

Takapourewa titiwainui (fairy prion; *Pachyptila turtur*)

How nest site selection affects breeding success, with
applications for translocation



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Abstract

Translocation of seabirds is used as a component of habitat restoration. This is often a complicated and expensive process, so maximising the likelihood that the translocation will succeed is important. Takapourewa is an island with vegetation at various stages of re-generation, and a large population of titiwinui (fairy prion; *Pachyptila turtur*). The titiwinui population on Takapourewa was studied to find how nest site selection (vegetation, aspect, burrow characteristics, and tuatara *Sphenodon punctatus* density) affected breeding success (burrow occupancy rates, chicks hatched, chicks fledged, chick fledge weight), and how soon titiwinui began nesting in an area after grazing was ceased or habitat restoration began. In order to test the hypotheses a new method of monitoring seabird burrows was designed and trialled; burrow utilisation monitoring boards (BUM boards). This method was compared with using study sticks. BUM boards were found to be a very promising, innovative method that yielded rigorous data quickly and easily. One hundred burrows were studied intensively to find out how nest site selection affected breeding success. There was a general trend of northerly-aspect and forest-covered sites having greater occupancy and more successful breeding conditions than southerly-aspect and pasture-covered sites. Burrow characteristics (complexity, temperature and length) did not appear to be critical factors for burrow occupancy or breeding success of titiwinui on Takapourewa. The density and feeding behaviour of tuatara is likely to have a greater effect on the breeding success of titiwinui on Takapourewa than vegetation, aspect or burrow characteristics. Belt transect surveys were undertaken at each of the accessible re-vegetated or retired pasture sites. It was found that titiwinui were more likely to re-occupy sites that had been without stock grazing for longer, irrespective of vegetation type. This knowledge is useful for restoration projects as reintroducing titiwinui does not necessitate expensive and time-consuming revegetation programmes, but there is no observed detriment to the establishment of titiwinui burrows by replanting sites. There are an estimated 1.83 million breeding pairs of titiwinui on Takapourewa.

Key words: seabird biology, titiwinui, (fairy prion; *Pachyptila turtur*), Takapourewa (Stephen's Island), island restoration, translocation, re-vegetation, burrow monitoring, nest site selection.

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For Charlie, with love xxx

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Chapter one: General introduction

Translocation as a tool

Biodiversity loss is a major global conservation issue. In response to this, translocation of organisms is often used at the species level to establish or enhance further populations with the intention of curbing continued decline (IUCN 1998; Fisher and Lindenmayer 2000). Translocation has been defined as the ‘deliberate and meditated movement of wild individuals to an existing population of conspecifics’ (IUCN 1998). In New Zealand, the term translocation encompasses this definition, as well as re-introduction, re-inforcement/supplementation, and conservation/benign introductions¹ (it was suggested by Armstrong and Seddon 2008 that the term translocation should revert to the original meaning of ‘the movement of any living organism from one area to another’). New Zealand has a long history of using translocation as a wildlife management tool (Atkinson 1990; Armstrong and McLean 1995, Clout and Saunders 1995), which can be credited with helping to prevent the extinction of several species, including the takahe (*Porphyrio mantelli*; Jamieson *et al.* 2000), black robin (*Petroica traverse*) and South Island saddleback (*Philesturnus carunculatus*; Towns *et al.* 1990; Armstrong and McLean 1995). Within New Zealand, offshore islands are often an important component of successful translocations. They provide a source of founder individuals to be translocated, and the sea barrier prevents unwanted introductions (Craig and Veitch 1990). Islands are also often used as release sites as it is possible to rid them of introduced predators, something yet to be achieved on the mainland (Veitch 1994, Clout and Saunders 1995).

Habitat restoration

Given the huge conservation potential of New Zealand’s islands, habitat restoration of island ecosystems has become a major focus (Saunders 1994; Clout and Saunders 1995). This approach has aims to restore whole ecosystems and associated processes, rather than focusing only on individual species or populations (Simberloff 1990; Towns *et al.* 1990; Clout and Saunders 1995). Restoration methods include eradication of introduced flora and fauna, reinstating previous species, and reverting pasture/exotic vegetation to the endemic vegetation (Lovegrove

¹ Re-introduction: an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct; re-inforcement/supplementation: addition of individuals to an existing population of conspecifics; conservation/benign introductions: an attempt to establish a species, for the purpose of conservation, outside its recorded distribution but within an appropriate habitat and eco-geographical area (IUCN 1998).

and Veitch 1994; Veitch 1994). Habitat repair may be an important pre-requisite for successful translocations outcomes (Lovegrove and Veitch 1994), as likelihood of success increases with habitat quality (Griffith *et al.* 1989; Saunders 1994; Wolf *et al.* 1996).

Seabirds are a keystone species (Clout and Saunders 1995) on many islands. They transfer oceanic nutrients ashore (Ward 1961), and burrowing activities homogenise soil horizons and aerate soil (Markwell 1997), while providing valuable habitat for other burrow-utilising species (Miskelly and Williams 2002). Consequently, seabirds are viewed as a key component in island restorations (e.g. Mana Island, Miskelly and Williams 2002; Miskelly and Gummer 2004, and Matakoho-Limestone Island, Gummer and Bishop 2004). The need to translocate seabird species is heightened by the decline in seabirds on oceanic islands due to predation and habitat destruction caused by grazing animals (Bell 1994).

Takapourewa history, habitat degradation and restoration

General description of island

Takapourewa/Stephens Island (previously known as Titapua, Campbell *et al.* 1984) is a small (150 ha) oceanic island located north of D'Urville Island to the west of Cook Strait, New Zealand (40° 40'S, 174° 00'E; Fig. 1). It rises to 280 m above sea level at the highest point, and is bounded on all sides by steep cliffs (Ward 1961; Campbell *et al.* 1984; Medway 2004). Takapourewa has a long history of isolation, and was possibly formed as early as the Triassic age (Campbell *et al.* 1984). Due to the buffering action of the surrounding ocean (Daugherty *et al.* 1990) the island has a temperate climate and frost is unusual (Ward 1961).

Early accounts of the vegetation described lowland coastal forest dominated by kohekohe (*Dysoxylum spectabile*); taupata (*Coprosma repens*); mahoe (*Melicytus ramiflorus*); and ngaio (*Myoporum laetum*). Nikau (*Rhopalostylis sapida*) were scattered throughout, and kowhai (*Edwardsia microphylla*) was common on exposed cliffs and ridges (Ward 1961). The vegetation is now 22% grassland (*Avena sterilis*, *Lolium perenne*, *Poa cita*), 20% vineland (*Muehlenbeckia complexa*, *M. australis*), 17% pasture (*A. sterilis*, *L. perenne*), 15% cliff (predominately bare rock), 14% shrubs (*A. sterilis*, *L. perenne*, *P. cita*, *C. repens*, *M. complexa*, *Hebe urvillea*), and 12% forest (*C. repens*, *M. ramiflorus*, *D. spectabile*, *Hedycarya arborea*, *Macropiper excelsum*, *Urtica ferox*, *Solanum nigrum*; East *et al.* 1995, Markwell 1997).

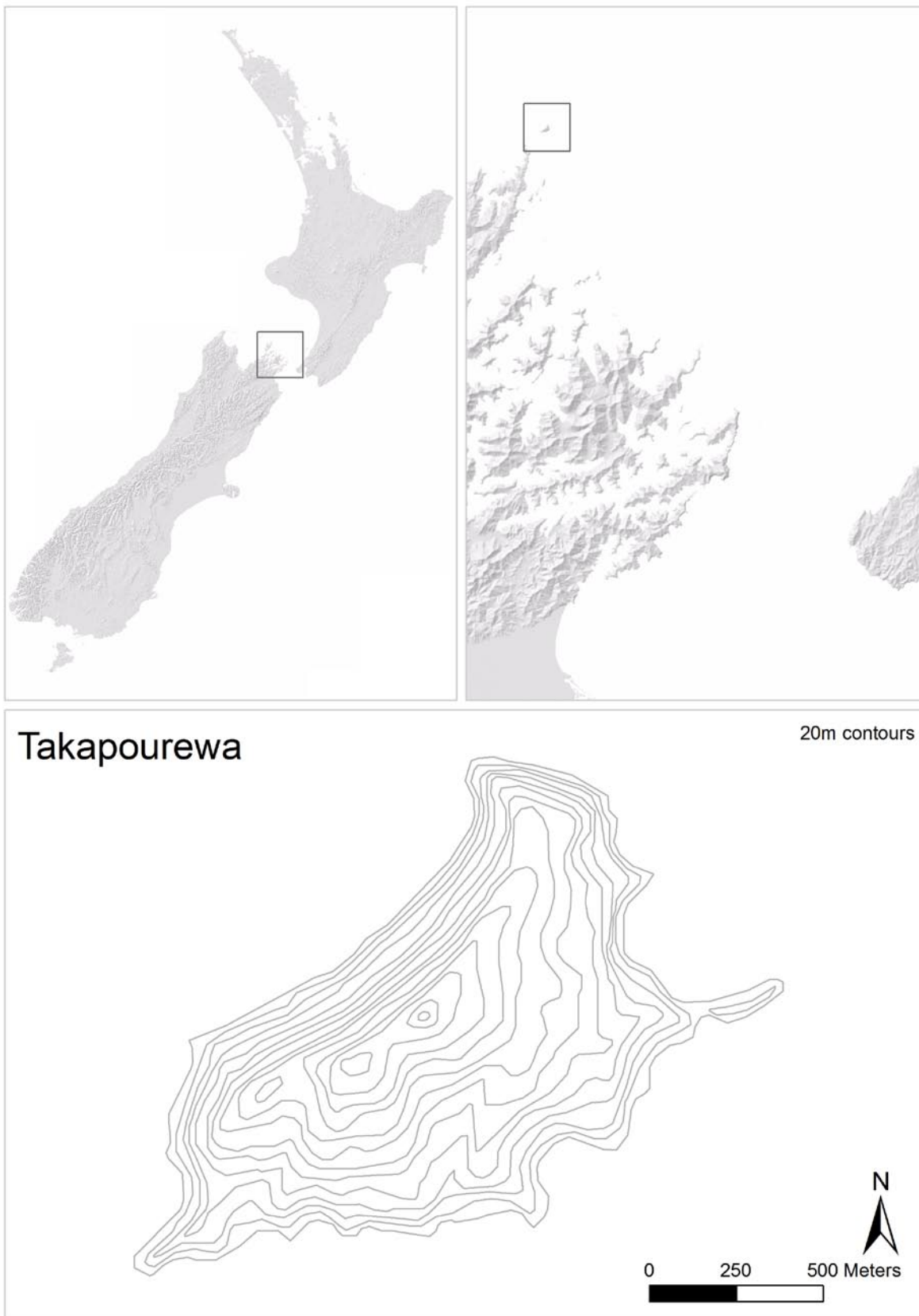


Figure 1. Location map of Takapourewa

Takapourewa has great conservation significance due to the absence of introduced mammalian predators and the presence of rare and endangered flora and fauna (Brown 2001).

History of degradation

Takapourewa was once encompassed within the rohe (tribal boundary) of Ngati Kuia, until the Battle of Waiorua in 1824, when Ngati Koata defeated Ngati Kuia. The island was duly gifted to Ngati Koata as a *tuku* (peace-offering) by Ngati Kuia chief Tutepourangi. In 1891 the island was acquired by the Crown under the Public Works Act as a site for a lighthouse (Brown 2001). Prior to the commencement of lighthouse construction the island was not continuously occupied (Medway 2004). The island was inhabited by lighthouse keepers until the lighthouse was automated in 1989 and the island changed ownership from the Ministry of Transport to the Department of Conservation (DOC). On the 29th of November 1994 a land claim by Ngati Koata was resolved, and the island was returned to Ngati Koata, who in turn gifted it to the people of Aotearoa/New Zealand. The island is now co-managed by Ngati Koata and DOC, and is protected with the highest environmental classification, a closed access nature reserve (Brown 2001). Takapourewa was first protected as a Wildlife Sanctuary in 1966, and reclassified as a Nature Reserve in 1997 (Medway 2004).

The forest of Takapourewa was pristine until a track was cut in 1879, followed by clearing during the early-mid 1880s for the lighthouse and other associated sites, and grazing for domestic stock (Ward 1961; Brown 2001; Medway 2004). The clearing exposed the remaining forest to strong winds which extended the cleared areas, human occupation led to forest fires, and the presence of stock prevented revegetation (Ward 1961). By 1916 the forest was confined to a belt along the summit, with the rest of the island in grass/tussock (Medway 2004). Only two small tracts of native vegetation remain (Keepers Bush and Ruston Bush; Brown 2001).

Cats (*Felis catus*) were introduced to the island around 1894 (Medway 2004). Before this there were no mammalian predators present on the island (Galbreath and Brown 2004). The cats became feral by 1895. Despite eradication attempts (by shooting) the population of feral cats remained high from the late 1890s to 1905. A small number persisted until at least 1916, but none were left by 1925. The extinction of the Stephens Island wren (*Traversia lyalli*), and local extinction of the saddleback (*Philesturnus c. carunculatus*) and piopio (*Turnagra capensis minor*) is attributed to feral cats. Twenty five native species of land bird were recorded on

Takapourewa in the early 1890s, which probably represented the original fauna (Medway 2004). Only a small proportion of these remain today due to habitat loss and predation (Brown 2001).

Restoration

Takapourewa is currently undergoing extensive habitat restoration. The first protective fence was erected in 1951, and the first attempt at re-vegetation began in 1953. Since the mid-1990s DOC has undertaken an annual programme to replant endemic forest (Brown 2001). The last of the stock (sheep *Ovis aries*) were removed in August 2004, and the redundant pasture left to go rank. Thus Takapourewa currently has various stages of successional forest and retired pasture.

Habitat alteration at restored sites is likely to have an impact on any translocated species. For example, agricultural use causes severe browsing of the under-story or complete deforestation, and compaction of the soil (Crook and Moran *pers. comm.*), so the successive vegetation may bear little resemblance to the original state. Thus the apparent habitat preferences of a restored species may not be a realistic guide due to a reduction of choice through habitat modification (Craig and Veitch 1990). It is not known how habitat alteration affects the likelihood of success of translocation projects. The IUCN (1998, Pp 8) recommends that 're-introductions should only take place where the habitat and landscape requirements for re-introduction are satisfied, and likely to be sustained for the for-seeable future. The possibility of natural habitat change since extirpation must be considered'. Where the release site has been subject to previous causes of decline (which may include habitat loss and competition with domestic livestock), habitat restoration should be implemented before any animals are released (IUCN 1998). Given that habitat refers to all aspects of the environment including predators and parasites (Armstrong and Seddon 2008), habitat restoration includes not only vegetation but also the removal of introduced pest species. Where possible in large areas, Craig and Veitch (1990) recommend multiple releases over patchy habitat and subsequent monitoring to ascertain the impact of release site features, specifically how this influences colonisation. I suggest that it is more beneficial to undertake this type of monitoring prior to release, so that sub-standard habitat types can be avoided. Given that Takapourewa has various stages of successional forest and retired pasture, and an abundant population of titiwinui, it is an appropriate site to identify those environmental variables resulting in the greatest breeding success. Additionally, establishing the pattern of titiwinui expansion into restored habitat will be useful for determining the habitat requirements of translocated titiwinui.

General titiwainui biology

Titiwainui (fairy prion; *Pachyptila turtur*) are a small (25 cm, weight 125 g; Heather and Robertson 1996, wing span 56 cm; Warham 1990), circumpolar, abundant seabird of the order Procellariiformes and family Procellariidae (with fulmars, petrels, gadfly petrels and shearwaters; Harper and Kinsky 1978). Titiwainui and fulmar prions (*P. crassirostris*) form the subgenus *Pseudoprion* (Prince and Copestake 1990). Titiwainui breed around the Southern Ocean, and are most concentrated in the sub-Antarctic zone. They have never been found (breeding or otherwise) north of the equator. Their breeding sites are Tasmania/Bass Strait; Macquarie Island; Auckland Island; Snares Islands; North and South Islands of New Zealand; Stewart Island; Chatham Islands; Antipodes Islands; Falkland Islands; South Georgia; Marion and Prince Edward Islands; Crozet Islands; Kerguelen; and St Paul and Amsterdam Island (Warham 1990). Like most petrels of temperate seas they are spring and summer nesters (Warham 1990). In New Zealand the titiwainui breeding range exceeds 1200 km (Harper 1980), and is restricted almost exclusively to offshore and outlying islands due to predation on the mainland by introduced mammals (Heather & Robinson 1996), although there is a small breeding colony at Otago Peninsular (Graeme Loh pers. comm.).

Titiwainui are reported as incubating their single egg between 44 and 54 days, and the mean fledging period is between 45 and 50 days (Heather and Robertson 1996). The parental incubation shifts are 2.4 days at the Poor Knights Island (Harper 1976), 3-6 days on the Snares (Miskelly *et al.* 2001), and 5.6 days on Whero Island (Richdale 1965).

Within the Cook Strait region there are three main breeding colonies (at Stephens, Trios and Brothers islands; Heather and Robinson 1996). Takapourewa has an estimated 250,000 (Daugherty *et al.* 1990) to 500,000 breeding pairs of titiwainui (Brown 2001). Little is known of the breeding biology or absolute population of titiwainui within this region (Miskelly & Williams 2002), although this information is known for the Poor Knights Islands (Harper 1976) and Whero Island (Richdale 1965). There were some fundamental differences in the breeding behaviour in these populations, for example titiwainui on Takapourewa nest in burrows, but elsewhere they are known to nest beneath rock slabs (to a depth of ~ 1 m, Falklands; Strange 1968), in caves (Poor Knights; Harper 1976), among coastal rocks (Kerguelen; Warham 1990) and between large boulders (South Georgia; Prince and Copestake 1990). Previous studies have reported that

titiwainui burrow occupancy rates differ between habitats on Takapourewa (Markwell 1997) and elsewhere (e.g. North Brother Island; Gaston and Scofield 1995).

Titiwainui on Takapourewa feed almost entirely on 1-2 cm long euphausiid (*Nyctiphanes australis*) crustaceans (Walls 1978; Harper 1980; Harper 1987; Warham 1990). They feed by surface-seizing or dipping (surface seizing: taking prey from the surface or just beneath it; contact dipping: taking animals at the surface while still airborne; Prince 1980) for prey (Harper 1980; Harper 1987; Warham 1990). Titiwainui begin to arrive on Takapourewa in June, pairing and burrow excavation begins in late July, egg laying begins in October with hatching in early December. Chick departure is completed during February (Walls 1978).

Titiwainui as a keystone species

Titiwainui provide a direct source of food, shelter (by excavating burrows), and improved foraging and hunting conditions (through understory depletion, nutrient enrichment and increased invertebrate density) for tuatara (*Sphenodon punctatus*) and other herpetofauna (Walls 1978). This is reflected in the abundance of reptiles on Takapourewa (tuatara; Stephens Island gecko *Hoplodactylus stephensi*; green gecko *Naultinus manukanus*; common gecko *H. maculates*; four species of skink *Leiopisma infrapunctatum*, *L. lineocellatum*, *L. nigriplantare polychrome*; *L. zelandicum*). This abundance is attributed to titiwainui and other seabirds, as the guano they produce develops rich soils that encourage a high diversity and abundance of invertebrates (East *et al.* 1995). Due to their keystone role ecological conservation projects could be based around seabirds, thus knowledge of their abundance and behaviour is especially valuable (Markwell 1997).

Titiwainui are a candidate for translocation for habitat restoration. They are one of New Zealand's most abundant seabirds (Heather and Robertson 1996), they occupy a large latitudinal and longitudinal range, breeding on islands around mainland New Zealand; as far south as the Snares and Auckland Island, and as far east as the Chatham Islands (Heather and Robertson 1996). They have been translocated previously (e.g. to Mana Island, Miskelly and Williams 2002).

Breeding systems

A thorough knowledge of all factors that contribute to survival and breeding is crucial to manage a species effectively (IUCN 1998; Gardner 1999) and to assess translocation success (Sarrazin and Barbault 1996). Understanding the importance of the external physical requirements of nesting birds has conservation and management value; determining which resources are selected more often than others provides fundamental information about how animals meet their needs for survival (Manly *et al.* 2002). As burrow selection affects the probability of breeding success (Thompson and Furness 1991) suitable areas with desirable qualities for nesting can be actively protected (Stokes and Boersma 1991).

This study aims to establish which selected environmental conditions are most conducive to the successful breeding of titiwainui; i.e. which conditions result in increased burrow density, occupancy rates and fledging success. This information will be useful for establishing, or reinstating titiwainui colonies. Selecting optimal breeding sites for new colonies will increase the probability of the translocation being successful, i.e. establishing a self-sustaining population (Seddon 1999).

