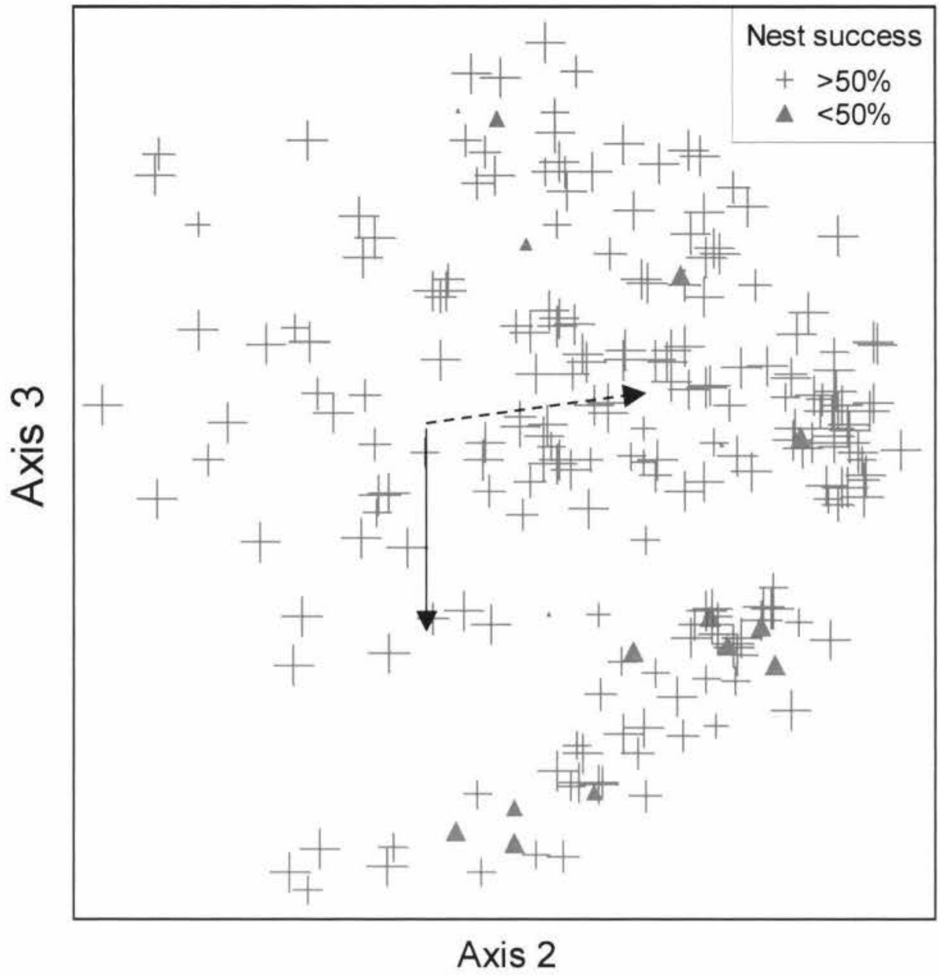


Figure 4. A two-dimensional nMDS plot of nest sites. Ordination was based on 9 microhabitat components scored for 229 nests sites within three reserves (arrows indicate the direction of the 2 habitat components (broken arrow = distance to clearing, solid arrow = aspect) that explain the largest proportion of variation in the data (given a cut-off of 0.5)). Individual nests are represented by symbols. Distance between symbols reflects level of dissimilarity in habitat structure between nest sites, the size of the symbol represents the value of nest success (larger the symbol the higher the success).

There is an even spread of symbols from each category of nest success spread throughout the ordination plot (Figure 4). This suggests that from the variety of differences in habitat structure found, no particular structural composition increased or decreased the probability of nest success. The absence of any strong relationship between habitat structure and likelihood of nest success (estimated using Mayfield method) is supported by the weak correlation with axis one (explaining 29% of the ordination) represented by $r = 0.20$, and axis two (representing 43% of the ordination) represented by, $r = 0.18$.

Outlier analysis recognized 15 nests as outliers with standard deviations ranging between 3.14 and -2.32 with corresponding weekly nest survival estimates ranging from 0.87 to 1.00. However, the nest success values for these sites lay within the range of values found for the remaining sites, revealing no connection between outlying nests and nest success.

The influence of macrohabitat on nest success

The overlap of error bars in Figure 5 suggests the structural composition of the habitat surrounding nest sites is similar among reserves. However, the degree of overlapping is not the same between all reserves. Tiritiri Matangi and Waipapa show some degree of isolation from the other reserves suggesting that there is some difference in the structural composition of nest sites compared with the other reserves. Tirtiri Matangi reserve has the majority of its nest sites placed at the top right-hand side of the nMDS plot, a location characterised by the close proximity to the edge and low canopy. Waipapa reserve has the majority of its nest sites in the mid right-hand side of the nMDS plot, a location characterised by greater distance from edge and high canopy. The range in habitat structure at nest sites within reserves is greatest for Tiritiri Matangi, Karori and Bushy Park and smallest for Waipapa. Nest successes for each reserve were as follows: Boundary Stream 96% (s.e.0.02), Bushy Park 77% (s.e.0.07), Karori 64% (s.e.0.09), Paengaroa 75% (s.e.0.06), Tiritiri Matangi 33% (s.e.0.05), Waimanoa 96% (s.e.0.03), Waipapa 77% (s.e.0.08), Waotu 90% (s.e.0.03). Boundary stream and Waimanoa have similar nest site structure and nest success whereas Waotu, while similar in its nest success, has different habitat structure at nest sites. Bushy Park and Paengaroa have similarities in nest site structure and nest success; Waipapa, while similar in nest success has a different habitat structure at nest sites. The relative isolation of Tiritiri Matangi produced nest success that is much lower than the other reserves. Karori, while sharing similarities regarding habitat structures at nest sites as Tiritiri Matangi has a nest success value that is almost 50% higher. There is no obvious trend between the range in habitat structure at nest sites and nest success.

