Variations in the Breeding Biology of the Grey-Faced Petrel *Pterodroma macroptera gouldi*

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Plate 1.1 A beautiful watercolour of a grey-faced petrel adult with its chick by Emma Scheltema.

Abstract

The Procellariiformes are a diverse seabird order that is well represented in New Zealand. Their conservation maintains both their intrinsic value and ecological function within island ecosystems. The grey-faced petrel is a New Zealand endemic sub-species; one of few Procellariiformes persisting as a large meta-population. However, colonies are variable in size with the majority small and prone to local extinction.

The aims of this study were to: (1) compare geographical and annual variations in grey-faced petrel chick growth; (2) investigate parental provisioning behaviours and; (3) investigate the effects of annual variations in breeding success on population dynamics.

The breeding attempts of grey-faced petrels from two islands were monitored weekly during the 2013 breeding season: Ihumoana (west coast of New Zealand) and Te Hāwere-a-maki (east coast of New Zealand). Chicks raised on Ihumoana grew significantly faster, fledged earlier and in better condition than Te Hāwere-a-maki chicks. Consequently, the chick rearing period on Te Hāwere-a-maki was significantly longer than on Ihumoana; 139 and 116 days, respectively. Chicks raised on Te Hāwere-a-maki in the 2011, 2012 and 2013 seasons had indistinguishable growth rates and similar chick rearing durations. Hourly weight loss for chicks from Te Hāwere-a-maki in the 2013 season declined asymptotically following a meal. Parents alternated between short and long foraging trips (2-5 days and >8 days, respectively) and appeared to take their chick into account when making decisions as to trip length. Chicks received a meal every 7.7 days, on average. Breeding success on Te Hāwere-a-maki has been similar among the 2011, 2012 and 2013 seasons (36.4%, 40.9% and 45.5%, respectively) despite causes of failure varying between abandonment coupled with starvation (2011, 2013) and predation (2012). Populations experienced growth, within the range of 1.4-9.8% per annum, in simulations with breeding success varied among values calculated for the 2011, 2012, 2013, hypothetical good and bad seasons.

Differences in chick growth between Ihumoana and Te Hāwere-a-maki are suggested to reflect differences in the foraging conditions experienced by parents. Results suggest that conditions experienced by chicks raised on Te Hāwere-a-maki in 2013 are relatively typical for this island based on data collected in the 2011 and 2012 seasons. However, it is encouraging that the small Te Hāwere-a-maki population appears to be increasing. These results will inform future conservation strategies for the grey-faced petrel and other closely related *Pterodroma* species.

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Glossary

(B)LM	(Before) last meal
DBF	Days before fledging (expression of chick age)
DSH	Days since hatching (expression of chick age)
DSLV	Days since last visit (in reference to adults)
DSLM	Days Since last meal (in reference to chicks)
ENSO	El Niño-Southern Oscillation
GPS	Global Positioning System
IUCN	International Union for the Conservation of Nature
SST	Sea surface temperature

Chapter One

Introduction

Plate 1.2 Mōmona: consistently our largest chick on Ihumoana during the 2013 breeding season, not to mention one of our cleanest. At approximately two weeks old Mōmona weighed the same as an underweight adult; Mōmona thought about regurgitating once but in the process decided food was too precious and refrained from doing so for the remainder of the year. This picture was taken on the last visit to the island before Mōmona fledged around the 1st of December, 2013; the first chick to leave the nest!

1 Introduction

Key words: Procellariiformes, *Pterodroma*, conservation, grey-faced petrel, *Pterodroma macroptera gouldi*

1.1 An Introduction to the Procellariiformes

With 137 species currently recognised, the Procellariiformes are a diverse avian order comprising four families: Diomedeidae, the albatrosses; Hydrobatidae, the storm petrels; Pelecanoididae, the diving petrels and; Procellariidae, the petrels and shearwaters (Onley and Scofield, 2007). After splitting from a shared lineage with the Sphenisciformes (penguins) some 47 million years ago, the Procellariiformes evolved large external tubular nostrils along with a high aspect ratio and low loading wings (Warham, 1990). These adaptations, distinguishable among the Procellariiformes, enable them to exploit the patchy and unpredictable at sea food resources on which all members of this order rely (Imber, 1973; MacLeod et al., 2008; Warham, 1996).

The Procellariiformes are among the most long-lived birds, with individuals in many species living up to 60 years (Bried et al., 2003). Annual survival rates can be as high as 96% in some species (Dobson and Jouventin, 2007). The Procellariiformes are colonial breeders most often found nesting on predator-free offshore islands, inside burrows, crevices or at the surface. All are socially monogamous throughout the breeding season, during which both parents contribute their time and resources to incubation and subsequent chick rearing (Bried et al., 2003). While divorce among breeding seasons is not uncommon, some species, such as the wandering albatross (*Diomedea exulans*), form particularly strong pair bonds that can last decades (Jouventin et al., 2007).