Although the breeding data collected were for only one season, the relative success between sites was able to be measured, thus data from multiple years were not necessary. This study also established patterns of colony expansion over time into the re-vegetated successional forest and un-grazed pasture. This information can be used to predict the long-term effects of re-vegetation on the breeding success of titiwainui on Takapourewa, and may also be applied to other, similar sites.

Impacts of and on revegetation

To achieve a successful translocation and manage a population of wildlife so that it may achieve self-sustainability with little or no further intervention it is vital to predict whether the new habitat meets the needs of the translocated individuals (Armstrong and McLean 1995; Strickland and McDonald 2006). It is generally thought the selection of resources disproportionate to availability indicates a benefit (e.g. fitness, reproduction, survival) in using the resources (Thomas and Taylor 2006). However, neither persistence in a habitat or seemingly preferential use are conclusive determinates of habitat needs due to the influences of external factors such as predation (Armstrong and McLean 1995). Prior to any species translocation

activity detailed studies should be made of the wild population, including habitat preferences, intraspecific variation and adaptations to local ecological conditions, shelter requirements, and predators (IUCN 1998). It is very important to measure vital rates (reproduction and survival) at sites featuring different habitat variables as vital rates are the only direct indicators of habitat quality (Armstrong 2005).

Once habitat requirements have been established the translocated individuals can be introduced to an area that fits these criteria to increase the likelihood of a successful translocation. This could potentially occur through habitat modification (the modification of habitats to favour nesting seabirds can maximize population size; Stokes and Boersma 1991), or the avoidance of sub-standard habitat (e.g. any attempt to establish a colony of small seabirds in an area of compacted soils would be jeopardised due to the difficulty of digging burrows; Atkinson 1990). Understanding what affects the survival of translocated nestlings is even more important in (presumably) small populations; any decline in numbers or dispersal from the translocation site (through high post-release dispersal or mortality, or low reproduction rates; Armstrong and Seddon 2008) may reduce heterozygosity (Stockwell *et al.* 1996), increase the risk of the Allee effect (when the population is insufficient for individuals to be able to locate each other to breed; Allee 1931), and undermine the entire project.

Likewise, it is important to understand the impact on the environment of the translocated species. Studies on Takapourewa suggest large increases in seabird numbers (and perhaps large tuatara numbers) may have negative impact on vegetation regeneration, by decreasing seed germination and seedling survival. Seedling survival may be decreased in an environment of high nutrient/low pH typical of dense seabird colonies, and physical damage to vegetation increases as seabird numbers increase (Mulder and Keall 2001).

Thesis Objective

The objective of this thesis is to ascertain which environmental variables result in the greatest breeding success for titiwainui on Takapourewa.

To address this objective, this study aims to test the following hypotheses:

- 1) Titiwainui burrow occupancy rates; chicks hatched; chicks fledged and chick fledge weight will be higher in forest sites than in pasture sites.

Rationale: Forest vegetation creates a micro-climate beneath the canopy (Taborsky and Taborsky 1995), offering greater protection than does pasture from weather variables such as wind, rainfall, and temperature variation (Walsberg 1985; Wachob 1996). This creates an environment more conducive to the successful fledging of seabird chicks, as it reduces the chance of the egg or chick being subjected to thermal stress (Garcia-Borboroglu and Yorio 2004; Lusk *et al.* 2006). Titiwainui burrow density varies between the forest (0.6 +/- 0.2 mean birds/m²) and the less protected shrub (0.4 +/- 0.1 mean birds/m²) habitats on Takapourewa (Markwell and Daugherty 2003), but it is not known how this relates to burrow availability.

- 2) Titiwainui burrow occupancy rates; chicks hatched; chicks fledged and chick fledge weight will be higher in north-facing sites than in south-facing sites.

Rationale: On Takapourewa it has been observed that titiwainui chicks are more numerous on north-east slopes than on south-east slopes (Miskelly and Williams 2002). On Takapourewa there are frequently winds of gale force or higher from both the north-west and the south-east. The winds from the southeast tend to carry more salt and be more damaging due to the orientation and topography of the island (Crook and Moran *pers. comm.*). Wind disrupts the thermal insulation of nesting birds (Walsberg 1985), thus nest temperatures are higher at sheltered sites (Storey and Lien 1985). The differences in microclimate due to aspect (Taborsky and Taborsky 1995) could affect the nestling period and survival of nestlings (Rauter *et al.* 2002).

- 3) Some burrow characteristics (increased temperature, increased complexity and increased length) positively affect chicks hatched, chicks fledged, and chick fledge weights.

Rationale: Burrows provide a different microclimate to external ambient conditions (Simons 1985; Warham 1990). For example, the chick body condition of sooty shearwaters (*Puffinus griseus*) was higher in more convoluted burrows, as increased burrow curvature protected against rainfall, wind and predation (McKechnie 2004); and longer burrows offer reduced temperature fluctuation (Simons 1985). Cory's shearwater (*Calonectris diomedea*) pairs with longer burrows had significantly higher hatching success than those with shorter burrows, possibly due to protection against rain and wind; Ramos *et al.* 1997).

- 4) Titiwainui burrow occupancy rates; hatch rates; and fledge rates will be highest in sites of low tuatara density.

Rationale: Tuatara are a known predator of titiwainui eggs and chicks (Walls 1978; Gaston and Scofield 1995). Tuatara density on Takapourewa is higher than anywhere else, with estimates of up to 1500 - 2000 individuals per hectare (Brown 2001), so it can be expected that their impact on their prey items is greater than elsewhere. As tuatara density varies between habitat types (East *et al.* 1995; Markwell 1997); impact on titiwainui will be greatest in areas of highest density.

Thesis structure

This thesis is divided into five chapters. Chapter 1 (this chapter) provides an introduction to the general topic, details of the study site and study species, a statement of aims, and an outline of thesis structure. Chapter 2 is a review of methods used to monitor seabird burrow use, and an investigation of the accuracy and reliability of burrow utilisation monitoring boards (BUM boards) to quantify burrow occupancy of Titiwainui on Takapourewa. Chapter 3 is the core data chapter; it applies intensive monitoring of burrows from four study sites on Takapourewa in a specific test of the four hypotheses outlined above. Chapter 4 explores how long it takes titiwainui to re-occupy sites after grazing stops/revegetation begins, and calculates the population of titiwainui on Takapourewa. Chapter 5 is a general discussion exploring management implications and making some specific recommendations that arise from this research.

Chapter two: Monitoring seabird burrow use

Why is accurate monitoring important?

It is necessary to collect base line data and undertake repeated monitoring to determine whether conservation programmes are achieving their objectives (Markwell 1997). For example, rigorous post-release monitoring is vital to gain clarity over which factors influence translocation success (Griffith *et al.* 1989; Lovegrove and Veitch 1994; Armstrong and McLean 1995; IUCN 1998). Monitoring not only helps to evaluate the outcome of a translocation, but can potentially explain patterns of mortality, social structure, reproduction and genetic relationships (Armstrong *et al.* 1999). In most cases it is not possible to measure the entire population under study, so a smaller sample is examined and the results extrapolated to the remaining population (Thompson 2002). In order to achieve this, the sample needs to be as large as practicable (Markwell 1997). In addition, if the sampling method used does not measure the variables within the whole population (i.e. a method used to check seabird burrow occupancy that only measures burrows less than x long) it is a sub-sample and may produce erroneous results (Thompson 2002). Hence it is imperative that the sample method chosen is as accurate as possible.

There is currently no ideal method to determine burrow occupancy in seabirds. As seabirds tend to nest down long and often convoluted burrows breeding activity is hidden from view (McKechnie 2004). Although it is relatively easy to estimate burrow density, this is of little use in biological studies unless occupation rates are known (Bull 1981; Warham and Wilson 1982; Warham 1990). In this chapter the most commonly used methods of monitoring burrowing seabirds will be discussed, and their pros and cons noted.

Direct reach

Direct reach is the method of feeling into a burrow by hand. This is a simple method as it requires no tools and minimal expertise. However, reaching an arm in doesn't work for long or twisting burrows (Warham and Wilson 1982). Given that this method only works for relatively short burrows with no acute angles, any data collected must be considered biased and should not be viewed as representative of the total population. In addition, arms can disturb the soil during

inspection and cause a weakening of the burrow or collapse (Warham 1990), so may have an impact on the results of the study.

Sign

Bull (1981) reported that sign of activity around a cavity can be used to verify it as a nest, and Simons (1985) found that down around the entrance of dark-rumped petrel (*Pterodroma phaeopygia sandwichensis*) burrows was almost always evident during the late chick-rearing phase, enabling an estimation of burrow activity. However, not all published results concur. A review of sooty shearwater (*Puffinus griseus*) monitoring methods by Hamilton (1998a) found that sign (odour, faeces, substrate digging, feathers/down) was only a poor indicator of burrow occupancy, and Cuthbert and Davis (2002) found that using field signs (presence of fresh diggings, scratches in the soil, faeces, feathers, broken fragments of fresh vegetation) to assess the occupancy status of burrow was likely to produce erroneous results in Hutton's shearwaters (*Puffinus huttoni*). Thus sign may be an appropriate method in some situations and at some stages of the breeding season but can not be relied upon to give accurate results in new or untested species or sites. This method requires no tools but some expertise in recognising sign.

Barricade

A barricade of small sticks or fine wires has been reported as the most practicable way to check movement in and out of a burrow (Warham 1990). This method is inexpensive and requires little expertise, and is regularly used to determine burrow use (e.g. Richdale 1963; Warham and Wilson 1982; Simons 1985; Chaurand and Weimerskirch 1994; Hamilton 1998b; Gardner 1999; Imber *et al.* 2003a). However, the barricade may record false positives by being displaced by factors other than breeding individuals (e.g. non-breeders; Warham and Wilson 1982, Moller *et al.* 2003b or other species; Warham 1990, Moller *et al.* 2003a), and once the barricade is knocked down it gives no indication of subsequent use (Markwell 1997; Moller *et al.* 2003b). Occasionally the target species can be identified using the barricade method; for example a lattice of grass was placed across the burrow entrance to monitor use by Manx shearwaters (*Puffinus puffinus*). Due to being a larger bird, the disruption to the lattice by Manx shearwaters could be distinguished from activity of Leach's storm petrels (*Oceanodroma leucorhoa*; Storey and Lien 1985). Also, the manner in which the barricade was knocked down and the condition of the tunnel (e.g. presence/absence of debris and nesting material) was used to confirm burrow use

by Chatham petrels (Gardner 1999). Generally though there is some ambiguity as to the cause when the barricade is displaced. There is a presumption that an intact barricade indicates no visit (Warham 1990), however this method has been known to record false negatives; a barricade of sticks was left intact after three days in 13.1% of occupied sooty shearwater burrows (Moller *et al.* 2003a). The reason for this is unknown. The reliability of the barricade method may change throughout the breeding season; Hamilton (1998a) found that $\geq 95\%$ of confirmed occupied sooty shearwater burrows had a barricade knocked down in eight nights during incubation; five nights during early chick rearing; and 16 nights during late chick rearing. Thus the accuracy of data collected can also be expected to change, for example if the barricades were left in place for seven nights around hatching they may record only those nests that had already hatched.

Pecking

Using a stick or wire to probe the burrow to encourage pecking can confirm occupancy (e.g. Hamilton 1998b) but as with direct reach this can be difficult in narrow and/or angled burrows (Imber *et al.* 2003a). This can sometimes be rectified by using bent or flexible wires, but they are not effective in soft earth or peat soil (Warham 1982). Eliciting pecks of known occupied burrows of sooty shearwater only worked 36% of the time on average ($n = 16$ chicks), and one chick did not respond by pecking on any of the nine days the burrow was monitored (Hamilton 1998a). Pecking response may be related to age or aggressiveness of the individual (Hamilton 1998a), so using this method may only sample some of the population. Using a stick or wire may also be useful to study individual birds as many petrels will grasp a wire pushed down to them and can be drawn out slowly as they will latch on to the wire with their bills (Warham 1990).

Acoustic response

Using acoustic playback to elicit a response can be useful in identifying occupied burrows (Warham 1982), as it is faster and less disruptive than most methods (Bull 1981). It was used successfully for white-chinned petrels (*Procellaria aequinoctialis*) at Bird Island, South Georgia (Berrow 2000). However, this method did not consistently produce a response in sooty shearwaters (*Puffinus griseus*), at Taiaroa Head, Otago Peninsular (nor did 'war whooping' or clapping promote a consistent response; Hamilton 1998b). Moller *et al.* (2003a) reported that the overall response rate to sound at occupied sooty shearwater burrows was far too low for the method to reliably measure occupancy levels; 3-6 visits detected only 34% (on Putauhinu) and

55% (on Whenua Hou) of chicks known to be present from burrowscoping and inspection hatches. Acoustic response can also result in false negatives; a chick response was heard at between 3.6% (on Whenua Hou) and 4.7% (on Putauhinu) determined to be unoccupied by burrowscope inspection (Moller *et al.* 2003a; however this may have been a reflection of inaccurate burrowscoping), so it is probably best suited to non-colonial species (Bull 1981).

Study lid

Study lids or inspection holes are simple and reliable, and have the advantage of allowing access to the contents for handling (Cuthbert and Davis 2002). Creating inspection holes over the nest chamber was an effective method for observing and extracting the occupants of burrows over 0.7m in length (Hamilton 1998a). However, the creation of and associated removal and replacement of study lids carries an increased risk of soil disturbance (Bell *et al.* 2005; particularly during periods of dry weather, Bell 1994) and in extreme cases chamber collapse (Seto and Jansen 1997). The seal around a study lid is seldom perfect, which can let water into the chamber and potentially cause breeding failure (Warham 1990). For long-term studies the study lids require maintenance most years (Cuthbert and Davis 2002). Study lids are very time intensive to create, for example it took approximately four hours to census 20 titiwinui burrows using a burrowscope, which was less than the time taken to dig observation holes (Markwell 1997). However, once they are in place monitoring is relatively easy. Due to the effort to construct them and the potential negative impact on the occupant, study lids are better suited to long-term or intensive studies than research that requires only determination of occupancy rates.

Burrowscope

A mini video camera with infra-red light attached to a long maneuverable tube while relaying a picture to a monitor (burrowscope) can be used to determine seabird burrow occupancy (Dyer and Hill 1991; Waugh *et al.* 2003). Burrowscopes don't interfere with burrow construction (Hamilton 1998a), and allow sufficiently large samples to be collected without excessive disturbance to burrow occupants (Markwell 1997). Burrowscopes are relatively accurate; they gave the correct description of burrow occupancy in 90.3% of Hutton's shearwater burrows (Cuthbert and Davis 2002), and correctly detected sooty shearwater chicks 82.4% (The Snares), 85.0% (Bench Island) and 85.7% (Putauhinu) of the time (McKechnie 2004). When burrows were classified as active during the first check of the season, there was a high likelihood of

accurately measuring breeding success with the burrowscope (Cuthbert and Davis 2002). However; the accuracy of this method can vary over the breeding season. Sooty shearwaters on the Snares were recorded but not present 1.1% of the time at egg, early incubation and late incubation phases; recorded twice from different burrow entrances at 6.6% of the time for eggs, 16.5% of the time during early incubation, and 23.1% of the time during late incubation; breeding was present but not recorded 33% of the time during egg stage; 34% of the time during early incubation phase, and 20% of the time during late incubation phase ($n = 91$ in all cases). Only 50% of burrows were recorded correctly for all three consecutive checks (Hamilton 2000). The probability of detecting a sooty shearwater egg, if present, using burrowscoping, varied from 0.42 to 0.96 (mean = 0.80, s.e. = 0.581); the range for detecting an early chick varied from 0.56 to 0.98 (mean = 0.87, s.e. = 0.102; Jones *et al.* 2003).

The accuracy of the method is also affected by the complexity of the burrow system; inaccuracies (i.e. missed nests, Hamilton 2000) were more likely in complex burrow systems (Cuthbert and Davis 2002). Burrow contents were usually unable to be classified in tight or twisted burrows, and burrows with branched chambers (Cuthbert and Davis 2002) or excessively long or narrow chambers (Seto and Jansen 1997). Chicks were usually undetected due to internal burrow divisions being missed, or tight corners preventing burrowscope insertion (McKechnie 2004). Tree roots could also block chambers and prevent burrowscope insertion (Seto and Jansen 1997). Inaccuracy was largely due to chicks remaining undetected, but also occurred when chicks were double-counted from more than one entrance (McKechnie 2004).

Burrowscopes are cumbersome (Hamilton 1998a) and time-consuming (a burrowscope required two people 15-20 minutes to examine one burrow; Seto and Jansen 1997), and take some degree of technical knowledge to use (McKechnie 2004). The outcome of burrowscoping is affected by the skill, efficiency (McKechnie 2004) and experience (Cuthbert and Davis 2002; Jones *et al.* 2003) of the operator. Thus the accuracy of burrowscoping may vary between operators, and between consecutive checks of the same burrow, dependent on conditions (Hamilton 2000). Additionally, burrowscopes rely on batteries (Seto and Jansen 1997), so may not be feasible for long-term use in isolated field conditions. As the accuracy of burrowscoping varies between users, species and sites, and throughout the season, it can not be viewed as an ideal method.

Electronic methods

There are some relatively sophisticated electronic methods also in use, for example electronic gate systems (Moller *et al.* 2003b) and television monitoring (Simons 1985). Although some aspects of these methods appear promising, they are not commonly used. This is probably because they incur a high initial cost, and require excessive labour and time to set up (Moller *et al.* 2003b).

Observer disturbance

There are multiple studies that show observance disturbance has negative impacts on seabirds:

- *Hatching success*: the proportion of observed eggs hatched may be lower than at undisturbed nests (Perrins *et al.* 1973). For example, observer disturbance accounted for hatching failures in 3.9% (three from 76) of manx shearwater study burrows (Brooke 1978);
- *Desertion*: Observer disturbance accounted for the desertion of little penguin nests after the adult birds were handled (Renner and Davis 2001);
- *Chick survival*: Observer disturbance may have accounted for the death of little penguin (*Eudyptula minor*) chicks when parent birds were extracted for weighing (Numata *et al.* 2004);
- *Chick weight*: Pycroft's petrel chicks were weighed once every day or every second night (study); or weighed only twice (control). At the first comparison (29 Jan) there was no significant difference between the two groups; at the second comparison (15 Mar) the control group significantly heavier. This was possibly due to handling stress, but may be due to age differences between the two groups (Gangloff and Wilson 2004).

However, there are also studies that report no negative impact due to nest monitoring:

- *Desertion*: Prions withstood handling (if done expeditiously) without deserting egg or chick (Warham 1982; Warham 1990);
- *Hatching and fledging success*: There was no significant difference in the hatching or fledging success of Hutton's shearwaters when checked via inspection hatches or burrowscopes. The inspection hatch method involved handling the eggs and chicks, the burrowscope method did not. No difference suggests that handling during incubation and

chick rearing didn't cause higher levels of disturbance or desertion than a burrowscope. However, both may cause high levels of disturbance or desertion (Cuthbert and Davis 2002). Fledging results of Pycroft's petrel study chicks also suggest that handling did not impair growth or survival (Gangloff and Wilson 2004);

- *Chick survival:* Survival of Jackass penguin (*Spheniscus demersus*) chicks was unaffected by frequent visits and handling (Seddon and van Heezik 1991);
- *Provisioning behaviour:* Repeated capture of sooty shearwater adults had no influence on their provisioning behaviour (Weimerskirch 1998); and feeding frequency of blue petrels (*Halobaena caerulea*) was similar in the control and more intensively monitored study burrows (Chaurand and Weimerskirch 1994);
- *General:* Observer intervention appeared to have no impact on breeding success of Manx shearwater (Storey and Lien 1985).

It is clear that the method used has to be carefully selected to gain the most information while causing the least disturbance. Some effort can be made to reduce the impacts of disturbance. For example, observer effect was likely to be less in burrow-nesting species where only one nest was disturbed at a time, rather than the whole colony of species which breed in the open (Renner and Davis 2001). Chatham petrels burrow in friable and unstable soil, so when found their burrows are replaced with artificial ones to reduce damage caused by observers (Gardner 1999). The impact of disturbance on individuals may reduce over time; when Atlantic petrel (*Pterodroma incerta*) chicks were initially handled some regurgitated, but after this they could be handled with no obvious detriment (Cuthbert 2004).