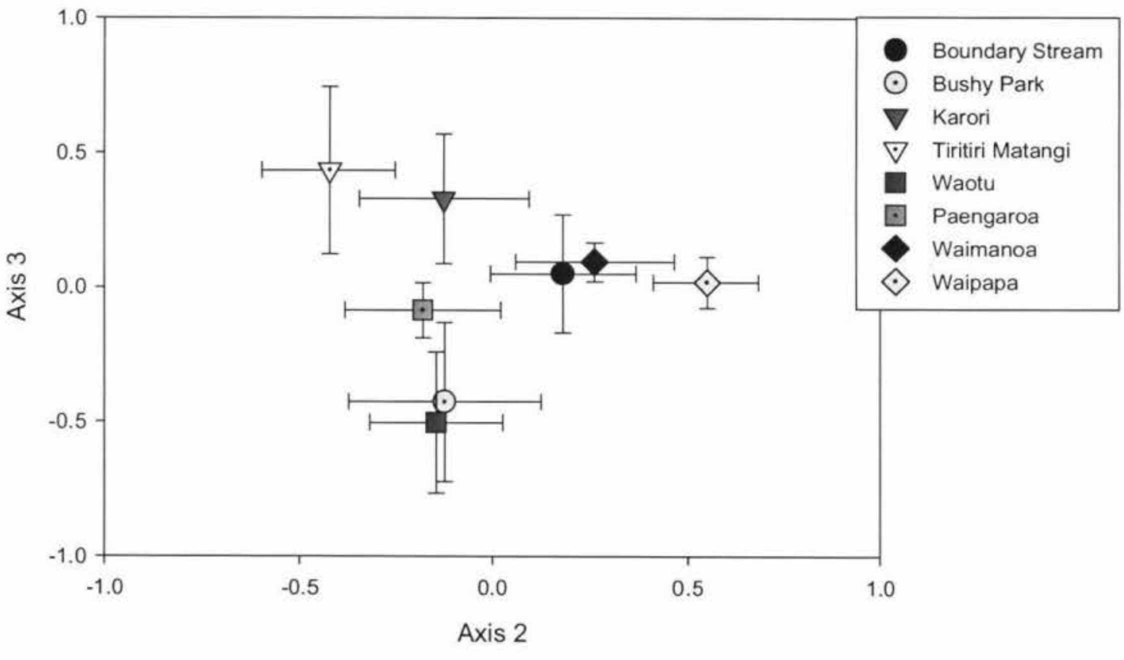


Figure 5. The mean scores with 95% confidence interval (generated from the ordination), illustrating the range of habitat structure found at nest sites for 8 reserves.

There was no obvious relationship between reserve size and nest success resulting from predation by avian predators (Figure 6). The reserve with the lowest nest success (Tiritiri Matangi) may be classed as a medium sized reserve from the sample, indicating that extremes in reserve size do not produce extremes in nest success. Additionally, the two reserves with high nest success (Waimanoa and Boundary Stream) have a large difference in area (500ha).

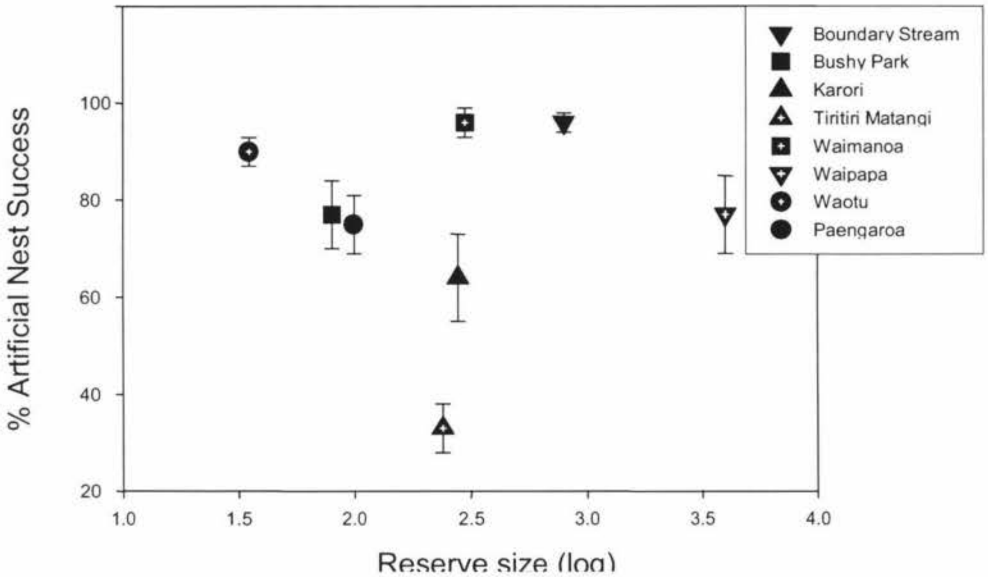


Figure 6. Estimates of nest success (with standard error) for 8 reserves resulting from depredation by birds.