Most Procellariiform species are highly philopatric, whereby adults will return to their colony of origin to breed (Warham, 1990). Juveniles spend several years at sea (up to 12 years in some species), before reaching sexual maturity and returning to their natal colony to breed (Dobson and Jouventin, 2007). The low lifetime fecundity characteristic of Procellariiformes means reproduction represents a key life history stage for these long-lived species (Gray et al., 2005; Serventy et al., 1989). Of great benefit to individual fitness is the ability to successfully raise high-quality offspring, likely to survive the initial post-fledging period during which they are faced with the challenges of learning to fend for themselves

(Asmussen, 2006). With the high levels of parental investment common in Procellariiformes, reproduction comes with extreme physiological costs. For a number of species a minimum weight threshold is required for breeding to commence (Chastel et al., 1995; Weimerskirch, 1992). It has been hypothesised that this ensures only those adults with sufficient reserves to maximise the chances of their own survival are physiologically capable of breeding. While this reduces overall reproductive rates, it ultimately promotes both chick and adult survival in the event that reproduction does occur.

The laying of a single egg, which is not replaced if lost, is followed by an extended incubation and chick rearing period; for some species these stages can last up to 79 and 278 days, respectively. Because of the costs associated with chick rearing, Procellariiform parents have the option to invest primarily in their own future maintenance or in provisioning offspring (Weimerskirch et al., 2001). Adjustments to parental provisioning may be necessary to reduce risks to adults whose loss, especially early in reproductive years, represents the loss of a substantial time and resource investment, while potentially resulting in no offspring to diversify the gene pool (Asmussen, 2006). Consequently, some Procellariiform species are only able to successfully raise a chick once every four years, though breeding success is often found to improve with age and experience (Dobson and Jouventin, 2007; Gray et al., 2005).

1.2 An Introduction to the Procellariidae and *Pterodroma*

The most diverse family in the Procellariiform order, the Procellariidae, comprises four sub-families: the fulmarine petrels, gadfly petrels, prions and shearwaters (Gaskin and Rayner, 2013; Onley and Scofield, 2007). Eighty or so species are recognised, though considerable taxonomic debate exists over this. The seas north of New Zealand are the centre of Procellariidae diversity with a high proportion of species found breeding, some exclusively, on the New Zealand mainland and offshore islands (Gaskin and Rayner, 2013; Warham, 1996).

The gadfly petrels comprise a single genus, *Pterodroma*, with 30-35 species recognised (Onley and Scofield, 2007). *Pterodroma* species are small to medium sized, long winged birds whose main prey are cephalopod species. All members are capable of feeding on the wing, though by alighting on the sea they are also able to feed on prey items at or near its surface. The *Pterodroma* are the most pelagic of the Procellariiformes; spending the majority of their lives at sea they return to land only to breed. Species breeding at higher latitudes nest primarily in burrows or crevices and are active at their colonies at night (Onley and Scofield, 2007). Conversely, those species breeding at lower latitudes are commonly found nesting on the surface and active at colonies during the day.

Pterodroma species are slow breeders laying a single egg, characteristic of Procellariiformes, which is not replaced if lost, with subsequent incubation and chick provisioning being shared by both parents. Though all *Pterodroma* species have historically been thought to attempt breeding annually, more recent observation suggests some species may only breed biennially. White-headed petrels (*Pterodroma lessonii*) have one of the longest incubation and chick rearing periods (61 and 112 days, respectively) of the *Pterodroma* (Zotier, 1990). Only adults whose breeding failed during incubation or early in the chick rearing period, attempted to breed in the subsequent year. There is some suggestion that this may also be the case for the grey-faced-petrel (*Pterodroma macroptera gouldi*) which has similarly long incubation and chick rearing periods (55 and 115 days, respectively; Imber, 1976a; Imber et al., 2000; G. A. Taylor pers. comm.).

Studies on chick provisioning behaviour across a range of Procellariidae species, including *Pterodroma*, have revealed that parents adopt a dual foraging strategy whereby they alternate between foraging trips of short and long durations (Baduini, 2002; Chaurand and Weimerskirch, 1994; Congdon et al., 2005; Pinet et al., 2012; Weimerskirch, 1998). The primary function of a short foraging trip, lasting between one and five days, is hypothesised to provide nourishment for the chick (Baduini and Hyrenbach, 2003). This comes at the expense of the adult, whose body condition deteriorates as a consequence of not adequately self-provisioning during short-trips (Congdon et al., 2005). The primary function of a long foraging trip, lasting between six and 29 days, is to allow the adult to restore its body condition, replacing lost reserves (Baduini and Hyrenbach, 2003; Congdon et al., 2005). However, a long trip results in lost opportunities to provision the chick, who receives significantly less food per day on average during the prolonged absence of at least one of its parents (Chaurand and Weimerskirch, 1994).