Given the difficulties in finding a method to ascertain the occupancy rates of seabird burrows, this study tested two methods on burrows of known occupancy to find the best method to use; a barricade of sticks ('study sticks'), and a new method; burrow utilisation monitoring boards ('BUM boards'). There was an initial pilot study to assess the feasibility of the methods (as recommended by Thompson 2002). The methods and results are discussed, and the pros and cons of the new method are noted. BUM boards record use of a burrow, and what was using the burrow. Study sticks record only use of a burrow. In this way BUM boards were expected to provide more information than study sticks.

Methods

Study sticks pilot

A barricade of four study sticks were fixed lightly in the soil equidistance across the burrow entrance of each of 13 burrows at each of four study sites (Pasture North [PN]; Pasture South [PS]; Forest North [FN]; and Forest South [FS]). ‘Forest’ sites were in areas of established endemic vegetation with a closed canopy; ‘Pasture’ sites were in areas of extensive rank grass; ‘North’ sites were in areas where the surrounding topography had a gentle slope facing 360°; ‘South’ sites were in areas where the surrounding topography had a gentle slope facing 180°. At each site direct reach/study lids were used to confirm the status of burrows. Ten burrows were confirmed used; three were confirmed unused. The barricades were left in place for four (n = three) or five (n = one) nights during the incubation phase (between the 21st and 26th of November 2004), and one (n = one), two (n = one), or four (n = two) nights during the chick-rearing phase (between the 11th and 15th of December 2004; the different lengths of time were due to logistical constraints). For each subsequent day the state of the study sticks and the occupant(s) of the burrow were noted. The state of the study sticks were defined as ‘in place’ if none or only one had fallen (as a titiwinui would not be able to pass through the burrow entrance and only disturb none or only one stick); ‘altered’ if two had fallen (as a titiwinui may have been able to pass through the burrow entrance and disturb only two sticks, but this was not likely); and ‘moved’ if three or four had fallen (as a titiwinui would have been likely to disturb three or four sticks if it had passed through the burrow entrance). Burrows with sticks ‘in place’ were considered not to have had a titiwinui pass through, and those with sticks ‘moved’ were likely to have had a titiwinui pass through. Burrows with ‘altered’ sticks could not be assigned either way. If the burrow contained an adult bird, it was identified by an individually numbered metal leg band each day. If the burrow contained a chick it was weighed each day as an increase in chick weight confirmed a visit from a parent bird. Chicks were placed into A4 sized 10 g unsealed plastic bags, and weighed using a 300g Pesola spring balance. The weight of the bag (10 g) was subtracted from the total weight to calculate the chick weight.

BUM boards pilot one

Another, previously untested, method of colour tracking was also used; burrow utilisation monitoring boards (BUM boards). This method consisted of placing a specially designed plastic tray (altered rodent indexing trays cut down to 25.5cm x 6.5cm and adhered with heavy-duty tape and silicon sealer) with three equal sized partitions (8.5cm x 6.5cm) just inside the burrow entrance. The middle partition held a piece of sponge soaked in diluted food colouring (kitchen sponge cut to 8.5cm x 6.5cm; dilution ratio: 1 part food colouring to 10 parts water). The two end partitions each held a piece of plain brown paper (8.5cm x 6.5cm), fixed in place with a paper clip (Fig. 2). Dye marks on the paper indicated the presence/absence of titiwainui in the burrow. This method followed the same design as tracking tunnels used for rodents and mustelids.

The method was tested on ten burrows of known occupancy over two nights (27/12/04 – 29/12/04) during the chick-rearing phase to see whether the method worked (i.e whether the tracks would show up on the paper, and whether the presence of the board would inhibit entry). The burrows used were from two study sites during the chick-rearing phase (Forest North and Pasture South, n = five per site). ‘Forest’ sites were in areas of established endemic vegetation with a closed canopy; ‘Pasture’ sites were in areas of extensive rank grass; ‘North’ sites were in areas where the surrounding topography had a gentle slope facing 360°; ‘South’ sites were in areas where the surrounding topography had a gentle slope facing 180°. At each site direct reach/study lids were used to confirm the status of burrows. Some burrows were unsuitable for the BUM board method as the entrances were sufficiently narrow that the BUM board could not sit flush with the bottom of the entrance and would potentially blocking the adult bird(s) from entering. There were four known occupied burrows and one known unoccupied burrow at each site. The chicks were weighed daily as an increase in chick weight confirmed a visit from a parent bird.



Figure 2. An example BUM board showing central compartment holding dye-soaked sponge and outer compartments holding paper.

Pilot analyses

A change of adult during the incubation phase would have the expected result of the study sticks being moved, whereas the presence of the same adults would have the expected result of the study sticks remaining in place. However, the same adult could have left the burrow and returned the same night. This would affect the results as the presence of the same parent would indicate the study sticks should be in place, but was not possible to control for. Titiwainui incubate their eggs over 1-5 day shifts (Harper 1976).

Weight gain of the chick was confirmation of adult visitation during the chick phase, as food regurgitated by adults is the only source of sustenance for chicks (Warham 1990; Gangloff and Wilson 2004; Pycroft's petrel chicks that experienced an overnight weight increase was taken to indicate the chick had been fed, whereas with no weight change from the previous day the chick was assumed to have not been fed). If weight remained the same or decreased the chick was classed as not being visited. Once hatched, titiwainui chicks are fed regularly (on 82% of nights on Whero Island, Richdale 1965; on 52% of nights at South Georgia, Prince and Copestake 1990). Titiwainui chicks fledge soon after they first emerge from their burrow (Colin Miskelly *pers. comm.*), so the chicks themselves were unlikely to interfere with the results. For both methods the data were analysed to see whether the state of the method applied and the weight gain or decrease of the chick concurred.

Pilot results

Egg phase

When the study stick data were collected daily during the egg phase, study sticks predicted occupancy of a known occupied burrow where the incubating adult was confirmed to have changed on only 27% of nights (Table 1). Results were classed as 'unknown' (study sticks were 'altered' so could not be assigned either way) on 27% of nights.

Chick phase

When the study stick data were collected daily during the chick phase, study sticks predicted occupancy of a known occupied burrow when chick weight increased on only 57% of nights (Table 1), and results were classed as 'unknown' (weights stayed exactly the same overnight) 22% of the time. There was a false positive result ('moved' study sticks at a confirmed unoccupied burrow) on 60% of nights (Table 2).

Table 1. Study sticks pilot study results (cumulative; used burrows expecting 'moved'; unused burrows expecting 'in place') showing percentage of correct responses, and percentage of correct responses excluding unknown, at egg stage and chick stage.

	Percentage of correct responses excluding 'unknown'	Percentage of correct responses total
Eggs	37%	27%
Chicks	72%	57%

Table 2. Study sticks pilot study results (each day separately) showing total nights, n burrows, and the result (moved, altered, in place) for used and unused burrows at the egg stage (n = 52 burrows), and used burrows at the chick stage (n = 52 burrows).

		Total				
		nights	n burrows	Moved	Altered	In place
Unused						
	burrows:	15	12	9 (60%)	5 (33%)	1 (7%)
Eggs	Used burrows:	130	40	83 (64%)	35 (27%)	12 (9%)
Chicks	Used burrows:	140	52	94 (67%)	32 (23%)	14 (10%)

BUM boards

When the BUM board data were collected daily, there was a correct prediction on 62.5% of nights in used burrows, and 100% of nights in unused burrows. Cumulatively, the BUM boards predicted the correct state of the burrow 100% of the time (Table 3).

Table 3. BUM boards pilot study results showing results from each day separately and the cumulative result. Results include the number and the percentage with the correct prediction.

BUM boards trial (each day separately)	Correct		
	prediction	n	%
Used & correct	10	16	62.5
Used & incorrect	6	16	37.5
Not used & correct	4	4	100
Not used & incorrect	0	4	0
BUM boards trial (cumulative result)	Correct		
	prediction	n	%
Used & correct	8	8	100
Used & incorrect	0	8	0
Not used & correct	4	4	100
Not used & incorrect	0	4	0

BUM boards main study

The results indicated that of the two tested methods the BUM board method was the more accurate. The pilot study was extended to gain a more rigorous understanding of the level of accuracy of the method (Thompson 2002). Twenty burrows were tested for three (n = 4 unused burrows) or four (n = 16 used burrows) consecutive nights. There were ten burrows selected at the FN and PN sites; eight confirmed used and two confirmed unused. The chicks were weighed daily as the method was applied. The method was then applied to 50 previously unstudied burrows within the four main study sites. The burrows were selected by walking a transect line through the main study areas and placing a BUM board in the entrance of all burrow within two meters of the line, excluding the study burrows. There were four unsuitable burrows at the PN site (the entrances were too narrow to allow a titiwinui to pass once the BUM board was in

place). All other burrows were suitable. The BUM boards were left out for three consecutive nights and checked on the fourth day. The sites weren't surveyed concurrently as there were only 50 BUM boards (FN: 14/01/05-17/01/05; PN: 18/01/05-21/01/05; PS: 21/01/05-24/01/05; FS 25/01/05-28/01/05).

From the BUM board extended trial, observations were classified into the following three groups:

- 1) Occupied and chick increased in weight (was fed)
- 2) Occupied and chicks didn't increase in weight (wasn't fed)
- 3) Unoccupied

For each of the three groups the probability of having a positive result on the BUM board (p_i) in a single night was estimated. For the second and third groups p_i was the probability of a false negative, as the chick was not fed. p_i can be estimated for each group by assuming that of the total number of burrows observed in each group each night (n_i), the number of burrows with a positive BUM board each night (n_i) is a random value from a binomial distribution, i.e., $x_i \sim \text{binomial}(n_i, p_i)$. The probability of a chick being fed in a single night ($pFed$) can also be estimated by considering the relative number of occupied burrows where chicks were and were not fed; $n_1 \sim \text{binomial}(n_1 + n_2, pFed)$. p_i and $pFed$ were estimated using Win BUGS (Lunn *et al.* 2000)².

Once the probability parameters were estimated, the fraction of the 200 study burrows that were likely to be occupied (using the BUM boards as a sampling device to determine occupancy) was calculated. Based on the initial pilot study there was the possibility of a false negative (burrow active but not tracked using BUM board), but not of a false positive (burrow not active but tracked). False negatives cause occupancy to be underestimated, false positives cause occupancy to be overestimated. By using data from the pilot study false results could be accounted for, thus correct estimates of occupancy could be obtained.

² WinBUGS is software that was developed for the application of Bayesian statistical methods to real data. The intent of Bayesian analysis is to obtain a posterior distribution for parameters (the probability distribution for the parameters after observing data and given prior understanding of the parameter distribution) rather than just point estimates, standard errors, and confidence intervals obtained from using maximum likelihood techniques.

As the 200 BUM boards were checked only after three consecutive nights rather than nightly, it was not possible to determine for how many nights a positive result was recorded. However, I could deduce that if a BUM board didn't track after three nights the results for each individual night was negative. Therefore, the probability of recording a positive track after three nights was one minus the probability of recoding a negative result on all three nights. The probability of recoding a positive BUM board on any night depended on whether the burrow was occupied, and whether the chick was fed each night (i.e. the probability was different depending on which of the three categories a burrow was classified as on any given night). If it was possible to determine which was the appropriate category for each burrow each night the probability of observing a negative result would have been $1 - p_i$. However, while the exact categories were unknown they were considered latent state variables and WinBUGS was used to predict the correct category. Given the predicted category, the probability of obtaining a negative result was obtained. The procedure for this modeling was:

- predict whether a burrow was occupied or unoccupied for the duration of the three nights (with probability P)
- predict whether the chick is fed or not for each night (with probability $pFed$)

The probability of a negative BUM board result each night was $1 - p_1$ if the burrow was occupied and the chick fed; $1 - p_2$ if the burrow was occupied and the chick not fed; and $1 - p_3$ if the burrow was unoccupied. The probability of a negative BUM board result after three nights is the product of the three respective probabilities: $(1 - p_i) (1 - p_i) (1 - p_i)$. Hence whether the BUM board was positive after three nights was a binary random variable with the probability $1 - (1 - p_i) (1 - p_i) (1 - p_i)$. As the probabilities of p_i and $pFed$ were estimated from the pilot study, the only remaining probability to be estimated was the probability of occupancy; P .

Using weight gain as the criterion for a chick being fed and no weight gain as the criterion for a chick not being fed is a substantial over-simplification and does not allow for small feeds or digestion rates (Prince 1980). If a chick was given a small feed, general weight loss through excretion may negate any observed weight gain. Thus the chick would incorrectly be recorded as not being fed. To counteract this, a proportion of expected daily weight loss was applied. Adult titiwinui weighed daily during their incubation shifts demonstrated a daily weight loss of $6.4 \pm 3.4\%$ (Gaston and Scofield 1995), so 6.4% was input as the expected loss, and any gain above this was recorded as a feed. Again, this is over-simplification as it doesn't allow for chicks

losing weight more rapidly during some periods than others (e.g. there was a rapid decline in the weight of titiwainui on the Poor Knights in the 10 days leading up to nest departure, due to physiological changes associated with feather development and increased movement at the nest; Harper 1976), it assumes that chicks of different sizes and in different burrows loose weight at the same rate, and it doesn't allow for chicks exploring pre-fledging. Previous studies have corrected weight data to allow for weight loss between being fed and weighed (e.g Gangloff and Wilson 2004).

When each night was analysed separately there was a correct prediction on 70% of nights. There was a false negative (the chick weight increased but there was no tracking on the board) only once (1.4% of the time). When a correction factor of a weight decrease of up to 6.4% was applied the number of correct predictions remained the same (70%), However, the number of false negatives increased to 10 (14%). For this reason the data were considered to be most accurate when adult visitation was deemed to have occurred only when chick weight increased overnight.

Results

Of the nights that the BUM boards were deployed, there was a determinate result 93.5% of the time. Of these results, 87.5% of the used burrows fitted the prediction, and 100% of unused burrows fitted the prediction. Both times that the BUM boards didn't track a titiwainui in a known occupied burrow the weight data concurred with the result – there was no chick weight gain thus no adult visitation during this time. On five (6.5%) occasions the results from the BUM boards could not be classified. One of these was due to the board being buried, potentially due to an adult entering the burrow, but possibly due to excavation from other species (i.e. tuatara), or digging from outside the burrow. One BUM board could not track due to the dye drying out. The remaining three had indeterminate marks present (marks were visible, but they were so faint it was not possible to determine what made them; Table 4.).

Table 4. BUM boards main study results.

	n	n total	%
Used and correct	14	16	87.5
Used and incorrect	2	16	12.5
Unused and correct	4	4	100
Unused and incorrect	0	4	0
Indeterminate result	5	77	6.49

The definition of whether chicks were fed each night was that the chick weight was greater than on the previous day. The BUM board method obtained a positive BUM (x_i) 76% of nights when the chick was fed, and 44% of nights when the chick wasn't fed (Table 5.).

Table 5. Summary of BUM board main study data given the number of burrows checked in each group (n_i) and number of a positive BUM (x_i).

	Chick weight greater than previous day	
	n_i	x_i
Occupied and chick was fed	21	16
Occupied and chick wasn't fed	43	19
Unoccupied	13	0

The posterior distributions have been summarised by their mean, standard deviation and 2.5th and 97.5th percentiles. P_X is the occupancy probability for the four groups. Despite the fact that no false positives were obtained for unoccupied burrows, the mean of the posterior distribution for p_3 is >0 (Table 6). Alternatively, p_3 could be set to 0. If this is done the following results in Table 7 are obtained.

Table 6. Posterior distributions summarised by mean, standard deviation and 2.5th and 97.5th percentiles, when $p_3 > 0$ (n = 76 nights; made up of 64 nights in known occupied burrows and 12 nights in known unoccupied burrows).

	Mean	SD	Lower 95% CI	Upper 95% CI
<i>p1</i>	0.74	0.09	0.55	0.89
<i>p2</i>	0.44	0.07	0.3	0.59
<i>p3</i>	0.07	0.06	0	0.23
<i>pFed</i>	0.33	0.06	0.23	0.45
<i>pFN</i>	0.53	0.1	0.32	0.72
<i>pPN</i>	0.58	0.1	0.37	0.77
<i>pFS</i>	0.22	0.1	0.03	0.41
<i>pPS</i>	0.45	0.1	0.24	0.65

Table 7. Posterior distributions summarised by mean, standard deviation and 2.5th and 97.5th percentiles, when $p_3 = 0$ (n = 76 nights; made up of 64 nights in known occupied burrows and 12 nights in known unoccupied burrows).

	Mean	SD	Lower 95% CI	Upper 95% CI
<i>p1</i>	0.74	0.09	0.55	0.89
<i>p2</i>	0.44	0.07	0.3	0.59
<i>p3</i>	0	0	0	0
<i>pFed</i>	0.33	0.06	0.23	0.45
<i>pFN</i>	0.6	0.08	0.45	0.76
<i>pPN</i>	0.65	0.08	0.49	0.8
<i>pFS</i>	0.34	0.07	0.2	0.49
<i>pPS</i>	0.54	0.08	0.38	0.69

When these results were plotted with the observed results of both the BUM board study and the study burrows, there wasn't concurrence. The observed study burrows had fewer chicks per burrow at all sites except FS (Fig. 3). This discrepancy between results may in part be due to the time of the season that the 200 BUM boards were placed. When the FN site was surveyed, none of the chicks were known to have fledged. By the time the FS site was surveyed, 75% of the chicks from the monitored nests had fledged. There was an attempt to correct for the proportion of chicks that had fledged at each site, but when the correction factor was applied the FS site ended up having >100% of chicks fledged (Table 8.).

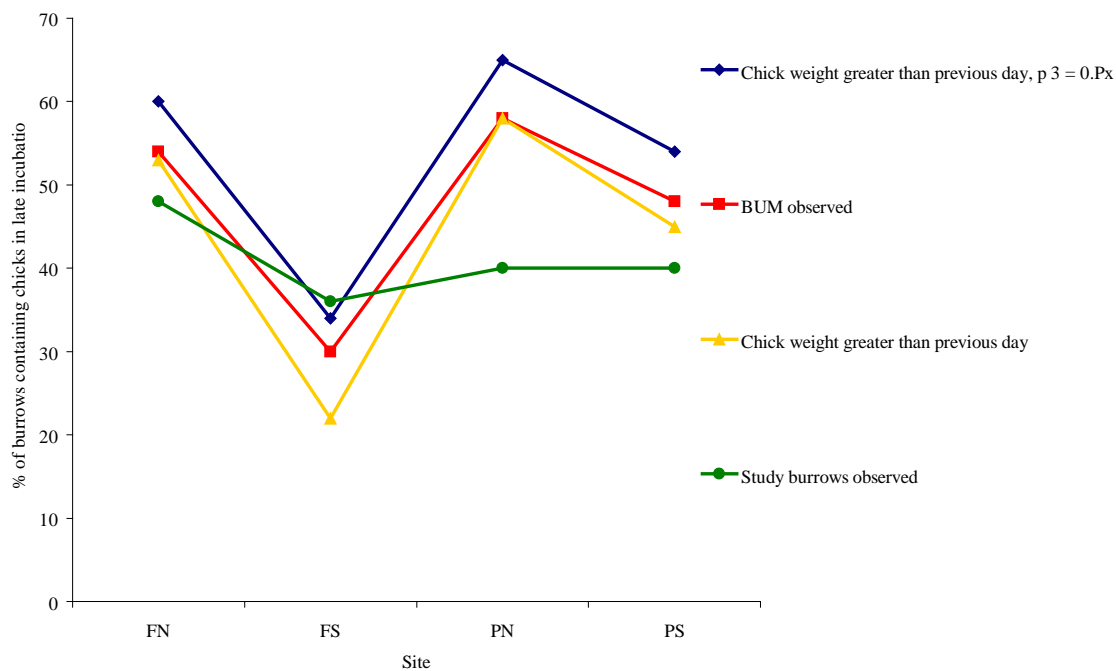


Figure 3. Observed state of burrows and chick weight change.

Table 8. Proportion of known chicks fledged at each study site (PN, PS, FN, FS) with BUM board result and correction factor applied for each site.

	PN	PS	FN	FS
Proportion of known chicks fledged	1/10	3/10	0/11	6/8
% of known chicks remaining	90%	70%	100%	25%
BUM board result x correction factor	32	34	27	60
Actual % occupied	58	48	54	30
Corrected % occupied	64	69	54	120
Intensively monitored burrows % fledged	37	36	48	36

Discussion

The results of the BUM boards could be quickly and easily interpreted almost all of the time, and they gave the correct result most of the time (87.5%) in used burrows and all of the time in unused burrows. Therefore this promising new method should be viewed as an accurate way of assessing presence/absence and breeding success of titiwainui borrows. It was not possible to fully test that accuracy of the BUM board method as it was used at one site (FS) after most (75%) of the chicks from that site had fledged. The attempt to correct the data to allow for some fledging to have occurred was unsuccessful. The trial of this method occurred late in the season due to the logistical constraints of completing field work at such an isolated site (supplies were delivered by ship every 4-6 weeks). It is recommended that this method should be tested at sites at the peak of the breeding season.