DISCUSSION

The influence of distance to bait stations on nest success

The results indicated that the proximity of individual nests to bait stations might influence the probability of nest depredation by rats and possums. However, the same result was not found for avian predators, with nest success showing no consistent change with distance to bait station. There are very few publications describing the influence of bait stations despite the fact that they are the most frequently used method of predator control in New Zealand. While the risk that the distance to bait station increases the likelihood of nest failure may be important when population numbers are very low, when populations are relatively high, overall nest success may not be detrimentally affected unless by chance a large numbers of nests are situated near bait stations.

The influence of microhabitat on nest success

Avian and mammalian predators

Results from the microhabitat analysis revealed no strong or consistent evidence to suggest that the structure of the nine habitat components measured at nest sites had a significant influence on the probability of artificial nests being depredated by either the rats and possums or bird predator groups. These results are consistent with previous studies that reject any association between nest fate and habitat structure at the microhabitat scale (Vickery *et al.*, 1992; Filliater *et al.*, 1994; Howlett & Stutchbury, 1996; Donovan *et al.*, 1997; Burhans & Thompson, 1998). More specifically, no relationship was found between nest success and the distance to the edge of the forest fragment, a question frequently addressed in previous publications. A review by Lahti (2001) suggested that edges do not always generate increased nest predation, a result supported by the lack of a correlation with distance to edge and nest sites in this study. It is also possible, that the effect of edge may be species specific (Rodriguez, 2001). Contrary to evidence from this and the previously mentioned research, it has often been suggested that habitat does influence nest success in ways specific to both avian and mammalian predators. For example avian predation rates have been linked to the availability of perch sites (Telleria *et al.*, 1991; Thurber *et al.*, 1994), residual tree density (Stuart-Smith & Hayes, 2003) and edge (Saracco & Collazo, 1999). Dense vegetation is thought to harbour more small mammals, leading to higher nest depredation (Johnson & Temple, 1990). For example, Cox *et al.* (2000) found that ship rats (*Rattus rattus*) preferentially use microhabitats providing a dense understorey, numerous vertical stems and dense leaf-litter cover which together create a structurally complex and dense local environment (Cox *et al.*, 2000).

Further investigation also revealed that nest sites from this sample exhibiting a combination of relatively unusual structural characteristics were not more or less likely to be depredated by either the avian or mammalian predator groups. A possible explanation for this result is given by Murphy (1997), who found that predators simply check all possible nesting sites, leading to no relationship between selectivity for a site and nest predation. Previous research has also shown nest depredation to be predominantly incidental (i.e., predators mainly encountered nests fortuitously while foraging for other food items (Githiru *et al.*, 2005).

Confidence in the results of this study can be found from the relatively accurate representation of the habitat structure expressed by the stress values for both of the ordinations and from the use of a large sample size. The coefficient values defining the relationship between habitat structure and nest success were also very low, leaving little doubt about the absence of any strong correlation between the microhabitat characteristics measured and nest success.

The influence of macrohabitat on nest success

Positioning the artificial nests in sites that resembled those chosen by the model species meant that, despite the spatial separation of the reserves, there would be some similarities in the structural composition of habitat at nest sites across all of the reserves. However, the results of the macrohabitat analysis did reveal some variation in the habitat structure at nest sites between reserves. It is assumed, however, that this variation would be similar for natural nests placed within these reserves as they are subject to the same differences in topography, floral community and conservation strategy and status influencing the habitat structure within each reserve.

Mammalian predators

For the three reserves used for analysis of rat and possum nest depredation and nest success, an increase in the level of dissimilarity of habitat structure at nest sites between reserves corresponded to an increase in the difference in nest success. As previously mentioned, there was no relationship between habitat structure at individual nest sites and nest success. Therefore, this connection with habitat must be on a larger scale (e.g. a result of differences in habitat between reserves rather than just the features at individual nest sites) or related to external factors. Evidence to support this effect was discovered by Hartley and Hunter (1998) who found through a meta-analysis of 13 studies that it was forest cover at the landscape scale that influenced the nest success at forest edges producing an edge effect. Paengaroa reserve is surrounded by farmland and has large sections of regenerating forest, whereas Waipapa is surrounded by forestry land and is mainly mature forest. Ship rats, which are responsible for the majority of nest predation events in reserves with no predator control, have been found to be absent from young plantations and present but not abundant in older exotic forest (Atkinson, 1973; King *et al.*, 1996). Additionally, differences in the surrounding landscape may also influence species diversity, distribution or carrying capacity within the reserves (Rodewald, 2003), differences that have been found to affect nest survival in previous research (Matessi & Bogliani, 1999). Based on the assumptions of the previously mentioned research, it is possible that the differences in the habitat structure between reserves, accompanied by additional forested areas surrounding the reserve may have increased the carrying capacity for rats in Waipapa, producing an overall lower nest success compared with Paengaroa reserve. This influence on nest success may be more likely to appear through analysis of associations with habitat on the aforementioned large-scale or macrohabitat, but not on the microhabitat scale, as found in the results of this research.