BUM boards were relatively quick and easy to use, especially when compared with laborious methods such as burrowscopes (Hamilton 1998a). The ease and speed at which BUM boards could be used meant it was easy to sample a large number of burrows. Large sample sizes are ideals as they give more rigorous estimations and descriptions of what is happening (Markwell 1997). Additionally, BUM boards didn't provide any false negative responses, so unoccupied burrows could be reliably interpreted as such. Unlike many other methods, the accuracy of BUM boards isn't affected by physical burrow characteristics (length, acute angles etc).

The use of BUM boards required little technical expertise. It was easy to place the BUM boards in the burrow entrances (although there was some judgement required on whether the burrow entrance was wide enough). There was some subjectivity in interpreting the BUM board papers, but unlike other methods that have to be examined and scored at the same time, they could be collected by anyone, carefully stored, and scored by an experienced person at a later date. The BUM board papers can be kept in perpetuity, so if there were future queries about the study the data could be referred to directly.

BUM boards give a picture over a period of time (the period of time that the board is left out for), other methods such as burrowscoping only record the state of the burrow at the exact time it is surveyed. In this way BUM boards can provide more information than simply presence/absence of the study animal. For example, BUM boards record results for all species

that use the burrow, not just the study animal. This ‘by-catch’ could have useful applications to the study (e.g. establishing the frequency of predators. Additionally, BUM boards could be used as a measure of breeding success; as an active burrow late in the chick phase had a high probability of fledge; 95.35% of burrows with chicks alive at 40 days (10 days prior to expected fledge at 50 days) fledged. If the object of survey is to obtain annual production then counts of chicks at or approaching fledging are necessary (Warham 1996).

There are also some limitations associated with the BUM board method. For example, it is not possible to use this method in inclement weather as rainfall would wash away the results, and wind could potentially dislodge the papers. Conversely, excessive sun or heat could dry the ink and prevent animals from tracking. Placing the BUM board right in the burrow instead of at the entrance could mitigate these issues. There is also a risk of soil being dislodged (by the study animal, by another animal, or by burrow collapse) and covering some or all of the BUM board. This was only observed once in this study.

Seabird burrow systems are often convoluted (e.g. McKechnie 2004), and as BUM boards don’t give any indication of whether the same entrance leads to multiple nests, or a single nest has multiple entrances, this method may not always provide an accurate picture of either burrow use, or breeding success.

The physical presence of the BUM board may be a deterrent to adults that would otherwise enter the burrow (due to an unknown object being in the burrow; and due to the burrow being slightly tighter). However, once a bird has sufficient investment in the nest it is unlikely to desert (Warham 1990). In the two cases where the known occupied nests weren’t visited during the four-day period of BUM board survey one returned to the burrow the day after the survey ceased, the other never returned and the chick perished. The last time there was evidence of that chick being fed was nine days before it was found dead, and again seven days before then, so the desertion is likely to be unrelated to the BUM board.

BUM boards provide an indication of burrow use, but don’t differentiate between breeders and nulliparous individuals (e.g. natal colony return by black petrels *Procellaria parkinsoni* tended to be 1-2 years before first breeding; Imber *et al.* 2003b). It may be possible to control for this depending on when the BUM boards were used. For example, non-breeders and pre-breeders are

more abundant early in the breeding season (Richdale 1963), but as chick-rearing progresses non-breeders and failed breeders leave (Warham 1990); failed or non-breeding titiwinui were ashore on the Snares from late Feb to early March 1986 (Miskelly *et al.* 2001); a colony of grey-faced petrels (*Pterodroma macroptera gouldi*) on Tiritiri Matangi Island contained both breeding and non-breeding birds at times, but non-breeders probably left during the pre-laying exodus and the end of chick hatching (Warham 1990; Ross and Brunton 2002).

Conclusions

In general, the BUM board method was applied with greater ease and accuracy than the study stick method. As the BUM board didn't detect 100% of known occupied nests it may be necessary to study a sub-sample of known occupancy burrows to calculate the detection probability of BUM boards at a given site. Using a corrected detection probability (a method that doesn't assume complete detection, and instead uses an applied ratio to calculate what proportion all individuals the detected individuals are likely to represent) reduces the likelihood of bias (Thompson 2002). If the detection probability was calculated this would be a very promising, innovative method that could be used to ascertain rigorous data about seabird burrow occupation rates and potentially breeding success.

Chapter three: Breeding biology of titiwainui on Takapourewa

Environmental effects on burrow density and breeding success

Nest site selection

Active selection of nest sites providing key attributes that increase breeding success is a well established process (Li and Martin 1991, Thompson and Furness 1991). Selection is the use of a resource by an animal disproportional to resource availability (Manly 1993). This process is observed through the preferential use of high quality sites (e.g. common guillemots *Uria aalge*; Kokko *et al.* 2004), variations in nest density dependent on specific habitat characteristics (e.g. Chatham petrel; Sullivan and Wilson 2001), and variation in population density related to habitat quality (Godfrey *et al.* 2003). Selection is driven by the perceived benefits of high-quality sites; for example individuals living in high-quality habitat may have lower daily energy expenditure than their counterparts living in lower quality habitat (Godfrey 2003a). It is plausible that the physical aspects of site quality may offer more reliable cues for nest site selection than the breeding success or failure of conspecifics (Kokko *et al.* 2004).

Selection appears to be for the function that the habitat element provides, rather than the habitat element itself (Lusk *et al.* 2006). This is true for seabirds selecting particular vegetation types, given that they aren't reliant on the surrounding vegetation for sustenance. There are some difficulties in assessing selection criteria:

- there is a assumption that nesting adults will select nest sites that maximise fitness of their offspring, but this may not always be the case (Lusk *et al.* 2006);
- maximum fitness is achieved by the trade-off of variables that affect energy expenditure (Godfrey 2003b), but selection for particular vegetation and aspect variables can be confounded due to the interplay between the two (for example, the canopy above successful mountain chickadee *Parus gambeli* nest boxes was more open in the southeast and less open in the northwest (Wachob 1996) masking the selection for and effect of both vegetation and aspect); and
- systems may have been altered by human-induced change (e.g. artificially large tuatara populations on Takapourewa due to the nesting benefits of the pasture habitat, Brown 2001), so selection may be masked by relatively recent and rapid change.

Vegetation

Seabirds preferentially select some vegetation types over others; for example on Rangatira/South East Island Chatham petrels actively selected nest sites within a vegetation height of 11-20m, and a canopy cover of 21-40%; and broad-billed prions (*Pachyptila vittata*) actively selected habitats where canopy cover was 61-80% and under-story cover was 21-40%, and actively avoided sites that were predominately grass (Sullivan and Wilson 2001). Nest site selection according to canopy height, shrub cover, and bare ground exposure was also observed in Northern bobwhites (*Colinus virginianus*). Vegetation affected not only nest site selection but also nesting success in this species (Lusk *et al.* 2006).

Selection according to vegetation may occur because vegetation buffers animals from thermal stress (Garcia-Borboroglu and Yorio 2004; Lusk *et al.* 2006) by shielding from wind and precipitation, reducing nocturnal radiation loss, and reducing diurnal heat gain from solar radiation (Walsberg 1985; Wachob 1996). Conversely, vegetative cover may be selected against in some cases to avoid the risk of entanglement and/or injury (Garcia-Borboroglu and Yorio 2004), and to maximise diurnal solar radiation (e.g. Mountain chickadees; Wachob 1996).

Aspect

Nest density may vary according to aspect (e.g. titiwinui on Falkland Island, Strange 1968; yellow-footed gulls at Bahia de los Angeles, Spear and Anderson 1989; Chatham petrels and broad-billed prions on Rangatira/South East Island, Sullivan and Wilson 2001; water pipit *Anthus spinoletta* in Switzerland, Rauter *et al.* 2002; grey faced petrels *Pterodroma macroptera gouldi* on Moutohora/Whale Island, Imber *et al.* 2003a). The preferred aspect tends to be northerly in the Southern Hemisphere, and southerly in the Northern Hemisphere, due to the greater solar radiation. An aspect preference tends to be away from the prevailing wind, as wind disrupts the thermal insulation of nesting birds (Walsberg 1985), thus nest temperatures are higher in sheltered sites (e.g. Manx shearwater, Storey and Lien 1985; tuatara on Takapourewa, Nelson *et al.* 2004). Variation in microclimate due to aspect can affect the duration of the nestling period and survival of nestlings (Rauter *et al.* 2002).

Temperature

Burrows, like other types of nest cavity, provide a different microclimate to external ambient conditions (Warham 1990). A study of the New Zealand long-tailed bat *Chalinolobus tuberculatus* found that mean tree roost burrow temperature was significantly higher than

ambient external temperature over a 24 hour period and ambient external temperature and humidity fluctuated to greater extremes, and more rapidly than cavity temperature and humidity (Sedgeley 2001). The tendency for burrow temperature to be more stable than external temperatures (Simons 1985) reduces thermal extremes. Exposure to thermal stressors can compromise the fitness of the animal inhabiting the burrow and make them more vulnerable to disease. Extremes of temperature can produce physiological reactions such as increased blood pressure and respiration; and long-term exposure can induce severe reactions, including cardiovascular disease and hypercholesteremia (Siegel 1980). Selection of sites that offer preferred temperatures reduce the exposure to stressors and promote faster growth of the occupants (Bakken and Kunz 1998). Although burrows offer shelter from excesses of wind and heat (Warham 1990), they do not entirely eliminate the effects of surface weather (Storey and Lien 1985), thus weather variables can still affect the daily survival of the occupant(s) (e.g. turkey *Meleagris gallopavo silvestris*, Roberts and Porter 1998).

Burrow characteristics

The physical characteristics of a burrow may affect breeding success. For example, nest site selection mediated by the physical characteristics of the immediate environment was observed in magellanic penguins (*Spheniscus magellanicus*); the distribution and density of their burrows was influenced by substrate depth, slope, and texture; and significantly more nested in burrows than above the ground (Stokes and Boersma 1991). Substrate may be selected for based on thermal properties (the insulating properties of earth vs. stone nests may have been responsible for differing chick survival rates of little penguins; Renner and Davis 2001), or due to the soil stability (the unstable soil on Takapourewa collapses titiwinui burrows, occasionally burying birds; Ward 1961).

The consequences of selection for particular physical characteristics may be enhanced breeding conditions. For example, the body condition of sooty shearwater chicks increased with more convoluted burrows, as increased burrow curvature protected against rainfall, wind and predation (McKechnie 2004); successful Mountain chickadee nest boxes had higher daily total solar radiation than unused boxes (Wachob 1996); Magellanic penguin fledging success was greatest in soil types least likely to collapse (Stokes and Boersma 1991); African penguin chick mortality was highest in open nests (Seddon and van Heezik 1991); and significant differences in little penguin chick survival was observed between nest types (tree nests; earth burrows; stone

nests; and open nests) due to rain-induced mortality being greater in some nest types than others (this was observed in 1995 but not in 1996; Renner and Davis 2001).

Cause of death

Tuatara

A further factor that may influence nest site selection and success is the density of predators. Tuatara and titiwainui share burrows (Mulder and Keall 2001), and tuatara are known to predate fairy prion eggs, chicks and adults, both above and below the ground, (Wright 1960; Gaston and Scofield 1995). Tuatara can also have non-lethal effects, as the presence of predators can increase the energy expenditure of potential prey through direct predator avoidance and effects on population density (Godfrey 2003a), and can deter parents from feeding their chicks (Godfrey 2003b). There are estimates of up to 30000 – 50000 tuatara on Takapourewa (Brown 2001), at densities up to 1500/ha (Newman 1987). As tuatara density differs between habitats (East *et al.* 1995; Gaston and Scofield 1995; Markwell 1997) they are likely to have an influence on nest site selection by titiwainui.

Poor parental synchronicity

Parental synchronicity affects the probability of a successful nesting attempt, as interrupted incubation can result in egg failure (Simons 1985; Jones *et al.* 2003). Seabird chick survival is also highly dependent on both parents being available for incubation and provisioning (Jones *et al.* 2003). Parent titiwainui were banded and their incubation patterns recorded to ascertain how their coordinated incubation and feeding affected the chick.

Aim

This chapter aimed to (a) identify those environmental variables mediating nest site selection by titiwainui on Takapourewa, and (b) determine how this selection affected breeding success. The following hypotheses were tested:

- 1) Fairy prion burrow occupancy rates, chicks hatched, chicks fledged and chick fledge weight, will be higher in forest sites than in pasture sites as the forest canopy offers protection from weather variables (Walsberg 1985; Wachob 1996) which reduces thermal stress on the egg or chick (Garcia-Borboroglu and Yorio 2004; Lusk *et al.* 2006).
- 2) Fairy prion burrow occupancy rates, chicks hatched, chicks fledged and chick fledge weight, will be higher in north-facing sites than in south-facing sites as southerly-aspect

winds in Takapourewa are more damaging than those from the north (Crook and Moran *pers. comm.*), and wind disrupts the thermal insulation of nesting birds (Walsberg 1985). The differences in microclimate due to aspect (Taborsky and Taborsky 1995) can affect the survival of nestlings (Rauter *et al.* 2002).

- 3) Some burrow characteristics (increased temperature, increased complexity and increased length) positively effect chicks hatched, chicks fledged, and chick fledge weights as burrows with these characteristics offer increased protection from rainfall, wind and predation (Ramos *et al.* 1997; McKechnie 2004).
- 4) Titiwainui burrow occupancy rates; hatch rates; and fledge rates will be highest in sites of low tuatara density as tuatara are a known predator of titiwainui (Walls 1978; Gaston and Scofield 1995) and tuatara density varies between habitat types (East *et al.* 1995; Markwell 1997).

Methods

Intensively monitored burrows

General field methods: Four study sites were selected: Pasture North (PN); Pasture South (PS); Forest North (FN); and Forest South (FS, Fig. 4). The sites were defined based on providing a representative sample for the variables vegetation (forest, pasture), aspect (north, south), and ease of access. ‘Forest’ sites were in areas of established endemic vegetation with a closed canopy; ‘Pasture’ sites were in areas of extensive rank grass; ‘North’ sites were in areas where the surrounding topography had a gentle slope facing 360°; ‘South’ sites were in areas where the surrounding topography had a gentle slope facing 180°. The sites were all in the northern half of Takapourewa (Fig. 4) as access is prohibited in the southern half due to fragile and unstable Titahi and Takapourewa soils, which are treacherous to walk on (Ward 1961).

One hundred study burrows were selected; twenty five at each of the four study sites. A central burrow was selected based on ease of access. Study burrows were systematically selected relative to a central burrow; all accessible burrows close to the central point were included (maximum area: 491 m²). One site (Pasture North) had two extra study burrows added during the course of the study (both on the 1st of November 2004), making this sample size 27. The burrows were added to replace non-viable burrows, to increase the sample size for chick data.

All entrances were initially checked manually to search for a nest chamber (the area where the burrow widens to accommodate the incubating adults and subsequent chick; Warham 1990). If the nest chamber was out of an arm’s reach of the entrance a study lid was added. This was constructed by reaching into the burrow as far as possible and digging a hole from directly above using a small metal trowel. The hole was used as a new point to try to reach the chamber. If it still couldn’t be reached a second hole was dug one arm’s length in from the study hole. If the chamber still couldn’t be accessed after two attempts it was considered that further digging would reduce the stability of the burrow, so the holes were blocked and the burrow not used in the sample. A ‘plug’ of soil or soil and vegetation was jammed into the superfluous hole(s), and filled in with soil to ground level. The plug ensured that soil did not fall in and block the burrow. If the soil was too friable for a plug to hold, a lattice framework of small sticks was placed in the

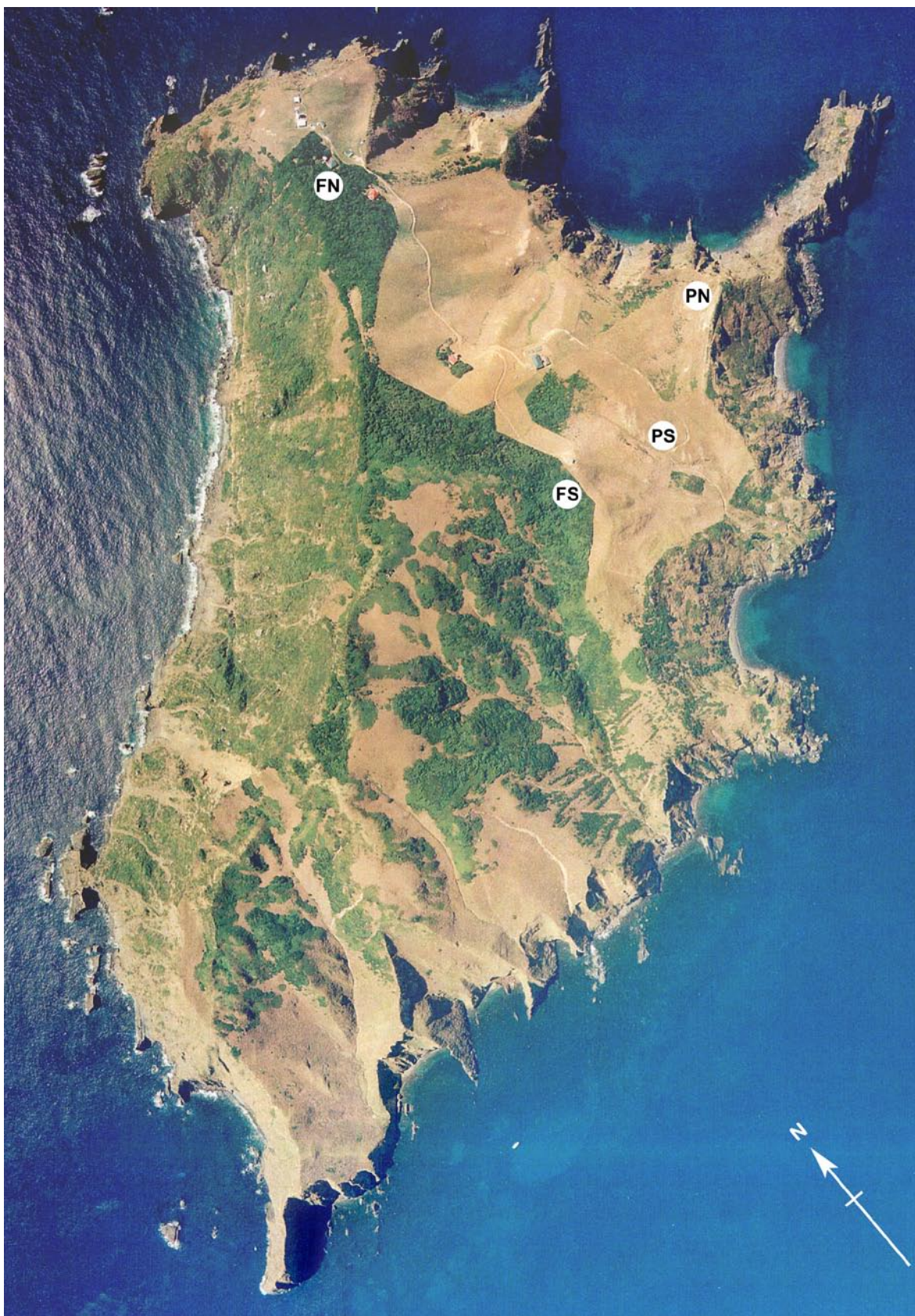


Figure 4. Aerial photograph of Takapourewa showing the four study sites (FN – forest with northerly aspect, PN – pasture with northerly aspect, FS – forest with southerly aspect, PS – pasture with southerly aspect; photo: DOC)

hole. This was then covered by leaves and filled in with soil to ground level. If the first hole allowed access to the chamber it was covered with a piece of timber weighed down with a rock or brick (study lid). If the second hole allowed access the first hole was blocked and the second hole covered with a study lid. The study lids varied in size according to the size of the hole, but they were approximately 30cm x 30cm. The edges of the lids were buried to reduce any light or water entering the burrow through the study hole. All burrows were numbered and labelled with a piece of blue 'flagging tape' attached to wire and pushed into the ground at the burrow entrance for sites with no study lid, or midway between the burrow entrance and study lid. The tag was placed far enough away from the entrance so as to not interfere with passing birds. The study burrows represented a sub-sample of burrows that were relatively easy to reach (between 460 and 1555 cm). This bias could potentially favour younger birds, as they tend to nest in shorter burrows (Warham 1996). However, the 102 burrows selected for study came from a sample of 109 that were considered for study, so 92% fitted the criteria. As rejected burrows only represent 8% of the total it is not considered their exclusion would bias the results. The burrows that were rejected were either too long or too deep for study holes to facilitate reaching the nest chamber. Burrows were monitored up to 60 times between the 17th of October 2004 and the 2nd of February 2005 (the day the last monitored chick fledged). The presence/absence of adults, eggs and chicks were noted; and adults and chicks weighed (see appropriate sections for further details). Adults and older chicks were returned to the nest chamber via the tunnel; young chicks were placed directly into the chamber. Monitoring ceased once an egg or chick had failed, or when a chick had successfully fledged. The forest sites had very friable and fragile soil that were prone to collapse (Ward 1961; Mulder and Keall 2001), so a series of boardwalks were installed to enable movement around these areas with the least risk of burrow collapse (follows West and Nilsson 1994; Markwell 1997). Burrow visits did not occur during or immediately after rain to avoid getting down/feathers and chambers wet (Gardner 1999), and to minimise the risk of collapsing the already fragile burrows. Wind interfered with weight measurements, so on particularly windy days the occupancy status of the burrows was checked, but no weighing took place.

General analyses: All data were analysed using SPSS 11.0 statistical software. All continuous data were examined for normal distribution using the Kolmogorov-Smirnov (K-S) test. All data exhibited normality so transformation was not necessary. All data were pooled by vegetation (forest and pasture), and aspect (north and south) where possible, as examining one variable at a time leads to a higher chance of encountering a Type I error (Zar 1999). This may

result in there being no perceived differences, although there may be real differences in the multivariate distribution (Thomas and Taylor 2006). All data was ‘censored’; i.e. if some of the data for an individual was missed (e.g. hatch date or fledge weight) the remaining data was only used to estimate the variables that were observed (follows Renner and Davis 2001). Data with categorical factors and a continuous response variable were analysed using univariate analysis of variance (follows Ramos *et al.* 1997). Data with categorical factors and a binary response variable were analysed using logistic regression. This study fits Manly *et al.*’s (2002) description of a type 2 study design; habitat use by individuals is observed, but non-use is described only at the population level. Type 2 designs allow examination of the variation in selection strategies.

Burrow occupancy

Field methods: The 25 study burrows at each site were monitored daily as weather conditions permitted, and the presence/absence of use recorded. Use was confirmed by the presence of adult(s) and/or egg(s). If the burrow was classed as used and the state later changed (e.g. an egg was encountered which later disappeared), the classification remained the same. If the burrow was classed as not used and the state later changed (e.g. no egg found initially, but one encountered later in the breeding season), the classification was changed.

Analysis: Burrow occupancy data had categorical factors (aspect and vegetation type) and a binary response variable (burrow used or not), so were analysed using logistic regression. A full factorial model was selected, which also tested for an interaction effect between aspect and vegetation.

Burrow occupancy rates per m² were calculated by establishing burrow density, and applying a factor of burrow use (after Markwell 1997).

Burrow density

Field methods: the density of burrows in all sites (PN, PS, FN, FS) were calculated along transect lines. Transects were used due to the fragility of the soil; quadrats were deemed to be too invasive and carried an increased risk of collapsing burrows. Transects were placed every 5 – 10 m at an angle that afforded the longest possible continual transect within the survey site. All burrows within 1 m either side of the transect line were counted, at 5 m increments. All transects followed a fixed compass bearing. Total transect lengths were 40 m (80 m²; FN and PN), 45 m

(90 m²; FS), and 70 m (140 m²; PS). Transects crossed the study sites two (FN and PN) or three (FS and PS) times. The samples were different lengths due to the differing shapes of the study sites. All data were collected on the 31st of January 2005.

Analysis: Burrow density data had categorical factors (aspect and vegetation type) and a continuous response variable (burrow density), so were analysed using a univariate analysis of variance. A possible interaction effect between aspect and vegetation was explored.

Chicks hatched

Field methods: As the study burrows were being monitored the presence/absence of a chick was recorded. Chicks were found by hand in the nest chambers. The first encounter with the chick was often in the absence of an adult bird, so they were directly visible. If the adult bird was still brooding the presence of a chick could sometimes be determined by hatch sign (e.g. egg shell visible in the chamber; peeping heard or down visible under the adult; follows Gardner 1999). If there was no hatch sign a hand was used to feel under the brooding bird.

Analysis: Chick hatch data had categorical factors (aspect and vegetation type) and a binary response variable (chick or not), so were analysed using a logistic regression. A full factorial model was selected, which also tested for an interaction effect between aspect and vegetation.

Chicks fledged

Field methods: As the study burrows were being monitored the presence/absence of the chick was noted. Any chick missing late in the chick phase after being found fully feathered and in good health was deemed to have fledged (follows Gangloff and Wilson 2004).

Analysis: Chick hatch data had categorical factors (aspect and vegetation type) and a binary response variable (fledge or not), so were analysed using a logistic regression. A full factorial model was selected, which also tested for an interaction effect between aspect and vegetation.

Breeding success

Analysis: Breeding success can be defined as mean number of birds fledged per pair nesting (Thibault 1994), or proportion of chicks surviving to the late chick phase per egg laid (Cuthbert and Davis 2002). For this study breeding success was defined as the number of chicks fledged per egg laid.

Breeding success data had categorical factors (aspect and vegetation type) and a binary response variable (egg survived to fledge or not), so were analysed using a logistic regression. A full factorial model was selected, which also tested for an interaction effect between aspect and vegetation.

Chick fledge weights

Field methods: Fledge weights were calculated by weighing the chicks in the study burrows during the last day of contact prior to fledging. A minimum of eight and a maximum of 11 chicks fledged from the 25 or 27 burrows at each site. It was considered that this was insufficient data to generate accurate mean fledge weight. The sample was increased by capturing chicks above the ground at night, just prior to fledging (follows Perrins *et al.* 1973). These were weighed in the same manner as the study chicks. At each of the study sites there was a focused ‘take-off’ area (with short or no ground cover and no canopy) that the extra samples were taken from so they could be assigned to a vegetation and aspect group. It is feasible that chicks travelled away from their natal zone thus were assigned to the incorrect vegetation or aspect group; however the study sites were relatively small areas in a much larger area of the same vegetation type and aspect, so even if they had moved they were still likely to have come from burrows with the defined variables. Chicks emerge from the burrow prior to fledging (e.g. Perrins *et al.* 1973; Imber *et al.* 2003b), so may have been captured on the surface *prior* to departure thus would not have been at fledge weight, and it is possible that the same animals were counted more than once. However, this seems unlikely as most chicks were observed flying off immediately after handling, and as most chicks get to sea on their first flight (Warham 1990) it was presumed they fledged. Titiwainui chicks tend to fledge soon after emergence, as was observed in a study of titiwainui transferred from Takapourewa to Mana Island 2003 and 2004 (Colin Miskelly *pers. comm.*). The chicks may have fledged prematurely due to observer disturbance in the current study but it is not possible to correct for this. Chicks were identified by the presence of down. This was often minimal amounts (e.g. only one or two wisps left on the nape or belly) so difficult to spot. Adults were identified by the complete absence of down and protruding bellies (the measurements took place during the first few hours of darkness when the adults were coming in from sea to feed the remaining chicks, and were carrying food to regurgitate for their young). All birds encountered could be easily classed in one of the two categories.

Analysis: Chick weight decreases asymptotically after a chick had been fed (Ricketts and Prince 1981; Weimerskirch 1998), due to defecation and respiration (Ricklefs *et al.* 1985; Warham 1990), so chicks continue to lose weight from the time of their last parental feed until they fledge and are able to forage themselves. The study burrow chicks were weighed prior to fledging, and the extra weight chicks at the point of fledging. To make these data comparable the average daily decrease in weight after the last feed before fledging was calculated for the chicks at each study site. The weight decrease ranged from three to 22 grams (PN 3-12; PS 9-21; FN 10-22; FS 6-21). Mean weight loss was 8.1 g (PN, n = seven); 12.8 g (PS, n = six); 14.6 g (FN, n = eight); and 15.3 g (FS, n = six). Two chicks (PN18a and FS8) gained weight just prior to fledging (one and three grams respectively). These were considered anomalies, so were excluded from average weight loss calculations. The mean loss figure was divided by three to represent eight hours (the estimated mean time between being weighed and fledging) and subtracted from the fledge weight for the study sites.

Fledge weight data had categorical factors (aspect and vegetation type) and a continuous response variable (weight), so were analysed using a univariate analysis of variance. An interaction effect between aspect and vegetation was tested for. Study fledge weights and extra fledge weights were pooled.

Burrow characteristics

Complexity

Field methods: Burrows were explored thoroughly by hand at first encounter and categorised as either single (one entrance, one chamber) or multiple (more than one chamber or entrance) burrows.

Analysis: Burrow complexity data had categorical factors (aspect and vegetation type) and a binary response variable (single or multiple), so were analysed using a logistic regression. A full factorial model was selected, which also tested for an interaction effect between aspect and vegetation.

Length

Field methods: Burrow length was measured for all study burrows by manually feeding a piece of string along the length of the burrow to the end of the nest chamber. The string was

marked at the entrance, removed from the burrow, and measured using a standard metric tape-measure. The burrow length measurements were taken during the egg phase, so the length from the burrow entrance to the egg (if present) was also measured, using the same method.

Analysis: Burrow length data had categorical factors (aspect and vegetation type) and a continuous response variable (burrow length), so were analysed using a univariate analysis of variance. An interaction effect between aspect and vegetation was also tested for.

Temperature

Field methods: the ambient air temperature one centimeter above the ground was measured in the centre of each of the four study sites (PN, PS, FN, FS). The inside air temperature one centimeter above the ground was measured in the nest chamber of ten arbitrarily selected burrows at each site. The measurement was taken from the area directly above the chick roost; or from the area where the burrow widens to a chamber for the out of use burrows. All temperatures were measured using a mercury thermometer. The thermometer was held in place manually for the time it took for the mercury to stop moving (approximately one to five minutes). Of the ten burrows, six were recently used and four were previously failed or never used. Samples were taken after the respective chicks had fledged, to avoid disturbance. The measurements were taken at all sites between 1400 and 1700 on the 27th of January 2005, and repeated at all sites between 1245 and 1530 on the 29th of January 2005. The samples were collected in the order of FN, PS, PN, FS on the first day, and PN, PS, FS, FN on the second day. The order of sample collection differed between the two days because time of day affects temperature.

Analysis: The data from day one and day two were analysed separately. Temperature was a continuous response variable, and aspect, vegetation type and whether the burrow was used were categorical factors, so data were analysed using a univariate analysis of variance. All interaction effects were tested for.

Cause of death

Field methods: Where possible the cause of failure of eggs and death of chicks from the study burrows were determined. Eggs were classed as predated (tuatara)/missing if the egg was absent from the burrow; poor synchronization/desertion if the egg failed following interrupted incubation and/or desertion; burrow collapse if the egg failed following burrow or chamber

collapse; and broken/evicted if the egg was found broken in the chamber or burrow, or cold outside the chamber or entrance. Any evicted eggs were measured to confirm they came from the associated burrow.

Chicks were classed as predated (by tuatara) if they were found dead in the chamber or burrow, or just outside the entrance either decapitated or with crushing injuries to the head and bruising and wounds on the body. One chick was missing from the burrow but there was down and blood evident at the entrance. The down and blood trailed 3 m up hill from the burrow to a second burrow. The dead chick was found inside with crushing injuries, in the mouth of a tuatara, so this was recorded as predation. In two cases a dead chick was found with injuries to the head, but these were not consistent with the crushing typical of tuatara, so were recorded as unknown. Chicks were classed as starved if they lost weight for several days before dying (follows Renner and Davis 2001); burrow collapse if the chick died following burrow or chamber collapse; and expulsion if the chick was found dead outside the burrow with no sign of external injury.

Analysis: The proportion of eggs or chicks that died at each site was calculated. Data were tabulated and explored, but results were insufficient to perform any statistical analyses.

Results

Intensively monitored burrows

Of the 102 burrow monitored, 10 were unused, 31 failed at the egg stage, 14 failed at the chick stage, 43 chicks fledged, and four burrows had unknown breeding outcomes. There were no unused burrows at the FN site, but almost twice as many eggs (ten) failed here than at PS (six). FN and PN each had 12 chicks fledge, slightly higher than the other two sites (Table 9).

Table 9. Results of the 102 intensively monitored burrows, grouped by site (percentages in parentheses).

	Burrow removed /results					
	Unused	Failed egg	Dead chick	Fledged chick	unknown	Total
FN	0	10 (40)	3 (12)	12 (48)	0	25
FS	3 (12)	7 (28)	5 (20)	9 (36)	1 (4)	25
PN	3 (11)	8 (30)	3 (11)	12 (44)	1 (4)	27
PS	4 (16)	6 (24)	3 (12)	10 (40)	2 (8)	25
Total	10	31	14	43	4	102

Burrow occupancy

The proportion of study burrows used was not significantly different when grouped by vegetation (LR $X_1^2 = 0.004$ $P = 0.95$) or aspect (LR $X_1^2 = 0.0$ $P = 1.0$), and there was no significant interaction between vegetation and aspect (LR $X_1^2 = 0.066$ $P = 0.798$; Table 10).

Table 10. Proportion of burrows used, showing SE and upper and lower 95% CI, grouped by vegetation type and aspect.

	n	Burrows used/			
		burrows studied	Standard error	Lower 95% CI	Upper 95% CI
Forest	52	0.917	0.040	0.836	0.998
Pasture	50	0.840	0.052	0.735	0.945
North	52	0.918	0.039	0.839	0.998
South	50	0.837	0.052	0.729	0.944

Burrow occupancy rates per m² were similar for FS and PN (1.40 and 1.41 respectively, but much more for FN (2.49) and much less for PS (0.75; Table 11).

Table 11. Used burrows/m², calculated using burrows used/burrows studied and burrows/m² data, grouped by site.

	N	Burrows/m²	Burrows used/burrows studied	Used burrows/m²
FN	27	2.49	1.00	2.49
FS	25	1.64	0.83	1.40
PN	25	1.68	0.84	1.41
PS	25	0.89	0.84	0.75

Chicks hatched

The number of chicks hatched was not significantly influenced by vegetation (LR $X_1^2 = 0.233$ $P = 0.629$), aspect (LR $X_1^2 = 0.347$ $P = 0.556$), or an interaction between vegetation and aspect (LR $X_1^2 = 0.002$ $P = 0.962$; Table 12).

Table 12. Chicks hatched/eggs laid, showing SE and upper and lower 95% CI, grouped by vegetation type and aspect.

	Chicks			
	hatched/egg laid	Standard error	Lower 95% CI	Upper 95% CI
Forest	0.622	0.073	0.475	0.770
Pasture	0.690	0.072	0.574	0.807
North	0.617	0.072	0.473	0.761
South	0.700	0.073	0.552	0.848

Chicks fledged

The number of chicks fledged was not significantly influenced by vegetation (LR $X_1^2 = 0.510$ $P = 0.475$), aspect (LR $X_1^2 = 0.931$ $P = 1.0$), or an interaction between vegetation and aspect (LR $X_1^2 = 0.822$ $P = 0.364$; Table 13).

Table 13. Chicks hatched/chicks fledged, showing SE and upper and lower 95% CI, grouped by vegetation type and aspect.

	Chicks fledged/ chicks hatched	Standard error	Lower 95% CI	Upper 95% CI
Forest	0.750	0.083	0.579	0.921
Pasture	0.769	0.084	0.596	0.943
North	0.815	0.076	0.658	0.971
South	0.704	0.090	0.520	0.888

Overall, there were no detected differences in either the incubation or nesting periods; or the dates that egg were laid and chicks hatched and fledged, between any of the study sites (Fig. 5).

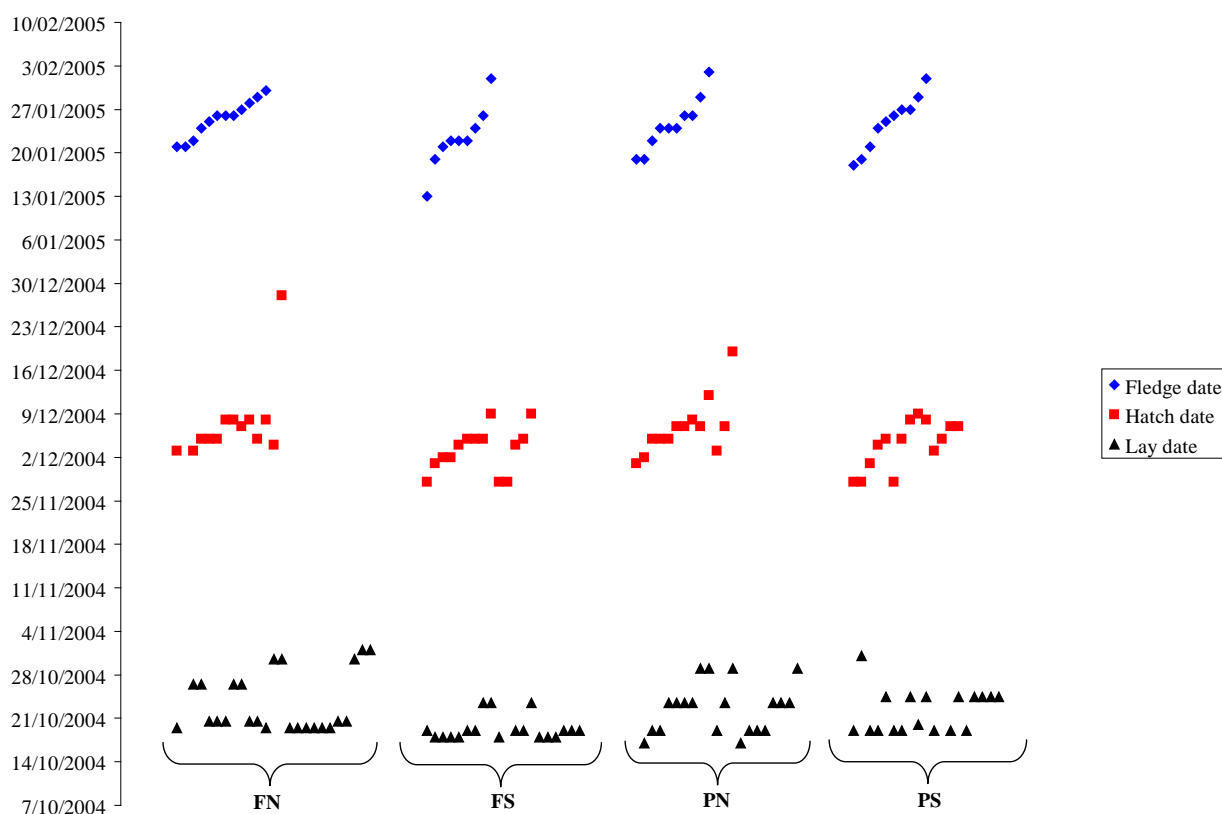


Figure 5. Lay date, hatch date and fledge date for all eggs and chicks, grouped by site.

Breeding success

The ratio of chicks fledged per egg laid was highest for Forest North (0.6) and lowest for Forest South (0.45). The ratio of chicks fledged per burrow used was also highest for Forest North (0.5) and lowest for Forest South (0.45; Table 14). The proportion of chicks fledged per egg laid was not significantly influenced by vegetation ($LR X_1^2 = 0.227 P = 0.634$), aspect (LR

$X_1^2 = 0.027$ $P = 0.869$), or an interaction between vegetation and aspect (LR $X_1^2 = 0.616$ $P = 0.432$).

Table 14. Burrows used, eggs laid and chicks laid, with fledge:burrow ratio and fledge:egg ratio, grouped by site.

	Burrows used	Eggs laid	Chicks fledged	fledge:burrow ratio	fledge:egg ratio
FN	24	20	12	0.5	0.6
FS	20	20	9	0.45	0.45
PN	21	20	10	0.476	0.5
PS	21	19	10	0.476	0.526
Mean				0.476	0.519

Chick fledge weights

There was no significant difference in mean fledge weights from forest sites and mean fledge weights from pasture sites ($105.92 \pm .79$ g and 103.55 ± 1.05 g, respectively; ANOVA, $F_1 = 0.129$, $P = 0.720$). There was no significant difference in mean fledge weights from south sites and mean fledge weights from north sites (104.93 ± 0.88 g and 104.39 ± 1.04 g, respectively; ANOVA, $F_1 = 1.085$, $P = 0.299$; Table 15). There were no significant interaction effects (ANOVA, $F_1 = 0.283$, $P = 0.595$).

Table 15. Mean fledge weight (g), showing SE and upper and lower 95% CI, grouped by vegetation type and aspect.