Distribution of predators may also be associated with developed and agricultural habitats that are interdispersed with forest habitat (Donovan *et al.*, 1997). Changes in nest predation within study sites may then be linked to changes in the productivity gradient between adjacent habitats (FenskeCrawford & Niemi, 1997). Predators that depend mainly on food resources in the farmland, and can often build up high population levels due to the high productivity of the agricultural landscape, can also exert pressure on nests in forest fragments. Such predators are known habitat generalists visiting forest fragments in the landscape regularly and preying upon birds' nests (Angelstam, 1986; Small & Hunter, 1988; Andrén, 1992). Paengaroa reserve is surrounded by farmland and may be subject to influxes of nest predators responding to food availability from surrounding agricultural land. As a result, the probability of nest success may be linked to nest predator abundance rather than habitat characteristics at nest sites as these predators are not established within the reserve itself therefore predation events are more likely to occur sporadically and be focused on areas of entry into the reserves rather than at specific locations throughout the entire reserve area.

The results also showed that when analysing nest predation by rats and possums, reserves with a larger range in habitat structure across nest sites tended to have higher nest success. In reserves where habitat structure around nest sites is uniform, predator searching may become more efficient as they learn to recognise and quickly locate nests. Results from my analysis also revealed an influence of reserve size, suggesting that large differences in reserve size may also influence nest success resulting from depredation by rats and possums. The association between reserve size, the corresponding 'edge effect' (resulting from habitat fragmentation) and nest success is by far one of the most frequently researched areas (Gates & Gysel, 1978; Chasko & Gates, 1982; Andrén *et al.*, 1985; Wilcove, 1985 Angelstam, 1986; Andrén & Angelstam, 1988; Small & Hunter, 1988; Moller, 1988, 1989; Gibbs, 1991; Gates, 1994; Saracco & Collazo, 1999; also see reviews by; Soderstrom, 1999; Lahti, 2001; Chalfoun *et al.*, 2002b; Bátáry & Baldi, 2004). A review by Paton (1994) concluded that nest predation increases near habitat edges. A change in the area to edge ratio as a result of fluctuations in reserve size may therefore result in changes in predation rates. Contrary to this, the results of this research revealed that as the size of the reserve increased so did the risk of nest failure, thus suggesting that an increase in edge does not result in an increase in nest depredation as supported by the results of the microhabitat analysis. This result may be attributable to the fact that larger reserves (e.g. Waipapa) have larger densities of nest predators. Consequently, interpreting the results of habitat analysis in this study may be confounded by reserve size when dealing with mammalian predators.

Avian predators

Of the eight reserves used for analysis of avian predators, while there are some similarities in habitat structure between these reserves, nest success does not follow the same pattern. This suggests that similarities in habitat structure might not act as a confounding factor when analysing factors influencing nest success between reserves. From the sample, Tiritiri Matangi and Waipapa reserves remained relatively isolated with regards to habitat structure when compared with the other reserves. The structural composition of nest sites on Tiritiri Matangi were characterised by having a lower canopy and, as a result of high fragmentation, the majority of nest sites were situated near the edge of a forest fragment. Tiritiri Matangi also had the lowest nest success.

However, there was no trend towards lower nest success association with such characteristics for all the reserves. It is therefore possible that the lower nest success estimates found for this reserve relate to factors not within the scope of this study (i.e. subject to pressures other than those imposed through macrohabitat structure or area), which may be attributable only to the circumstances found within this reserve. Tiritiri Matangi is the only off-shore island reserve used in this study and is composed of many small patches of forest, most of which consist of regenerating forest. It also houses a dense population of birds, including predatory moreporks and harriers. The spatial restriction together with the high number of birds may increase the risk of nest detection regardless of habitat structure. Nest sites in Waipapa reserve were characterised by having low to zero incline and a high canopy. However, nest success at this site was similar to other reserves in the sample exhibiting different habitat structure.

Habitat structure in Karori reserve shared some similarities with Boundary Stream reserve; however, nest success for these two reserves is very different (0.64 versus 0.96 respectively). Karori reserve is situated within a major city whereas Boundary Stream is surrounded by a matrix of farmland and forest fragments. Although Karori reserve is contained within a mammalian predator-proof fence, it may be subject to invasions of opportunistic avian predators able to penetrate the reserve, increasing the incidence of nest depredation by avian predators. Previous research has shown that landscape scale influences can occur when reserves are situated near towns where opportunistic predators may be in greater numbers and therefore pose more of a problem (Sasvari *et al.*, 1995; Matthews *et al.*, 1999; Jokimaki & Huhta, 2000; Schneider, 2001). However, the different species responded differently to the proportion of forest in the landscape. Research into factors affecting nest depredation of sparrow nest boxes (Huhta *et al.*, 2004) also found that landscape-level fragmentation affected nest predation more than fragmentation on the territory scale (Robinson *et al.*, 1995; Chalfoun *et al.*, 2002a).

The results of this research revealed no evidence to suggest a relationship between the range in habitat structure at nest sites in reserves and nest success resulting from predation by birds. Analysis of the influence of reserve size also suggested that reserve size had no influence on nest success for avian predators. Andrén (1992) found that the density of corvids increases as forests become fragmented and intermixed with agricultural land, causing an increase in nest predation in small forest fragments. However, nest depredation events in this research were attributed mainly to smaller avian species.

Alternative explanations

If, as the results suggest, the structural composition of the habitat at nest sites has no strong or consistent influence on the risk of a nest being depredated there must be an alternative explanation for fluctuations in nest success found between both nest sites and reserves. Eggs and chicks are thought to provide only a secondary food source for most nest predators, and nests are principally encountered opportunistically by generalist predators while searching for other prey (Cooper *et al.*, 1999). As a result, nest depredation levels may fluctuate in response to the availability and distribution of alternative food supplies (Bealey *et al.*, 1999; Bety *et al.*, 2001). When alternative food supplies are plentiful and predictably located, nests may be less vulnerable to depredation as the predators' foraging/search areas are decreased and they need not rely on a secondary food source. Alternatively, if the food supply is plentiful but unpredictably located the likelihood of opportunistic nest depredation may increase, as the predator is required to search more extensively for food increasing the probability of encountering a nest. When alternative food supplies are low and highly dispersed, nests may then be at their most vulnerable to depredation as predators rely more on secondary food sources and expand their search efforts. Research into factors affecting gadwall (*Anas strepera*) nest predation discovered that an increase in nest success found was attributed to a decrease of striped sunk (*Mephitis mephitis*) foraging activity in nestling habitats because of an abundance of alternative prey (Crabtree and Wolfe, 1988). Nests located in areas where the primary food supply for the predator is plentiful may dictate nest survival rather than the aspects of habitat structure surrounding the nest site.

One consistent feature of previous research has been the establishment of a connection between forest seed crop and mammalian predator populations, with temporal heterogeneity of the seed crop frequently setting the stage for dynamic fluctuations in mammal population density. White-footed mouse, eastern chipmunk, and grey squirrel (*Sciurus carolinensis*) populations were significantly correlated with annual fluctuations in the acorn crop (Crabtree *et al.*, 1989; McShea, 2000). Likewise, Schmidt and Ostfeld (2003) found that populations of small mammals, such as the white-footed mouse (*Peromyscus leucopus*) and eastern chipmunk (*Tamias striatus*), greatly increased in response to mast production of acorns, and as a result, nest predation rates on songbirds increased. Seed crops have also been shown to impact on predators in temperate forests of New Zealand (King, 1983), where stoats (*Mustela erminea*) are significant predators on nestlings and their annual abundance is correlated with fluctuations in mice and beech (*Nothofagus* species) seed production (Alterio *et al*, 1999). Schmidt & Whelan (1999) observed that during fruit maturation the number of artificial nests depredated decreased by 36%, survival of woodland songbird nests increased by 21% and predation on artificial ground nests switched from density dependant prior to fruit maturation to density independent coinciding with fruit maturation. Fluctuations in the productivity of dominant plant species may also have a significant impact on complex food webs in forest ecosystems (Power *et al.*, 1992). It is possible then that species composition within the habitat rather than the structure may influence nest survival, i.e. reserves dominates by floral communities that are highly productive, hence supply potential nest predators with an ample supply of food, may dictate the risk for nesting species.

Changes in the predator-prey community may influence predators' search effort and strategies, nest encounter rates and thus ultimately in the rate of nest predation (Schmidt & Whelan, 1999). An explanation for differences in nest success may also be explained by the habit, dynamics and trophic levels present within the predator-prey community. A predator with a wide searching foraging mode is most conducive to finding immobile and unpredictably located but clumped prey sources such as nests, while predators that use the sit and wait mode are adapted to locating and capturing mobile and more predictably located prey (Huey & Pianka, 1981; Crabtree *et al.*, 1989; Picman & Schriml, 1994; Bayne & Hobson, 1997). Nest success may therefore be dependant or influenced by the foraging mode of the predators within the community (Lima & Zollner, 1996). Innes and Skipworth (1983) found that the home ranges of ship rats (*Rattus rattus*) are inversely related to rat density. Additionally, Blackwell *et al.* (2002) reported that rats in low density populations may become more active and cover larger areas. Small reductions in predator numbers may therefore not reduce nest depredation rates as rats expand their territories.

Biological control and competition for resources within the habitat may be mediated by the trophic levels present within the predator community. It is known that the behaviour of low-level predators may change when top-level predators are removed (Dion *et al.*, 2000). In New Zealand, the main mammalian predators threatening nest survival were introduced into a system that lacks top predators to mediate their numbers and alleviate the threat to nest survival through biological control. As a result, rats are extremely abundant in New Zealand forest fragments. In systems where predator populations are not subject to control, the over-riding influence on nest mortality may then be related to the predator density (Zanette & Jenkins, 2000), as opposed to the fine scale structural attributes within the habitat. Predator density may also peak in landscapes that offer ample feeding and breeding opportunities (Donovan *et al.*, 1997).

The aforementioned alternative explanations may be responsible for the fluctuation in nest success, the effect of which may override any observable effect of habitat. Alternatively, as concluded by the results of this and other research, it is possible that habitat, or habitat alone, is not be the driving force behind nest success.

Limitations of this study

Lack of any relationship between microhabitat structures and nest success does not mean that a relationship does not exist just that it is not apparent from the information provided in this research. The inclusion of nine habitat components in this study only provides a simple assessment of nesting habitat and may lack the information needed to determine the factors involved in predation. In addition to this, the amount of dissimilarity between nest sites was heavily governed by two habitat components, canopy height and tree type, in reserves looking at mammalian nest depredation and distance to clearing and aspect in reserves looking at avian nest depredation. Interpretation of the results is then heavily influenced by the strength of these factors. Consequently, the mechanisms linking predation and nest site features may be masked by the strength of these components. However, responsibility for this result lies in the fact that nest sites were chosen to mimic those selected by the model species, hence not selected to test the influence of varying attributes of specific components of habitat structure. The results were then expected to reflect the effect of habitat structure in natural robin nests, not the effect of habitat components themselves.