		Mean fledge weight (g)	Standard error	Lower 95% CI	Upper 95% CI
Forest	85	105.92	0.79	104.35	107.49
Pasture	93	103.55	1.05	101.47	105.64
North	80	104.39	1.04	102.33	106.45
South	98	104.93	0.88	103.18	106.67

Burrow characteristics

Burrow complexity

The percentage of multiple-chambered burrows ranged between 29.5 – 41.3%; Pasture sites had 11.8% more multiple burrows than Forest sites, North and South sites were similar (34.1 and 37.0% respectively; Table 16). One burrow (PS 12) had a single chamber and two entrances, but there were no observed burrows with both multiple entrances and multiple nest chambers (this was also observed by Markwell 1997). The proportion of single or multiple burrows was not significantly influenced by vegetation (LR $X_1^2 = 2.279$, $P = 0.131$), aspect (LR $X_1^2 = 0.802$, $P = 0.371$), or an interaction between vegetation and aspect (LR $X_1^2 = 0.983$, $P = 0.321$). Although the ratio of multiple chambers to single chambers changed at all sites between all burrows, and only those burrows that fledged chicks, the overall ratio remained the same (Table 17). There was no relationship between burrow complexity and fledge weight (Fig. 6; t -test $P = 2.03$).

Table 16. Percentage of burrows with multiple chambers, showing SE and upper and lower 95% CI, grouped by vegetation type and aspect.

	% multiple chambers	Standard error	Lower 95% CI	Upper 95% CI
Forest	29.5	7.0	15.5	43.6
Pasture	41.3	7.3	26.5	56.1
North	34.1	7.2	19.5	48.7
South	37.0	7.2	22.5	51.4

Table 17. Ratio of multiple chambers to single chambers for all burrows (n = 102), and for burrows that fledged chicks (n = 43).

Site	All burrows	Burrows that fledged chicks
FN	0.50 : 1	0.43 : 1
FS	0.35 : 1	0.13 : 1
PN	0.53 : 1	0.50: 1
PS	1 : 1	3 : 1
Total	0.57 : 1	0.57: 1

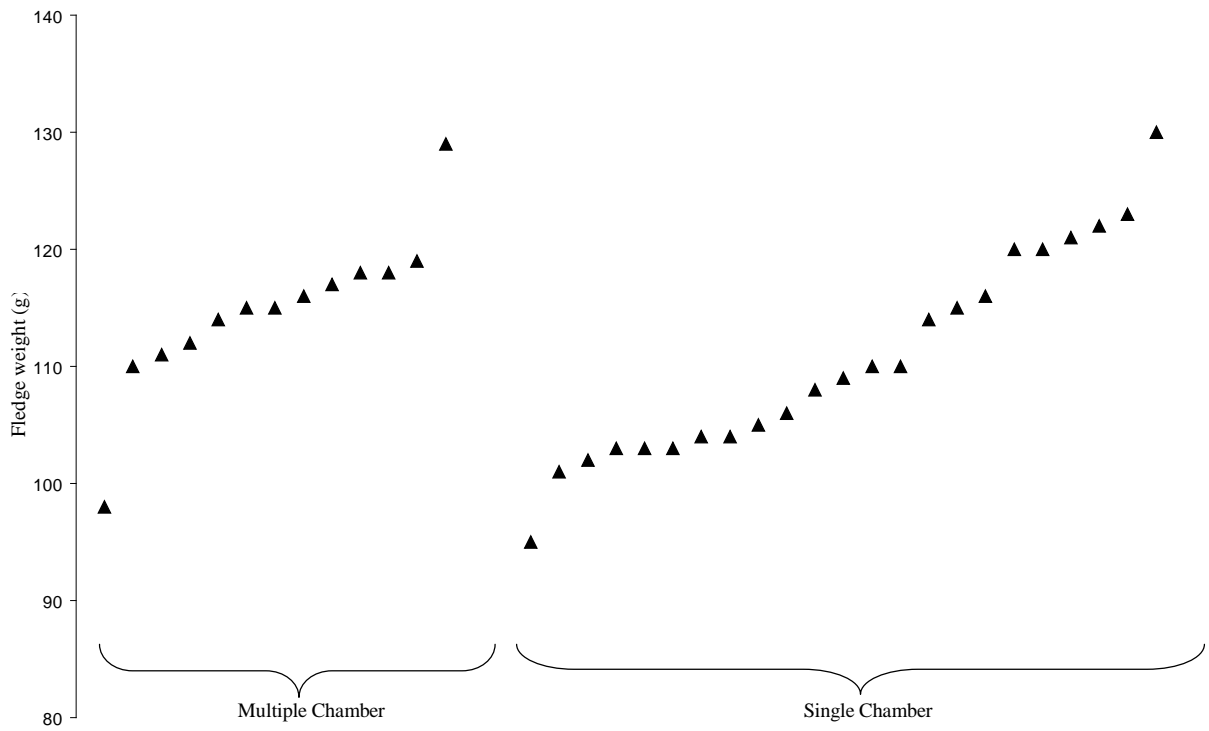


Figure 6. Fledge weight of chicks grouped by single and multiple chambered burrows.

Burrow length

Burrow length ranged from 460 mm to 1555 mm. Burrows were significantly longer in pasture sites (845.11 ± 31.13 mm) than forest sites (745.11 ± 26.97 mm; ANOVA, $F_1 = 7.397$, $P = 0.008$). There was a significant interaction effect (ANOVA, $F_1 = 20.590$, $P = 0.000$; Table 18).

The mean distance from the burrow entrance to the egg was not significantly different for any of the variables studied (pasture and forest 654.41 ± 28.81 mm and 584.08 ± 30.58 mm, respectively; north and south 641.72 ± 2.46 mm and 597.11 ± 30.63 mm, respectively; Table 19; ANOVA, $F_1 = 3.314$, $P = 0.73$; ANOVA, $F_1 = 1.330$, $P = 0.253$, respectively), however there was a significant interaction effect (ANOVA, $F_1 = 6.908$, $P = 0.010$).

Table 18. Mean burrow length (mm), showing SE and upper and lower 95% CI, grouped by vegetation type and aspect.

Mean burrow length				
	(mm)	Standard error	Lower 95% CI	Upper 95% CI
Forest	745	26.98	690.71	799.52
Pasture	845	31.13	782.40	907.81
North	807	24.94	756.40	856.86
South	785	34.94	714.87	855.81

Table 19. Mean distance from burrow entrance to egg (mm), showing SE and upper and lower 95% CI, grouped by vegetation type and aspect.

Mean distance from entrance to egg (mm)				
	entrance to egg (mm)	Standard error	Lower 95% CI	Upper 95% CI
Forest	584	30.58	522.12	646.04
Pasture	654	26.81	600.13	708.70
North	642	27.46	586.12	697.32
South	597	30.63	535.04	659.17

Burrow characteristics

The distance from the burrow entrance to the egg was not significantly associated with whether the egg hatched (LR $X_1^2 = 0.602$. $P = 0.438$) or chick fledged (LR $X_1^2 = 0.410$. $P = 0.522$). The distance from the burrow entrance to the egg did not have a significant relationship with fledge weight (Pearson Correlation -0.206 , $P = 0.247$; Fig. 7).

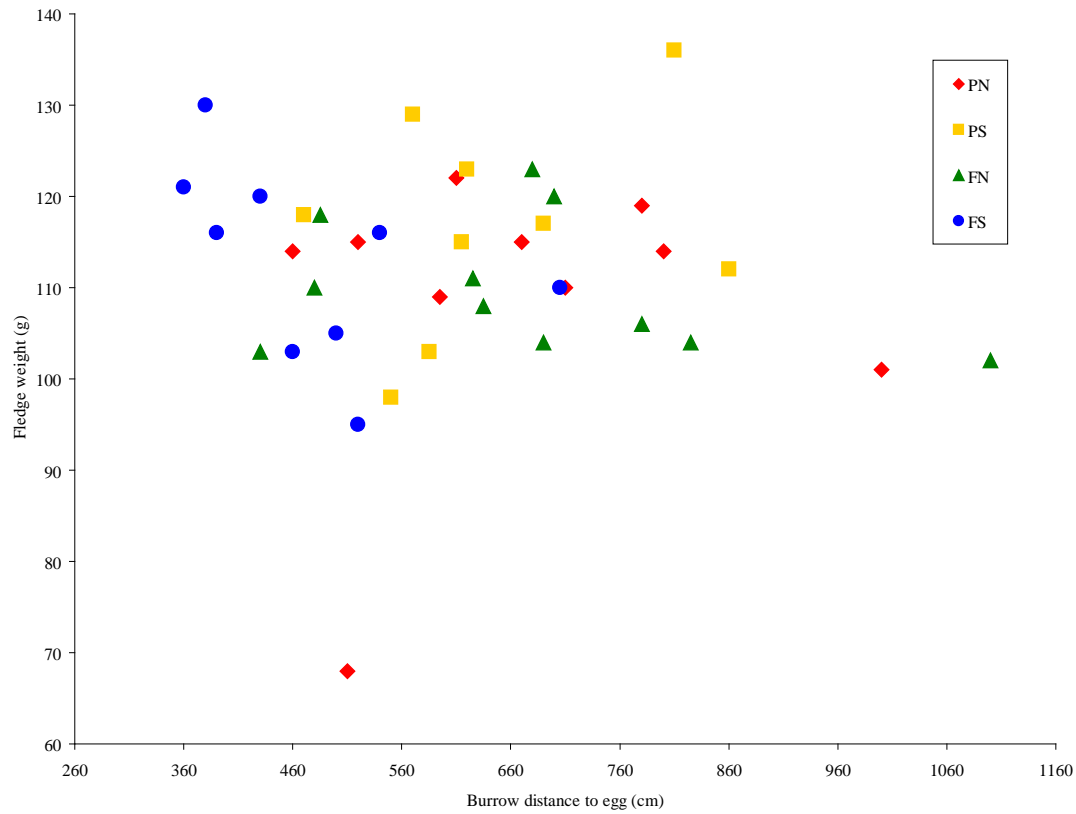


Figure 7. Relationship between fledge weight (g) and burrow distance to egg (cm), grouped by site.

Temperature

The mean burrow temperature was significantly higher in the pasture than the forest sites and in the north than the south sites on both the 27th and 29th of January 2005 (Day 1 vegetation: $17.89 \pm 0.22^{\circ}\text{C}$ and $15.63 \pm 0.12^{\circ}\text{C}$ respectively; Day 1 aspect: $17.31 \pm 0.34^{\circ}\text{C}$ and $16.21 \pm 0.22^{\circ}\text{C}$ respectively; Day 2 vegetation: $17.55 \pm 0.25^{\circ}\text{C}$ and $15.44 \pm 0.06^{\circ}\text{C}$, respectively; Day 2 aspect: $16.98 \pm 0.37^{\circ}\text{C}$ and $16.01 \pm 0.13^{\circ}\text{C}$, respectively; Table 20). There was a significant interaction effect between vegetation and aspect on both Day 1 and Day 2 (ANOVA, $F_1 = 14.998$, $P = 0.001$) and ANOVA, $F_1 = 132.076$, $P = 0.000$) respectively). There were no other significant differences detected.

Table 20. F and P values for measured temperature differences for vegetation, aspect and use variables, for day 1 and day 2.

	Day 1		Day 2	
	<i>F</i> ₁	<i>P</i>	<i>F</i> ₁	<i>P</i>
Vegetation	215.200	0.000	512.569	0.000
Aspect	45.714	0.000	103.193	0.000
Use	0.015	0.903	0.029	0.867
Veg*Asp	14.998	0.001	132.076	0.000
Veg*Use	0.063	0.804	1.098	0.303
Asp*Use	2.137	0.154	1.297	0.263
Veg*Asp*Use	0.015	0.903	3.368	0.076

Cause of death

The most common cause of death at all sites was predation, followed by poor synchronicity of the parent birds resulting in death of the embryo due to incubation failure or starvation of the chick. Tuatara were responsible for nearly half (20/45 – 44%) of all titiwinui egg failures and chick deaths. At the study sites, losses caused by tuatara were similar at FN, PN and PS (54%, 50% and 50% respectively), but less for FS (25%). Losses caused by tuatara were similar at Pasture (50%) and North (52%) sites, but less at Forest (40%) and South (36%) sites. Predation at the egg or chick stage differed between sites; at the North sites the majority of predation events involved eggs (10/12; 83%); at the South sites the majority of predation events involved chicks (5/8; 63%, Fig. 8). All other results were similar regardless of aspect or vegetation type (Table 21).

Table 21. Cause of death (classed as predation, poor synchronicity, burrow collapse, eviction or unknown) for eggs and chicks (combined and separately) for all sites.

	Poor		Burrow			
	Predation	synchronicity	collapse	Eviction	Unknown	Total
<u>Eggs and chicks:</u>						
FN	7	4	1	0	1	13
FS	3	3	2	2	2	12
PN	5	3	0	2	0	10
PS	5	3	1	1	0	10
Total	20	13	4	5	3	45
<u>Dead egg:</u>						
FN	6	4	0	0	0	10
FS	1	3	2	1	0	7
PN	4	2	0	2	0	8
PS	2	2	1	1	0	6
Total	13	11	3	4	0	31
<u>Dead chick:</u>						
FN	1	0	1	0	1	3
FS	2	0	0	1	2	5
PN	1	1	0	0	0	2
PS	3	1	0	0	0	4
Total	7	2	1	1	3	14

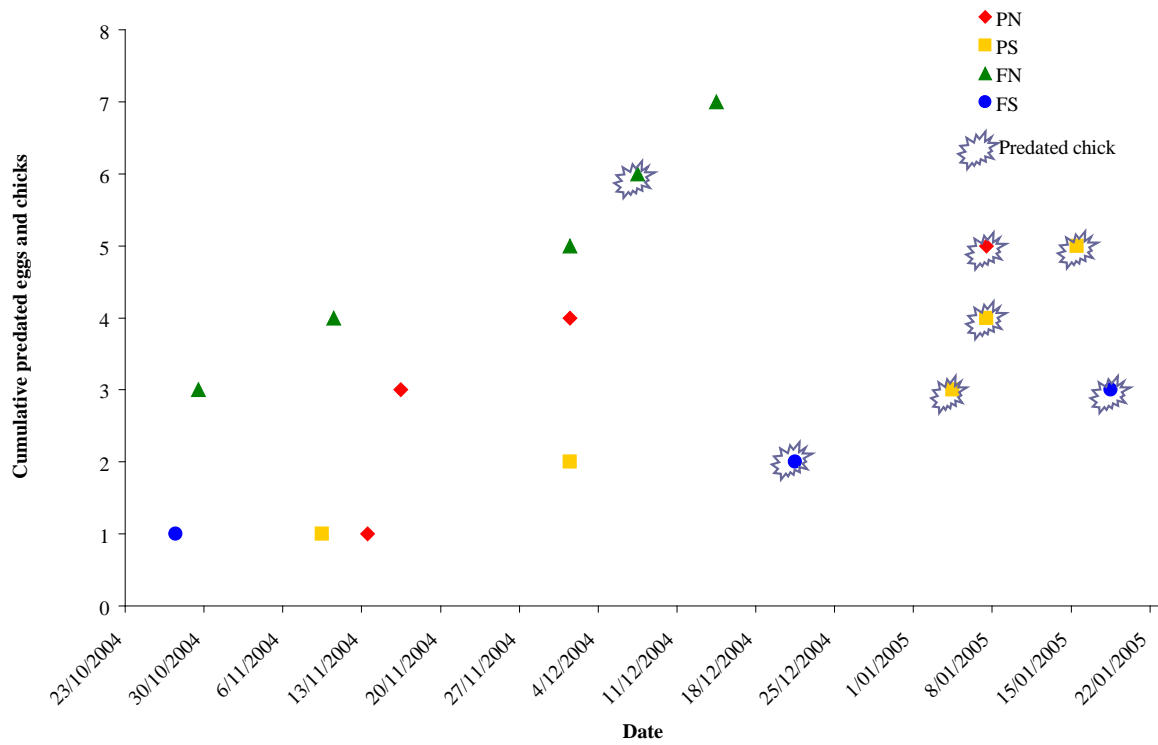


Figure 8. Cumulative predated eggs and chicks ($n = 20$) over time, grouped by site. Multiple deaths at the same site occurred 29/10/04 (FN) and 16/11/04 (PN).

Discussion

Intensively monitored burrows

Burrow occupancy

Observed burrow occupancy rates in Forest and North sites were not significantly different than Pasture and South sites. This finding supports the null hypotheses, and was not expected as Forest sites offer greater protection from wind and precipitation, and Northern sites offer greater protection from prevailing winds and increased solar radiation. On Takapourewa there are frequent north-west gales, but these winds are deflected and dissipated by the western cliffs. The lower eastern cliffs do not offer the same deflective ability, so south and south-east winds are more damaging (Ward 1961). When examined independently, the effect of vegetation and aspect on burrow occupancy was more marked; although the FS and PN sites were similar, the FN site had more than three times the number of occupied burrows per m² than the PS site.

However, this result does not accord with previous studies:

- Newman (1987) reported that Ruston Bush (where the FS site is located) had a lower proportion of burrows not used by titiwinui than Keepers Bush (where the FN site is located; 13.9 and 26.1%, respectively), the inverse pattern to that recorded in the current study;
- Markwell (1997) reported titiwinui burrow occupancy rates as 68.2% in Pasture; 71.4% in grassland; 79% in shrubs; and 67.6% in Forest, all less than the 83.7 – 91.8% occupancy recorded in the current study;

The differences between studies may be due to real biological differences in occupancy, as observed in Hutton's shearwaters (*Puffinus huttoni*; occupancy rates changed by 31% (between 56% and 87%) over ten years; Cuthbert and Davis 2002). However, burrow occupancy would not be expected to change dramatically in such a philopatric species (Warham 1990), as the same individuals would generally be returning to the same or nearby burrows and thus should be detected by burrow occupancy surveys over time (Richdale 1965). Unless there was a significant directional shift these birds should still have been recorded in occupancy surveys of the selected environmental variables. It seems more likely that the observed differences are due to variation in methodology.

The differing results between the current study and previous studies may be due to seasonal effects (Verner 1985), since burrow occupancy declines as the season progresses (Warham 1990). Newman (1987) collected data in Ruston Bush in February, April, July and September 1975 and in Keepers Bush in July 1977, December 1978, and November 1980. The data collected during September 1975 was at the time of highest burrow occupancy, as this is during the courtship period of the prion breeding cycle when all breeders and many non-breeders are present at colonies (Warham 1990), and before pairs have a chance to have failed their breeding attempts. April and July are relatively quiet times in the titwainui breeding cycle, and November, December and February would have increasing numbers of failed breeders and fledged chicks (February), so reduced burrow occupancy (however, failed and non-breeding titiwainui were abundant ashore at the end of the breeding season (February – March) on the Snares; Miskelly *et al.* 2001). The observation that Ruston Bush had higher occupancy than Keepers Bush (Newman 1987) was probably due to non-comparable data being collected at different times of the year. Markwell (1997) made four trips to Takapourewa in June, September, November and December, but used only data collected during November and January for occupancy estimations, when the titiwainui were breeding. November was during the late incubation phase so would not have included those pairs that failed early in incubation, and January was during the late nestling phase so would not have included those pairs that failed during incubation or early nestling phase, or those that had already fledged. Burrow occupancy results in the current study being greater than the occupancy rates observed by Markwell (1997) are probably due to the current study occurring during peak burrow use. The time of season can also make burrows more or less obvious conspicuous (Verner 1985).

Chicks hatched

The proportion of chicks hatched per eggs laid varied between the sites from 62% (Forest and North) to 69-70% (Pasture and South, respectively). Sites that were perceived to be preferred (highest burrow density and highest occupancy rates) had the lowest proportion of chicks hatch. This is probably due to predation (see below), but may be due to the experience of the parents (e.g. Storey and Lien 1985).

There is inconsistency in previous studies about how stable hatching success is over time. A ten year study of Hutton's shearwaters showed a 28% change in hatching success (range 34% -

72%) over ten years (Cuthbert and Davis 2002), yet Prince (unpubl. data in Reid *et al.* 2000) reported identical hatch rates (77%) in one year of low and one year of high food availability (fledge weights differed during this period; 37% and 77%, respectively). It is not known whether the data in the current study are comparable with other years.

Chicks fledged

The proportion of chicks fledged per chick hatched was similar between Forest and Pasture sites (75% and 77%, respectively). Although not significant, 82% of chicks at North sites fledged, versus only 70% of chicks at South sites. Titiwainui fledge rates were similar to that observed at the Snares was (78.6%; 22/28) in 1986-87 (Miskelly *et al.* 2001).