To reduce the number of confounding factors in this study introduced by human disturbance at nest sites and to reduce the effort required for volunteers to check nests, all the nests were placed between 1.5 and 2 m high. As a result, the influence of nest height was not a factor included in this study and did not fully represent nest heights chosen by the model species. This is one of the major limitations of this study as nests within different height classes are exposed to different predator assemblages and often vary in success rates (Martin, 1987; Martin & Geupel, 1993; Wada, 1994; Soderstrom, 1999; Burhans *et al.*, 2002). The cost associated with reaching nests located at different heights might be higher for mammalian compared to avian predators, because mammals have to climb to reach nest. Encounter probabilities should therefore decrease with increasing nest height for ground foraging mammals but may have little influence on avian predators.

The problem with the method of habitat analysis used in this research is the presence of outlying nests which may not allow the bulk of the data to be analysed, hiding the effects of habitat characteristics found at other nest sites. Such a result may also affect the correlation coefficient, producing a significant correlation based on the outlying nests that has little to do with the bulk of the data. The structural components included in this analysis included those previously found to influence nest success. However, there are an immeasurable number of factors not included in this study that may potentially affect nest success. The potential problem with adding too many factors is that the interpretation of the findings becomes very time consuming. Perhaps more importantly, too many factors can lead to over-fitting, providing no weight for interpretation from the model without testing and consequently further research. The results of this type of analysis are also very specific to the circumstances in the reserves used in the study. Increasing the sample size by a small amount may have a large impact on the results. However, ordination analysis does provided an excellent method of visually representing differences between reserves with regards to overall habitat structure at nest sites.

This use of artificial nests in this study is unable to account for any factors relating to parental activity. Nesting birds may modify their behaviour to compensate for the risk of predation. For example, nesting blackbirds have been found to alter their level of nest defence to compensate for the predation risk associated with a nest's location (McNamara & Houston, 1987; Moller, 1989; Cresswell, 1997). Additionally, birds commonly change nest site microhabitat choices following early failure (Rowley, 1965; Martin & Li, 1992; Morton *et al.*, 1993). It is therefore possible that the shortcomings of habitat features will be compensated for in natural nests by parental activity (Forstmeier & Weiss, 2004). The detection of any relationship between habitat components and nest success using artificial nests may have to be interpreted with caution as the influence of certain habitat components may be redundant in the presence of defending parents.

Management implications and recommendations

Evidence from the results of this study show that nest sites that were near bait stations were marginally more likely to be depredated than those further away. After ingesting the poison (e.g. Brodifacoum) rats may take up to a week to die, giving them time to depredate nearby nests. When the numbers of the species you are trying to conserve is very low, the success of every nest is very important. Given such circumstances it would be advisable to use a poison that kills its host within a shorter space of time (e.g. cyanide) leaving less time for the predator to depredate nearby nests.

New Zealand provided a unique environment in which to conduct this research and may have provided circumstances where nest success may be linked to factors other than fine-scale habitat structure. Before human settlement New Zealand's animal community evolved without mammalian predators. Consequently, its avian occupants evolved no anti-predator adaptations effective for many mammalian predators (Vickery *et al.*, 1992). Following their introduction, rats underwent a population explosion that ripped through the New Zealand forest decimating bird numbers (Atkinson, 1973; King 1984, Atkinson & Cameron, 1993; Moors 1985; Clout, 2001). Following predator control, rats have the propensity to recover rapidly (Blackwell, 2003). It is possible that the best predictor of nest success in this instance is not the structure of the habitat at nest sites but the sheer number of predators and the lack of any biological control. The results of this research may therefore be specific to circumstances within New Zealand forest only.

Knowledge of the identity and abundance of dominant predators in a habitat or landscape is necessary to target conservation efforts to reduce nest predation or to interpret results of research on factors affecting nest success (Thompson & Burhans, 2003). Forest and land managers can reduce predator populations using a range of methods, e.g., baiting, shooting, trapping and fencing (Reynolds & Tapper, 1996). However, for this to be effective most of the predators have to be killed and predator removal conducted every year. This approach requires intensive effort and in most cases the results are effective only at a local scale and for a short period of time (Pressey, 1994). In New Zealand, the predator community is composed of introduced species and lacks the trophic levels in the food chain effectively controlling their numbers. Leaving the system to develop with no predator control regime is therefore not a viable strategy to conserve endangered prey in landscapes where predator density is high and where predator assemblage is subsidised by humans clearing vast areas of habitat. Humans have created an artificial system requiring ongoing management and until the predators are completely eradicated this management needs to continue. However, if the interaction of multiple species is mediated through the productivity or abundance of a single species, then the effective management of this species can help maintain ecosystem stability (Pressey, 1994; Polis & Strong, 1996; McShea, 2000).

The accuracy of artificial nests as a tool for monitoring natural nest success may not be greatly influenced by differences within the habitat at nest sites in New Zealand forest fragments. However, these results may depend on the relative similarity between nest sites within and between reserves and the consistency in nest height. If the reason for using artificial nests is to predict the predation pressure for natural nests then it may therefore be necessary to place nests in positions that mimic those chosen by the model species. This being the case, the problem of habitat confounding interpretation of the results may not be an issue. Problems may arise with this technique if the habitat in which artificial nests are used to predict natural nest success varies greatly between nest sites (i.e. microhabitat) and or reserves (macrohabitat), especially when mammalian predators are involved. To assess the influence of microhabitat, artificial nests should be placed in different locations within one area of forest (subject to the same predator community). To assess the influence of macrohabitat, artificial nests should be placed in similar microhabitats i.e. nest sites, within different reserves with similar predator communities.