The pattern of chicks fledged relative to aspect was the inverse pattern of chicks hatched; more eggs survived at South than North sites, and more chicks survived at North than South sites. The most likely cause of this pattern was predation (see below). Vulnerability at specific age stages is a known factor (e.g. sooty shearwater survival was greater during the egg-early chick stage than the early chick-late chick stage; Jones *et al.* 2003). It is feasible that titiwainui eggs and chicks have variable likelihood of surviving at different age stages dependent on nest location.

A ten year study of Hutton's shearwaters showed a 21% change in fledging success (the proportion of hatched chicks that survived to late chick-rearing stage; range 73% - 94%) over nine years (Cuthbert and Davis 2002), so these data should not be considered comparable with other years.

Breeding success

The rate of breeding success was similar across all four sites. These results may not be indicative of breeding success rates over time, for example a ten year study of Hutton's shearwaters showed a 29% change in breeding success rates (measured as the proportion of eggs that survived to the late chick-rearing stage; range 27% - 66%) over nine years (Cuthbert and Davis 2002). This result may be affected by age, as the reproductive output of seabirds increases with age, before levelling off. This effect may be caused by a lack of breeding and/or foraging experience in younger birds, increased reproductive effort to counter-balance diminishing reproductive opportunities in older birds, or higher quality individuals surviving longer and

producing more offspring (Wooller *et al.* 1992). Seabirds have the ability to withstand periods of reduced fertility (e.g. following a catastrophic event) due to the longevity of their reproductive span (Wooller *et al.* 1992).

Chick fledge weights

The mean fledge weights were similar across all four sites, and there was no difference between Forest and Pasture sites, or North and South sites.

Greater fledge weights can be used as a measure of the likelihood of a chick surviving as the trend for heavier chicks to have a greater chance of survival and recruitment than lighter chicks has been observed in many seabird species, including Manx shearwater (Perrins *et al.* 1973), sooty shearwater (Sagar and Horning 1998), grey-headed albatross (*Diomedea chrysostoma*; Reid *et al.* 2000), titiwinui (Miskelly and Williams 2002), black petrel (Imber *et al.* 2003b), common diving petrel (*Pelecanoids urinatrix*; Miskelly and Taylor 2004), yellow-eyed penguin (*Megadyptes antipodes*; McClung *et al.* 2002) and fluttering shearwater (*Puffinus gaviat*; Bell *et al.* 2005).

Burrow characteristics

Mulder and Keall (2001) suggest that titiwinui on Takapourewa demonstrated a preference for burrowing in certain areas due softer soil from previous digging, rather than a selection of particular environmental characteristics. However, the environmental variables other than those studied (slope, aspect, soil moisture and light levels) may be correlated with burrow location. Likewise, factors other than those recorded in the current study may have been significant.

Burrow complexity

Habitat did not affect titiwinui burrow complexity on Takapourewa (this was also observed by Markwell 1997). Burrow complexity did not affect fledge weight, and there was no observed change in the ratio of multiple to single burrows in either total burrows studied, or in only those that fledged chicks.

Newman (1987) found that most burrows in Keepers Bush (FN) were simple (one or two entrances leading to a single nest chamber; 93.3% of 66 burrows), and most in Ruston Bush (FS) were complex (three or more burrows leading to multiple nest chambers; 61.4% of 44 burrows). However, as Newman had different criteria to define simple or complex burrows than the current study, these data are not directly comparable. The overall rates of burrow complexity (29.5% - 41.3%) were higher than those recorded by Markwell (1997); of 180 burrowscoped burrows, 20.6% were complex (14/7.8% had an additional entrance, 22/12.2% had two nesting chambers from one entrance, and 1/0.6% had three nesting chambers from one entrance. These differences may represent real differences over time, or may be observed due to the different methods used.

Burrow length

Burrow length ranged from 460 mm to >1555 mm, mean 745 – 845 mm. These results are comparable with previous measurements of titiwinui burrows on Takapourewa (range 600 – 2000 mm, averaging about 1200 mm, Walls 1978; range 200 mm - >2000 mm, mean 760±70 mm, Markwell 1997), Aorangi (750 mm – 900 mm, n = 11 burrows; Harper 1976) and North Brother Island (range 400 – 1200 mm, mean 645 mm, n = 26 burrows; Gaston and Scofield 1995).

The significantly longer burrows in Pasture than Forest sites were probably to gain protection from weather in lieu of a vegetation canopy, as longer burrows offer reduced temperature fluctuation (Simons 1985). Burrow length has previously been recorded as being associated with nest site selection (Manx shearwater burrows with eggs were significantly longer than other burrow types; Storey and Lien 1985, and sooty shearwater nest sites increased at distances from burrow entrances; McKechnie 2004) and breeding success (Cory's shearwater *Calonectris diomedea* pairs with longer burrows had significantly higher hatching success than those with shorter burrows, possibly due to protection against rain and wind; Ramos *et al.* 1997). Alternatively, the burrow length differential may be due to previous failures, as was observed in Manx shearwaters; pairs tended to extend burrow length following breeding failure (Thompson and Furness 1991).

Personal observation suggested the rank grass at the Pasture sites may have had a stabilising effect by holding the soil in place, whereas the Forest sites had very little ground cover hence increased collapse and erosion. Therefore burrow length may be a by-product of the immediate

environment rather than a factor that is selected for or against based on any biological consequence.

Despite a perceived selection for longer burrows in Pasture sites, the distances from the entrance to the egg had no relationship with egg weight or fledge weight; or the probability of hatching or fledging, so there was no apparent effect of burrow length on breeding success.

Temperature

As expected, temperatures were significantly greater in North than South sites. Temperatures were also significantly higher in Pasture than Forest sites. This result conflicted with the hypothesis that mean temperatures would be greater at Forest sites, but as temperature data were collected during the middle of the day during one of the typically warmest months of the year the result may be a reflection of greater thermal extremes at the Pasture sites. Although petrel eggs and chicks can withstand extensive chilling (Warham 1990), temperature extremes make nest site a critical component of reproductive success (Stokes and Boersma 1991). This is probably due to the burrow temperature being more stable than ambient temperature (e.g. dark-rumped petrel *Pterodroma phaeopygia sandwichensis* burrow temperatures in Hawaii were cooler and fluctuated less than ambient temperatures; Simons 1985). Although there was no observed indication of cold stress in Adélie penguin (*Pygoscelis adeliae*) chicks, excessive heat could be lethal (Chappell *et al.* 1990). To accurately calculate the effect of temperature on titiwinui chick survival extremes of temperatures would need to be ascertained.

There is evidence that parent birds will actively select burrows according to temperature. For example, temperature in Mountain chickadee (*Parus gambeli*) nest boxes was greater in used boxes than unused boxes. In this species breeding was most successful in nest boxes with a warmer environment, and temperature was not significantly different between unsuccessful nests and unused boxes (Wachob 1996). This observed difference is probably due to the inability of the chicks to regulate their body temperature when the ambient temperature reaches extremes. Chicks of burrow-nesting seabirds become homoeothermic within one or two days of hatch (Warham 1990), and significant amounts of energy may be required to maintain their temperature (this is also seen in non-burrow nesting birds; for example, once they reach thermal independence Adélie penguin chicks use 10-11% energy for thermoregulation; Chappell *et al.* 1990). If the chick has

insufficient energy (i.e. through not enough provisioning by the parents) or there are extremes of temperature in which the chick can not remain homoeothermic it may perish. There were no observed accounts of chicks in the current study dying through heat stress or hypothermia, but if chicks had become weak due to requiring extra energy for thermoregulation they may have been more vulnerable to predation (Walls 1978). Body size effects thermoregulation, as larger birds have relatively less surface area, thus a greater ability to retain heat, but smaller birds have better ability to facilitate cooling (Clark 1979). Thus the relatively smaller chicks from the PN and FS sites may have been more susceptible to hypothermia; and the relatively larger chicks from the PS and PN sites more susceptible to heat stress. This could affect the overall breeding success of these sites in years of climatic extremes.

Cause of death

Of the failed nests of Hutton's shearwaters, 30 (of 86; 35%) failed at the egg stage and 13 (of 86; 15%) failed at the chick stage. More breeding failures also occurred during the egg phase (367 from 1002 eggs; 37%) than the chick phase (93 from 506 chicks; 18%; Cuthbert and Davis 2002). Of the nests that had eggs, 50% successfully fledged chicks; similar to the 55% previously reported for successful titiwinui fledging on Takapourewa (Walls 1978). Walls (1978) listed desertion, interference, predation by tuatara and other mortality as responsible for the titiwinui nest failures on Takapourewa, as was also observed in the current study. A cause of death that this study does not consider is infertility. Of the failed eggs, all that were investigated were fertile, but Richdale (1965) found that 3.6% of 166 titiwinui eggs were infertile.

Tuatara

Tuatara have a detrimental effect on the breeding success of titiwinui on Takapourewa (tuatara were responsible for the loss of more than 25% of titiwinui eggs and chicks on Takapourewa through predation and interference; Walls 1978), and the degree of effect appears to vary according to nest site selection; nests in the FS site are predated only about half as regularly as all other sites. Predation events being less common at the FS site could be a reflection of tuatara density and occupancy rates there - like titiwinui, the density of tuatara varies dependent on vegetation. Tracking using BUM boards in the current study (see chapter 2) indicated tuatara in 18% (9/50) of burrows in FN, but only 4% (2/50) for both PS and PN, and none for FS. The result of less tuatara predation at the site with least tuatara makes inherent sense, but as the tuatara density data generated through the BUM board study was a by-product of

collecting titiwainui data it shouldn't be treated conclusively. This is especially true given that there are some anomalies between the BUM board results and previous published results; Newman (1987) reported estimated tuatara density as 1500/ha in Ruston Bush (FS) and 1420/ha in Keepers Bush (FN). However the higher burrow density in Ruston (FS) meant tuatara occupancy was lower than in Keepers (FN; 10.8 and 14.1%, respectively). Tuatara were found in all vegetation types on Takapourewa, but at significantly greater density in mature bush than in pasture (East *et al.* 1995; Markwell 1997). Tuatara (*Sphenodon guntheri*) on North Brother Island also occurred in greater density in areas where the dominant vegetation was more than 29 cm high than in areas with shorter vegetation (Gaston and Scofield 1995).

So although tuatara occupancy was less in FS than FN, it was probably greater than in either of the Pasture sites. The tuatara that live in pasture are primarily juvenile (East *et al.* 1995), except for during the spring when breeding tuatara are most abundant in pasture for egg-laying (Butler 1989 in East *et al.* 1995; tuatara construct shallow subterranean nests in open area as they have higher temperatures than forest habitat, and the higher temperatures are needed for successful development of the embryo, Nelson *et al.* 2004). As the titiwainui predation data was collected in summer it can be presumed that the adult tuatara would have returned to their usual Forest territories. The high occurrence of tuatara predation at the Pasture sites relative to tuatara density may be due to juvenile tuatara being more likely to predate titiwainui, or it may be because there are fewer invertebrates available in pasture areas than forest areas, so titiwainui are a more important food source for tuatara in these areas (Walls 1978).

Tuatara predation was the cause of death for six eggs in FN ($6/20 = 30\%$), but only one chick; and four eggs and one chick in PN. Perhaps the observed pattern of having the greatest number of egg predation events at the North sites where tuatara density was relatively high was due to a cost-benefit analysis; there may have been no incentive to leave eggs to become bigger chicks as the risk that another tuatara may eat the egg in the interim was too high (Hardin 1968). Alternatively, it may be that there were so many other food sources available to the FN dwelling tuatara (Walls 1978) that they could afford to feast (on eggs) due to no fear of famine. Emaciated titiwainui chicks more vulnerable to tuatara predation on Takapourewa (Walls 1978), so it may be the physical condition of the chick that predicts predation, rather than any conscious decision making by the tuatara. The same tuatara can use several different burrows (Newman 1987), so the same individual may have predated more than one titiwainui chick. If this was the case a rouge

animal could have skewed the results at any of the sites by artificially increasing the proportion of titiwainui deaths to tuatara density. The sample sizes in the study are too small to formulate any conclusive reasons for the pattern of less predation at some sites than others.

Tuatara are more likely to be found in burrows not occupied by prions (Newman 1987), which indicates there may be selection by titiwainui against burrows containing tuatara. However, adult titiwainui are able to evict tuatara from burrows (Brown 2001), and Newman (1987) suggests that tuatara density is determined by the number of burrows *not* occupied by titiwainui (greater unoccupied burrows equals higher tuatara density), rather than total number of burrows. If this is the case areas of lower titiwainui occupancy should see greater tuatara occupancy, but in the current study highest tuatara occupancy and greatest titiwainui occupancy were observed at the same site.

Poor parental synchronicity

The principle proximate cause of interrupted incubation is the delayed return of a parent bird, possibly caused by decreased food availability or contrary weather conditions. The incubating bird eventually needs to leave to feed (Warham 1990). Of 57 Chatham petrel eggs laid over two seasons, four out of five cases of abandonment were due to a partner not returning to relieve the incubation shift (Gardner 1999). In titiwainui the incubation changeover takes place soon after dusk, with 1-5 day shifts. Titiwainui on the nest are visited by their partner most evenings, but will not give up the egg willingly until the end of the shift. If the supporting parent has not reappeared after 5 days the brooding parent will leave for at least one day to feed (Harper 1976).

Synchronised incubation and provisioning are clearly imperative for seabird breeding success, but synchronised incubation may be less important for the chicks of burrowing species as they become homoeothermic within a day of hatching and are left alone by day after this time (Warham 1990). In the current study poor parental synchronicity was responsible for 11 failed eggs and two dead chicks (29% of all failed nests; 15% of all nests with eggs). Poor parental synchronicity was responsible for similar numbers of failed eggs at all four sites, but was the cause of chick mortality only at the Pasture sites. Although interrupted incubation would increase the effect of ambient temperature and wind, titiwainui eggs can withstand extensive chilling and can still be viable in these conditions (Walls 1978; Warham 1990), so the 11 failed eggs probably

reflect a very poor level of synchronicity (or potentially the death of one of the parent birds). Poor parental synchronicity also affects chicks. The most likely cause of death in little penguins was starvation. In total, 16.8% of studied little penguins died of starvation because the adult at sea did not return to feed then in time. This accounts for 73% of all chick deaths during the first six days, and 34% of all chick deaths (Renner and Davis 2001). The results of the current study indicate that the incubation of eggs was more important than the provisioning of chicks, but it is probable that the pairs with insufficient coordination to successfully incubate an egg would also have insufficient coordination to feed a chick. Of course none of the parents of failed eggs produced chicks to test this theory.

The probability of successful breeding increases with established pairs in most seabird species (e.g. Manx shearwater *Puffinus puffinus*; Brooke 1978). This success may be experienced due to timing, as established petrel pairs tend to lay eggs and fledge chicks earlier than inexperienced pairs, and earlier chicks may have a better chance of survival (Warham 1990). The experience of the parent titiwainui in the current study was not known, so this could not be factored in.

Burrow collapse/flooding

Burrow collapse and flooding are common phenomena in seabird colonies (e.g. Manx shearwaters, Storey and Lien 1985; titiwainui, Newman 1987; sooty shearwaters, Hamilton 1998a). As expected, burrow collapse/flooding occurred most at the FS site (twice), followed by the FN and PS sites (once each), and no burrow collapse/flooding occurred at the PN site. Newman (1987) has previously reported burrows in Ruston (FS) and Keepers Bush (FN) lost to collapse, Ward (1961) reported that the unstable soil on Takapourewa collapses titiwainui burrows, occasionally burying birds, and Richdale (1965) found that 39% of titiwainui burrows were lost each year through collapse. Warham 1990).

Substrate saturation makes burrows more susceptible to collapse (Stokes and Boersma 1991). Burrow collapse can have dire consequences, for example an adult dark-rumped petrel died due to burrow collapse during excavation (Simons 1985), and at least two (3.5%) of sooty shearwater chicks studied at Taiaroa Head probably died when their burrows collapsed (Hamilton 1998a). Burrow flooding can also negatively effect breeding success, flooding was a substantial cause of magellanic penguin egg and chick mortality in some years (Stokes and Boersma 1991); and 25%

of studied little penguin nests were susceptible to flooding (however no chicks ever drowned in the nest as most were destroyed during the incubation period; Renner and Davis 2001). Burrow collapse and flooding may also cause breeding failure indirectly, for example collapsing walls and flooding were possible causes for burrow abandonment by Manx shearwaters (Storey and Lien 1985). The nature of the weather and the physical location of burrows can effect flooding (a cause of egg-failure of short-tailed shearwater *Puffinus tenuirostris* was flooding of burrows caused by unusually heavy summer rainstorms, and the physical location of their burrows altered the effect of the rain; Serventy and Curry 1984). Burrow density and vegetation also make a difference; roots may impede digging but help to stabilize soil and reduce the probability of collapse, and burrows dug too close together are liable to cave-in (Warham 1990). Burrow collapse was more likely in high density areas of Jackass penguin nests, probably due to continued digging and the physical weight of the birds in and around burrows (Seddon and van Heezik 1991). Burrow density is greatest in compact or friable soils (West and Nilsson 1994), exacerbating this problem. The availability of dry burrows affected reproductive success of Manx shearwaters (Storey and Lien 1985). Thus although burrow flooding and collapse clearly have negative repercussion for the occupants; the potential effects are altered by many variables.

Cause of death conclusions

More nests failed at Forest than at Pasture (25 vs. 20) sites, but the presumption was that the Forest sites were of better quality, and when quality is related to breeding it is largely measured by survival. So for the survival in the Forest sites to be less than the Pasture sites is perplexing. The apparent anomaly may be explained by;

- The pairs nesting at the Forest sites may have included more inexperienced breeders, as first time breeders and newly formed pairs tend to lay later than experienced pairs, and as earlier chicks may have a better chance of survival (Warham 1990) later chicks would have been more likely to perish. However, if the Forest sites offer enhanced breeding conditions (as expected), the previous pairs from these sites should have had greater than average probability of successfully fledging a chick, thus increased site fidelity (Perrins *et al.* 1973; Warham 1990), so were unlikely to be inexperienced breeders;
- Tuatara occupancy was higher in Forest than Pasture sites. Although tuatara predation events were equal in Pasture and Forest sites (ten each), the increased occupancy may

have increased the energy expenditure of adults or chicks through predator avoidance (Godfrey 2003a), and tuatara presence may have deterred parents from feeding their chicks (Godfrey 2003b). Thus the chicks may have been compromised by the tuatara, but as there was no direct predation event the loss was attributed to another cause;

- The presumption that Forest sites offer improved breeding conditions (Walsberg 1985; Wachob 1996; Garcia-Borboroglu and Yorio 2004; Lusk *et al.* 2006) may not be true for Takapourewa. For example, temperatures were higher in Pasture than Forest sites. As long as the increased temperatures did not cause thermal stress in the chicks they may have improved breeding conditions by reducing the energy needed for thermoregulation;
- The current study only measured a limited number of variables. The observed results may be caused by an unknown and unmeasured variable (e.g. slope);
- The observed results may not be a true representation by chance due to small sample size. For example, the results may be confounded by random events that are unconnected to the nest site (such as adult death causing nest failure). With such small numbers random events could skew the results and mask the true effects of the nest site (Zar 1999).

Limitations

The duration of this study (one breeding season) limits the broader applicability of the results obtained. A study over one season may not be indicative of breeding systems over other years. For example, a study of Hutton's shearwaters showed a 31% change in occupancy rates (56% - 87%) over ten years; a 29% change in breeding success rates (measured as the proportion of eggs that survived to the late chick-rearing stage; range 27% - 66%) over nine years; and a 28% change in hatching success (the proportion of eggs that hatched; range 34% - 72% over ten years (Cuthbert and Davis 2002).

One of the problems of drawing conclusions from only one breeding season is the increased probability of one factor skewing results. For example, in short-tailed shearwaters (*Puffinus tenuirostris*) the proportion of individuals present rose with breeding age for about the first ten breeding years, then declined; the proportion of individuals present with eggs increased throughout life; and breeding success (fledglings per egg) increased until the seventh year after breeding then decreased (Bradley *et al.* 2000). A similar pattern was observed in Buller's albatross (*Thalassarche bulleri*) females; fledging success appeared to increase for those with

less than ten years breeding experience, then decrease for those with more than 20 years breeding experience (Sagar *et al.* 2005). The proportion of pairs breeding per year may be affected by food availability (Sagar *et al.* 2005) or the ability of individuals (Bradley *et al.* 2000).