Chapter Five

General Discussion

The battle to save New Zealand's endemic bird life from extinction through predation by introduced mammalian predators and habitat loss has attracted a wide variety of scientific research. However, this ecological tragedy, has inavertedly lead to the engineering and testing of many innovative and forward thinking conservation techniques, the implementation of which have provided some of the greatest success stories in conservation (Merton; 1992; Clout, 1995). Realising the potential for artificial nests is perhaps another important step forward for the conservation of avian species both in New Zealand and overseas. The results of this research show that there are many factors to consider when using artificial nests to predict the predation pressure on natural nests. However, the results also show that when such factors are taken into consideration artificial nests make an efficient and accurate monitoring tool that may benefit avian species conservation both in New Zealand and internationally.

The variation in spatial distribution, area, topography and conservation practice included in the reserves chosen for this study introduced a variety of possible confounds (e.g. variation in reserve size, habitat, and nest success). Despite these possible confounds, rigorous testing in Chapter 2 (Using artificial nests to predict the predation pressure in natural nests), provided enough evidence to suggest that artificial nests could be used to predict natural nest success with some accuracy. Previous research testing the ability of artificial nests emphasised the importance of mimicking the construction, placement and visual and olfactory cues associated with natural nests. The techniques used in this research aimed to follow this lead by using similar materials in the construction of nests and eggs and following the exposure period and positioning of nests used by the model species. In New Zealand, where mammalian predators pose the main threat to nest success, consideration of olfactory cues associated with the artificial nests was particularly relevant in the design of this study (Whelan, 1994; Rangen, 2000). The statistical methods used for estimating nest success for both natural and artificial nests, produced estimates with standard errors. Although the original estimates of artificial and natural nest success produced a relatively strong relationship, the uncertainty provided by the error meant that confidence in the results was not achieved. This uncertainty was accounted for by using a parametric bootstrap procedure utilizing 10,000 data sets, the results of which paralleled those from the original estimates, providing confidence in the results.

One of the most important results to come from Chapter 2 was the need to identify predator type. The materials used in the nest and egg construction enabled predators to be identified into mammalian and avian predator groups with relative ease, through simple observations of the imprints in the clay eggs. Further separation of the mammalian predators into 'high risk', i.e. rats and 'low risk', i.e. mice, was possible using the statistical technique of discriminant analysis. Although several of the eggs collected had unidentifiable (unknown) markings this sample only accounted for 4.1% of the entire sample. The fact that the eggs were tied to the nest also reduced the instance of missing eggs.

If this research was to be repeated, suggested improvements such as monitoring of natural nests in the same year as artificial nests for all reserves and reducing the number of people collecting the eggs may reduce some of the variability in the data. However, the inclusion of a large number of widely distributed reserves made it necessary to employ the help of many people to be able to collect the eggs simultaneously at regular intervals. A compromise may be to supply each 'egg collector' with photographs illustrating the variety of marks made by each potential predator to cut down the variability and amount of eggs collected that were not depredated by nest predators. While this method may reduce the variability, it is still open to the influence of differences in human interpretation. The results from this research suggest that this technique is viable, and while repetition over several years may add further confidence in the results, it may not be necessary prior to its use as a monitoring technique.

Variation and the methodology used in the design of artificial nests may be responsible for the variety of results and controversy over the accuracy of the technique (Davidson, 2000). There are two possible scenarios: one, that consistency is required i.e. that one uniform method should be used for successful implementation of the technique, or two, that the methods used should be designed to suit the predator community and circumstances within each country or indeed reserve they are to be used in. The only way to solve this issue is to test what methods work for each circumstance, i.e. in different countries, and collaborate to compile a guideline recommending techniques to be used in each circumstance. Chapter 3 (Methodological technique required to gain meaningful results using artificial nests to monitor natural nest success: a case study in New Zealand forest fragments) aimed to arrive at a conclusion as to what components of the methodology used in Chapter 2 make a difference to the results obtained for artificial nests used in New Zealand forest fragments. This question was divided into four areas of methodology, each addressed individually.

The main conclusion from Chapter 3 was that the accuracy of artificial nests in New Zealand forest fragments is influenced by the methodology used. From the factors tested, monitoring intensity, exposure period, and, for identification purposes only, egg type, were found to influence the results. A low intensity monitoring regime (in this case one week as opposed to four) was found to increase the accuracy of artificial nests at predicting natural nest success. The frequency and intensity of monitoring carried out within each reserve often depends on the amount of funding available and time allocated. Besides an increase in accuracy, a low intensity regime also means a reduction in the financial output and time required to apply the technique. Such a result has important consequences for conservation bodies when considering whether to include this technique in their monitoring programmes. A reduction in the amount of time artificial nests are exposed for was also found to have important benefits for artificial nests. Reducing the exposure period from 3 weeks to 1 week not only provided further support for the low intensity regime, but, more importantly, increased the probability of accurately identifying predators. Extending the exposure period increased the probability that imprints in the clay eggs would fade or be obscured by multiple markings, the result being an increase in the number of 'unknown marks'. An important consequence of this is the miss-identification of predators, potentially leading to underestimation of the impact of certain types of nest predators.

The addition of real eggs was found to have little influence on the probability of nests being preyed on by rats and possums. This result was somewhat surprising as it was assumed that mammalian predators located nests using olfactory cues associated with the eggs. Nevertheless the inclusion of a real egg in artificial nests did not increase (or reduce) nest depredation rates in reserves dominated by these mammalian predators. While egg combination was found to influence nest success resulting from predation by birds in several of the reserves, there was inconsistency in the egg combination chosen, suggesting that egg type was not the factor influencing nest depredation by birds. The ramifications of these results are positive, as handling real eggs in any monitoring technique can be problematic due to their fragility and longevity. Finding real eggs that are similar in size and shape to the model species is also problematic. Artificial eggs on the other hand can be moulded to the required dimensions. During this study a delivery of quail eggs arrived with 60% of the eggs broken, an outcome which cost both time and money. This finding is therefore an added benefit to the technique, avoiding additional problems such as egg decay and egg loss prior to its application.

Egg combination was highlighted as an important factor for predator identification in this research. Destruction of both quail and clay eggs occurred in all predator types and was sufficient to cause egg failure. However, identification of predator type through nest and egg remains was not found to be a reliable method of identifying the type of predator, a view supported by the majority of previous research (Marini, 1998; Lariviere, 1999). The results also highlighted the importance of including a clay egg in every nest to enable clear identification of predator type. Marks left on the quail eggs were not species specific (all predator types left similar markings), whereas marks left on the clay eggs could be separated into each predator type with relative ease. Egg size, deemed to be an important factor for accurate representation of the predator community, was not found to be important in this study. The size of natural eggs used in artificial nest research was previously thought to limit predation by small-mouthed mammals (DeGraaf, 1996; Ettel, 1998). However, small mouthed mammals, in this case mice, did manage to break open the larger quail eggs. It is important to note that at least one clay egg should be attached to each artificial nest to avoid removal and therefore, facilitate predator identification.

It is not just the methodological technique that needs to be considered when using artificial nests as a monitoring technique. Factors such as habitat structure may exert an additional pressure on nest success, confounding interpretation of the results from artificial nests. The effect of the habitat was analysed in Chapter 4 (Determining the influence of habitat structure on the probability of artificial nest depredation by avian and mammalian predators in New Zealand forest fragments; consequences for using artificial nests) to determine whether the positioning of artificial nests influenced the probability of nest survival, confounding interpretation of the results from research using artificial nests. To establish the extent to which habitat influences nest predation two spatial scales were used, microhabitat (habitat structure surrounding each nest site) and macrohabitat (habitat structure within each reserve). As avian and mammalian predators were assumed to respond to the habitat structure in different ways the influence of habitat was assessed for the two major predator groups, “rats and possum” “and birds, separately.

The results from this research concluded that proximity to bait station can influence the probability of nest success. Bait stations are the dominant technique used to control predator numbers in New Zealand, hence the results of this research are cause for concern. This result indicates that nests located near bait stations were less likely to survive. However, to my knowledge, there have been no previous publications addressing this problem. It would be highly beneficial, therefore, to design a quantitative study to address this problem and quantify the threat to nest survival. Secondly, habitat was found to have no influence on the probability of nest depredation from either mammalian or avian predators on the microhabitat scale. However, nest failure resulting from depredation by mammalian predators only was found to be slightly influenced by the macrohabitat. Macrohabitat influences on nest depredation probability for the mammalian predator group show a decrease in nest success with a large increase in reserve size and an increase in nest success with an increase in the range in habitat structure at nest sites between reserves.

The ramifications from the microhabitat results from Chapter 4 for artificial nest use are that the differences found between artificial and natural nest success in Chapter 2 were not confounded by artificial nest placement (based on the 9 components measured around each nest site). However, the findings in these results do highlight the importance of considering the habitat within the reserve as a whole as well as the surrounding landscape when assessing the risk to nest success resulting from predation by rats and possums. However, consideration should be given to the possibility that while macrohabitat may influence both natural and artificial nests in a similar way, it is possible that changes in the macrohabitat may influence the predator community, which may differentially influence depredation rates on the two nest types. For example, if artificial nests were preferentially depredated by certain predator types, for instance birds, and habitat fragmentation increased exposure to avian predators, the resulting nest success may be lower for artificial than natural nests.

In summary, this research has highlighted the influence of certain methodological and external factors influencing the precision of artificial nests in New Zealand forest fragments. Although the results are relevant to forest fragments in New Zealand, the questions asked and methods used are relevant anywhere. An important consideration when establishing the relevancy of these results to an international audience is the predator community involved. Establishing the predator types, preferences and habits may be crucial when interpreting the results of artificial nests. There are many factors that influence the predictive capability of artificial nests as a technique for monitoring natural nest success. However, the influence of one factor is often linked by changes in another. For example, the probability of nest success may be influenced by the type and abundance of predators. This in turn may be influenced by the level of habitat fragmentation and the subsequent exposure of individual fragments to different land-use, and available food supply. While the methods used for artificial nests can compensate for some factors, others (such as the influence of parental activity and nestling stage) cannot be. As a result, the absolute values for artificial and natural nest success are unlikely to be exactly the same. However, artificial nests were able to detect the differences in natural nest success between the reserves demonstrating that artificial nests can be used to predict predation pressure in forest fragments.

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I'm truly sorry man's dominion,

Has broken nature's social union,

An' justifies that ill opinion,

Which makes thee startle

At me, thy poor, earth-born companion

An' fellow mortal!

To A Mouse, Robert Burns (1785).