Weather variables may have been outside the normal range during the duration of the study. This could have affected all aspects of breeding behaviour; from adult survival and condition due to food stocks at sea, to the effect of nest site selection to the survival and condition of nestlings. NIWA (2005) described the 2004-05 summer as a summer of extremes; it was the coldest December since 1945, February was the 8th warmest on record, and there were severe or significant moisture deficits through most of the country for January and February. October had 62% of average rainfall and 85% of average sunshine hours in the Wellington area. November had 113% of average sunshine hours, 64% of average rainfall and above average temperatures in the same region. December saw 133% of average rainfall and record low temperatures in the Wellington region. It is not known how the weather extremes (particularly the high rainfall) affected the results of this study.

The current study assumes that high-quality nest sites will be selected based on a higher likelihood of fledging a healthy chick than a low-quality site. However, when ideal nest sites are scarce, birds may use sub-optimal sites (Renner and Davis 2001). If parents are forced to use low-quality sites the results become confounded. For example, if high-quality parents nest in a low-quality site the result of their breeding attempt may be the same as that of low-quality parents in a high-quality site. The result will not be a reflection of just nest site or parent quality, but a combination of both.

General conclusions

- Neither vegetation nor aspect caused a significant difference to the breeding success of titiwainui on Takapourewa.
- Burrow characteristics (complexity, length and temperature) do not appear to be critical factors for burrow occupancy or breeding success of titiwainui on Takapourewa.
- More nest failed (45) than fledged (43). As tuatara predation was the cause of almost half of the failed nests (20), the density and feeding behaviour of tuatara is likely to have a

bigger effect on the breeding success of titiwainui on Takapourewa than vegetation, aspect or burrow characteristics.

Chapter four: Burrow creation over time and population estimation

The current study was in-situ, at a site at various stages of vegetation restoration; hence it was possible to record the pattern of self-induced burrow expansion into the restored vegetation over time. Conditions for seabird burrows are known to vary with vegetation type (e.g. sooty shearwater; Warham and Wilson 1982), so this can provide valuable data on how restored habitat affects the abundance of titiwainui, and this knowledge can be applied to future translocations of this species to sites being restored.

Most of the recently grazed blocks and revegetated sites on Takapourewa are in areas of Ketu hill soils (Ward 1961). These are soils that have developed on Maitai rocks (sandstones, muddy sandstones, and siltstones of the Maitai series; Dr H. W. Wellman *pers. comm.* in Ward 1961). Ketu hill soils do not support burrows whilst they are grazed due to trampling and soil compaction from the stock (Crook and Moran *pers. comm.*) Thus all sites had no burrows (or at most, very few) at the time of being planted (forest) or retired (pasture), so burrows present now will have been established since the change in state. Small blocks of pasture were retired, and small tracts of forest planted every year since the mid-1990s, so patterns of establishment can be determined over time. Concurrently, it is possible to test the hypothesis that titiwainui breeding colony expansion will extend into the forested areas before pasture areas, based on the presumption that forest habitat offers greater shelter from weather variables than pasture (Walsberg 1985; Wachob 1996; Garcia-Borboroglu and Yorio 2004; Lusk *et al.* 2006).

Additionally, the density of titiwainui in different vegetation types and the overall abundance of titiwainui on Takapourewa can be estimated. Knowledge of the overall population and how density changes based on vegetation will also enable this population and any new populations sourced from this site, to be managed more effectively.

Methods

Burrow creation over time

Belt transect surveys were undertaken at each of the accessible re-vegetated or retired pasture sites. A compass bearing and starting point were selected systematically to encompass the greatest continual transect and ecological gradients within the survey site to calculate burrow density (follows Brower and Zar 1977). All burrows within 1 m either side of the transect line were counted, at 5 m increments. All transects followed the fixed compass bearing, and the compass was referred to throughout. This method assumed that all burrows within the transect were detected (Verner 1985). There were 19 sites surveyed, ranging from 15 to two years since being planted or grazed. The area surveyed at each site ranged from 40 m² to 400 m² (mean 139 m²), the total combined length of the transects was 1325 m, the total area surveyed was 2650 m². The burrow density index (D_i) was calculated as: $D_i = n_i / (L * W)$, where n_i was the total number of burrows i counted, L was the length of the belt transect, and W was the width of the belt transect. The sites were all in the northern quarter of Takapourewa as access is prohibited in the southern three-quarters due to fragile and unstable Titahi and Takapourewa soils, which are treacherous to walk on (Ward 1961). Data were analysed by comparing burrow density across different years and vegetation using an ANOVA.

Population estimation

Burrow density and habitat use was calculated by analysing burrow count data collected on Takapourewa by Richard DeHamel between the 15th and 19th of August 1994 (unpublished data). DeHamel undertook seven transects spanning the width of the island and recorded all burrows within 1 m (0.5 m either side) or 2 m (1 m either side) of the line (specified in each case, and dependent on vegetation/visibility), at 10 m intervals. The increments were measured by using a 10 m piece of string. All transects followed the fixed compass bearing of 346°. This method assumed that all burrows within the transects were detected (Verner 1985). The transects totalled 3495 m and covered 5435 m². The transects covered all vegetation types and the entire topographical spread of the island. The vegetation was briefly described for each 10 m section of transect. I classed each 10 m section of transect into one of the following vegetation classes; bare ground, grazed pasture, rank pasture, muchlenbeckia, scrub, forest (follows East *et al.* 1995). Data were analysed by comparing burrow density across different habitats using an ANOVA.

The impact of individual vegetation types was calculated by using paired t-tests. The mean densities for each vegetation type were extrapolated to reflect the total island cover of the given vegetation type, thus total burrow abundance could be calculated (follows Harper 1976; Brower and Zar 1977). The proportion of vegetation types were calculated by East *et al.* (1994), who used aerial photographs taken in 1990 and hand-drawn maps made in April 1992 to calculate percentage cover of vegetation types on Takapourewa (tall grass 22%; vineland 20%; grazed pasture 17%; bare cliff 15%; scrub 14%; mature bush 12%). The method of calculating vegetation cover from photographs follows West and Nilsson (1994). There is no evidence for deviation from these proportions of vegetation types between 1990, 1992, 1994, and for the duration of the current study, with the exception of grazed pasture which can now be presumed to be rank pasture as there are no longer stock present on the island (Mike Aviss *pers. comm.*). The proportion of occupied burrows in different habitat types and the proportion of entrances with multiple chambers (as calculated in the current study), were applied to determine the population of titiwainui in Takapourewa.

Results

Burrow creation over time

Year since grazed had a significant effect on the density of burrows (ANOVA, $F_1 = 10.398$, $P < 0.000$). Vegetation however, had no effect (ANOVA, $F_1 = 1.913$, $P < 0.168$), and no significant interaction effect was detected (ANOVA, $F_1 = 1.811$, $P < 0.166$). Thus titiwainui were more likely to expand in to sites that had been without stock grazing for longer, irrespective of vegetation type (re-vegetated areas or retired pasture).

Population estimation

Burrow density varied significantly with vegetation (ANOVA, $F_5 = 9.270$, $P < 0.00$), with rank pasture having the greatest density, and bare ground the least (Table 22). Scrub, muehlenbeckia and forest had similar burrow densities, with grazed pasture about a third of the density of this group. Grazed pasture had significantly fewer burrows than either forest (0.4931 burrows m^2 and 1.3585 burrows/ m^2 , respectively, $t = 2.891$, $P < 0.014$) and scrub (0.4931 burrows m^2 and 1.3846 burrows/ m^2 , respectively, $t = -6.231$, $P < 0.000$). There were no other significant differences detected.

Table 22. Burrows/ha, vegetation cover (ha), and total burrow for the 6 categories of vegetation type on Takapourewa.

	Burrows/ha	Vegetation cover (ha)	Total burrows
Bare ground	167	22.5	3750
Grazed pasture	4933	25.5	125791
Forest	13870	18	249653
Muehlenbeckia	14692	30	440755
Scrub	15363	21	322633
Rank pasture	20847	33	687941
Total			1830523

Of the six vegetation categories, the proportion of used burrows and the proportion of multiple chambers from a single entrance were known for two vegetation types; forest and rank pasture. When these factors were considered (presuming that a single entrance with multiple chambers equals two nests), the population estimates for both vegetation types increased by a similar

percentage; 18.69% for rank pasture and 18.75% for forest. If the same correction factor (18.7%) was applied to the whole study, the estimated population size would increase to 2160017 active nests on the island, representing 4.32 million breeding titiwainui (Table 23).

Table 23. Initial estimate of titiwainui, proportion of burrows with multiple chambers, proportion of used burrows, percentage change and corrected estimate for rank pasture and forest vegetation types on Takapourewa.

	Proportion of burrows			Corrected estimate	Percentage change
	Initial estimate	with multiple chambers	Proportion of used burrows		
Rank					
pasture	687941	41.3%	84.0%	816531	+ 18.69%
Forest	249653	29.5%	91.7%	296467	+ 18.75%

Discussion

Burrow creation over time

The clearing of endemic vegetation for the establishment of pasture can be considered a massive disturbance for the seabirds that originally nested there, especially considering that compaction of soil from stock prevents burrow nesting as long as stock are present (Crook and Moran *pers. comm.*). After the complete destruction of all burrows, a colony of sooty shearwater burrows recovered completely the following season (McKechnie 2004). This fast recovery was not observed in the current study, with no burrows being detected at one site that had been retired from stock use for 12 years, nor at another site that had been replanted six years previously. The shortest period observed between a site being replanted or retired and there being a burrow present was four years. Overall, the burrow density in the replanted/retired sites was much lower than that observed at the main study sites (mean 1.675 burrows/m², range 0.89 – 2.49 burrows/m²); the greatest observed density was 0.371 burrows/m², the mean of all sites was 0.095 burrows/m², and the mean of only sites containing burrows was 0.15 burrows/m². This suggests that titiwainui on Takapourewa are slow to expand their breeding colony into replanted/retired areas. This could be due to several factors:

- Seabirds are strongly philopatric so return to their natal site to breed (Perrins *et al.* 1973; Simons 1985; Warham 1990; Thibault 1994). As there would have been no successful breeding at the observed sites since the area was used for stock there would be no returning off-spring to inhabit these areas. Forest was cleared and stock introduced from the late 1800s to the early 1900s (Brown 2001), so there was a considerable time lag since breeding occurred at these sites and the current data were taken. If all titiwainui on the island were able to find burrows in their preferred sites there would be no need to expand in to new or marginal areas.
- Soil compaction may still be having an impact, even though all stock has been removed. Paddocks were gradually being retired prior to the last few stock being removed in August 2004 (Mike Aviss *pers. comm.*), but they still could have been used relatively recently before being retired or planted. It is not known how long it takes for the impact of soil compaction to dissipate. Sooty shearwater chick density decreased and had not recovered after seven years following a massive disturbance, suggesting a decrease in the

quality of the site. However, results were confounded by a short-term reduction in fecundity in the other sites (McKechnie 2004).

- The more open and sunny conditions that occur in pasture or revegetating/sparsely vegetated areas are also the areas favoured by tuatara for breeding (Butler 1989 in East *et al.* 1995, Nelson *et al.* 2004). Tuatara were most abundant in these areas during spring (Butler 1989 in East *et al.* 1995), which coincided with the return of titiwainui for the breeding season (Walls 1978; Miskelly *et al.* 2001). The food sources for tuatara are not as abundant in open areas as forest (Walls 1978), so the tuatara may predate on any titiwainui adults, eggs or chicks that do attempt to breed in these areas. The tuatara may be effectively suppressing the titiwainui population in the surveyed areas.

In conclusion, the results indicate areas that cease to be grazed by stock are more likely to be burrowed by titiwainui over time, irrespective of whether they are planted. This knowledge is useful for restoration projects as reintroducing titiwainui does not necessitate expensive and time-consuming revegetation programmes. However, the presence of seabird burrowing activities may inhibit natural succession (from short pasture to tall grass and vineland to mature bush; East *et al.* 1995). As forest habitats often represent greater biodiversity values than pasture habitats (for example, as forest succession on Takapourewa advances, reptile species richness increases; East *et al.* 1995), replanting forest trees may well be an aspect of ecological restoration projects. When this is the case there is no observed detriment to the establishment of titiwainui burrows by replanting sites.

Population estimation

Titiwainui abundance

The estimated 1.83 million breeding pairs of titiwainui on Takapourewa is much greater than previous estimates of 250, 000 (Daugherty *et al.* 1990) to 500, 000 breeding pairs (Brown 2001). However, this should be considered a conservative estimate as it does not consider the burrow use or multiple chambers from the same entrance. The presence of more nest chambers than burrow entrances is not unusual. For example, of 180 burrowscoped fairy prion burrows on Takapourewa 14 had an additional entrance, 22 had two nesting chambers from one entrance, and one had three nesting chambers from one entrance. Thus there were approximately 5% more

nesting chambers than burrows on the surface (Markwell 1997). If these variables were factored in the population estimation could change (as was observed with the two sites where these variables were known; each increasing by 18%). The perceived underestimation of the previous attempts at determining the population size are probably due to Daugherty *et al.* (1990) making a general estimation of population size rather than being able to draw on data. Brown (2001) derived his estimation from De Hamel's data, but did not take into account variation with habitat type. Given that rank pasture had at least one third more burrows per hectare than the next most densely burrow vegetation type (scrub), and was also the dominant vegetation type, this lead to an underestimation of total population.

Titiwainui density in different habitat types

As expected, grazed pasture was not densely burrowed by titiwainui. This was probably due to compaction of the soil through trampling by stock (Crook and Moran *pers. comm.*). Rank pasture was the most densely burrowed vegetation types. This was not expected; as it was presumed that the greater protection from environmental variables offered in the forest sites (Walsberg 1985; Wachob 1996) would make this the most densely burrowed vegetation type. Sooty shearwater burrows on The Snares were at the highest density (nearly 2 per m²) in tussock grass, probably due to less obstructive roots and easier burrowing, and there was low variability in the 10 m x 10 m quadrats of this vegetation type, probably due to the even distribution of tussock density (Warham and Wilson 1982). These factors may also make rank pasture a preferred nesting site. However, these results could be confounded as rank pasture may be over-represented due to the high winds and seabirds burrowing activity on Takapourewa suppressing natural succession (East *et al.* 1995). The rank pasture sites may be selected based on the time since stock was present, rather than an actual preference for this vegetation type.

Limitations

Burrow creation over time

Expansion may be affected by other variables, for example seabird burrows on Takapourewa were largely restricted to areas of Quaternary sand deposits (Campbell *et al.* 1984). Of the heavily burrowed areas on the island, the majority were initially Ketu hill soil, friable variant. This was probably due to this soil being friable thus easy to burrow into. This theory is further

validated by the presence of abandoned scrapings and short burrows in the separately classified firm Ketu hill soil. These were possibly abandoned due to it being too difficult to dig a burrow. Over time the burrowing activities and guano deposits of the seabirds changed the soil structure to Titahi and Takapourewa soils. These are characterised by their extremely friable consistency (Ward 1961). The current study did not consider soil type, so this variable may confound results.

Additionally, sample sizes were generally small (due to the small areas that were retired/revegetated), and were not consistent in size across sites in the current study. This may have resulted in bias from small samples, or non-comparable data due to different sample sizes (Zar 1999).

Population estimation

The method of population estimation presumes little or no variance in population density within a habitat type. However, this does not consider substrate, aspect, predator density etc so should only be considered a coarse estimate and treated with caution. These recommendations are not absolute – other factors for success need to be considered, e.g. both El Niño and La Niña events are known to affect seabird abundance (Ribic *et al.* 1992), presumably by affecting fledgling survival. It is not possible to predict what impact these other variables have on results.

The data were collected in 1995, so may no longer be accurate ten years later, especially considering that one of the vegetation types (grazed pasture) is no longer represented on the island. However, published reports of burrow density on Takapourewa show that density may have increased in past decades, but has stabilised (Mulder and Keall 2001).

The direct count of titiwainui burrows can be adjusted to allow for multiple chambers and unoccupied burrows. The proportion of unoccupied burrows was calculated from the current study. These data were extrapolated out to the total vegetation type, but breeding success varies so the extrapolated estimate may not be accurate and must be considered cautiously (follows Wiltshire and Hamilton 2003). Likewise, there may be factors affecting the proportion of multiple chambers with a vegetation type that make extrapolation unviable.

Duration of the study

The duration of the current study may be insufficient to detect patterns of burrow creation over time. In general, either the population monitored must represent a large proportion of the population, or data replication must be sufficient to be applicable to the species as a whole (Wooller *et al.* 1992). Neither of these criteria were met in the current study. Long-term studies which consider age-specific issues, year-to-year variation and the influence of infrequent events/cyclic phenomena are more useful than short term studies examining basic biology (Wooller *et al.* 1992).

Chapter five: General discussion and recommendations

As habitat restoration continues to be used as a tool to restore ecosystems (Saunders 1994; Clout and Saunders 1995), it is likely we will see an increase in the translocation of species that provide important functions in the restored environment. Transferring titiwainui (or any abundant seabird with a track record of successful translocations) to an area devoid of seabirds but outside the original breeding grounds, and with no other likely candidates for seabird reintroduction (i.e. if the seabirds that originally bred on the island are now extinct or endangered and with no record of successful translocation) is still considered to be restoring the habitat as it is restoring the *functional role* of seabirds. Given that complete restoration is difficult to achieve due to the dynamic nature of ecosystems, and the fact that for most ecosystems very little is known about their 'pristine' state (e.g. age structures, genetic make-up etc); it is important to restore a system to a state where the structure and function, interactions and processes of the original are replicated (Simberloff 1990).

To achieve the successful restoration of a habitat it is essential that we understand the ecosystem intimately, because if we can't define the component of an ecosystem that is being restored, we can't know when a goal has been reached (Simberloff 1990). In the past insufficient monitoring pre- and post-translocation has led to failed attempts at reintroduction without the benefit of knowing what caused the failure (e.g. weka *Gallirallus australis greyi*, kiwi *Apteryx mantelli* and red-crowned parakeet *Cyanoramphus novaezelandiae* to the Waitakere Ranges, MacMillan 1990; and hihi *Notiomystis cincta* to Taranga/Hen and Cuvier Islands; Boyd and Castro 2000). Without identifying causes of failure it is not possible to mitigate against these same causes in future operations. Thus if translocation as a conservation tool is to be used for the greatest benefit, scientific experimentation must be used to provide useful and applicable data (Armstrong *et al.* 1994; Seddon *et al.* 2007; Armstrong and Seddon 2008). We must understand all aspects of the mechanisms that drive breeding success (Renner and Davis 2001) to enable replication of the factors that result in the greatest success. For example, knowledge of nest site selection allows for more effective conservation and management through tailoring and manipulating environmental variables to suit a particular species (Lusk *et al.* 2006).

This study has shown that titiwainui breeding success on Takapourewa is dependent on multiple variables. Northerly-aspect and forest-covered sites had greater burrow occupancy and

greater titiwainui breeding conditions than southerly-aspect and pasture-covered sites, and tuatara predation had a detrimental effect on breeding success. Titiwainui began to re-occupy sites based on how long they had been free from grazing (and associated soil compaction), regardless of vegetation type. This study recommends that the ideal potential release site for titiwainui translocated from Takapourewa will be an un-grazed forested area with a northerly aspect free of predators including tuatara. However, not being able to meet all of these criteria at a release site does not preclude the chance of a successful translocation. The absence of tuatara is likely to be the most significant factor, followed by aspect, a lack of grazing, then vegetation type.

This study found there were an estimated 1.83 million breeding pairs of titiwainui on Takapourewa. It is unlikely that the translocation of some of this population to new sites would have a significant negative impact on such a large founder population. However, the time, effort and expense required for a translocation, and the associated management and monitoring, dictate that all efforts should be taken to ensure the translocation is successful. This should include selecting the release site to give the translocated individuals the best possible chance of surviving and breeding successfully.

Application of the study

The results and recommendations of this study can be applied to any titiwainui being translocated from Takapourewa. The results and recommendations may also have wider application potential, as understanding mechanisms may have broader conservation benefit than the immediate study animal or environment. For example it is possible to apply knowledge of a common study animal to a sympatric species in similar ecological circumstances (Githiru 2007). However, determining which conditions are selected for by titiwainui may not be applicable to other seabirds (Caro *et al.* 2005). Re-location of non-endangered related surrogate species can be used to identify key translocation problems that may affect the key species, but may only give a partial picture of what is needed for success, due to species reacting differently to environmental conditions (Fischer and Lindenmayer 2000).

The innovative method of using BUM boards to assess burrow occupancy and possibly breeding success has wide application potential. This method could be used for titiwainui on

Takapourewa and at other sites, and probably for other seabird species (as long as the physical presence of the BUM board in the burrow doesn't interfere with the behaviour of the occupant).

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