1.3 *Pterodroma* Conservation

The gadfly petrels are the most threatened group of seabirds after the albatrosses (Croxall et al., 2012). Due to rapid decline or small populations and ranges, the International Union for the Conservation of Nature (IUCN) recognises 25 of the 30-35 species as near threatened, vulnerable, endangered or critically endangered (Croxall et al., 2012; IUCN, 2013). In New Zealand, numerous impacts threaten populations at breeding grounds, including introduced predators (e.g. *Felis catus*, *Mus musculus* and *Rattus* species) and human population pressures (Croxall et al., 2012; Gaskin and Rayner, 2013). As a result, a number of species have become restricted to island groups or single islands. While *Pterodroma* species tend not to follow ships and so are not generally at risk from long-line fishing as larger Procellariiform species often are, their primary food sources may become depleted as a result of large scale fisheries (Carlile et al., 2003). Phases in the El Niño-Southern Oscillation (ENSO) can also have consequences for breeding success due to alteration in the productivity and distribution of prey items (Wolff et al., 2012). This is presumed to be a consequence of adults under-provisioning chicks as they are faced by less than optimal foraging conditions at sea (Cruz and Cruz, 1990a). It is unknown how the increasing frequency of the extremes in this global event will affect more vulnerable populations and species into the future.

A lack of basic biological knowledge for many *Pterodroma* species results in effective conservation efforts often being hindered (Pinet et al., 2009; Rayner et al., 2012). However, due to similarities in their physiologies, breeding biologies and diets, the management techniques developed for one species are often transferrable to others. The grey-faced and Pycroft’s (*Pterodroma pycrofti*) petrels have been used as analogue species in refining management techniques for their near relatives, the critically endangered Chatham Island taiko (*Pterodroma magentae*) and the endangered Chatham petrel (*Pterodroma axillaris*). The grey-faced and Pycroft’s petrels have been shown to respond strongly to human vocal lures (‘war-whooping’; Tennyson and Taylor, 1990). This technique has since been used to find previously unknown and inaccessible colonies of grey-faced petrel as well as locate burrows of rare *Pterodroma* species.

Like all Procellariiformes, the philopatric nature of *Pterodroma* species presents challenges in establishing populations at historical breeding sites (Gangloff and Wilson, 2004; Priddel and Carlile, 2001). After determining the appropriate age to translocate grey-faced, Pycroft’s and Gould’s (*Pterodroma leucoptera*) petrel chicks, translocations have become a common and important conservation tool. A number of vulnerable New Zealand species have since benefited, including the Chatham Island taiko and the Chatham petrel (Lawrence et al., 2008; Miskelly et al., 2009; Rayner et al., 2012). Feeding regimes and artificial burrows developed for translocated grey-faced petrel chicks have similarly been employed for other *Pterodroma* species (Miskelly et al., 2009).

1.3 An Introduction to the Grey-Faced Petrel

1.3.1 Taxonomic Status

There is some disagreement as to whether the grey-faced petrel constitutes its own, separate species. Gill et al. (2010), Imber et al. (2000), Macleod et al. (2008), Rayner et al. (2009) and Taylor (2013) consider the grey-faced petrel to be conspecific with the great-winged petrel (*Pterodroma macroptera macroptera*). In comparison, the grey-faced and great-winged petrels are considered separate species by Onley and Schofield (2007) due to their different breeding biologies and distributions. The grey-faced petrel is considered here as *Pterodroma macroptera gouldi* in the absence of evidence for genetic differentiation between the grey-faced and great-winged petrels. The grey-faced petrel is also known as Ōi, Tītī and the Northern Mutton-bird (Lyver et al., 2008; Taylor, 2000b).

1.3.2 Morphology and Identification

The grey-faced petrel is an endemic New Zealand sub-species from the Procellariidae family. It is medium in size, with adults weighing between 460 and 750 grams and having an average wingspan of 1020 mm (Imber, 1976a; Marchant and Higgins, 1990; Onley and Scofield, 2007). Sexes are monomorphic, displaying a uniform dark grey-brown plumage with the exception of the base of the bill and throat which are pale grey to buff white in colour (Taylor, 2013). The eyes, bill and legs are black.

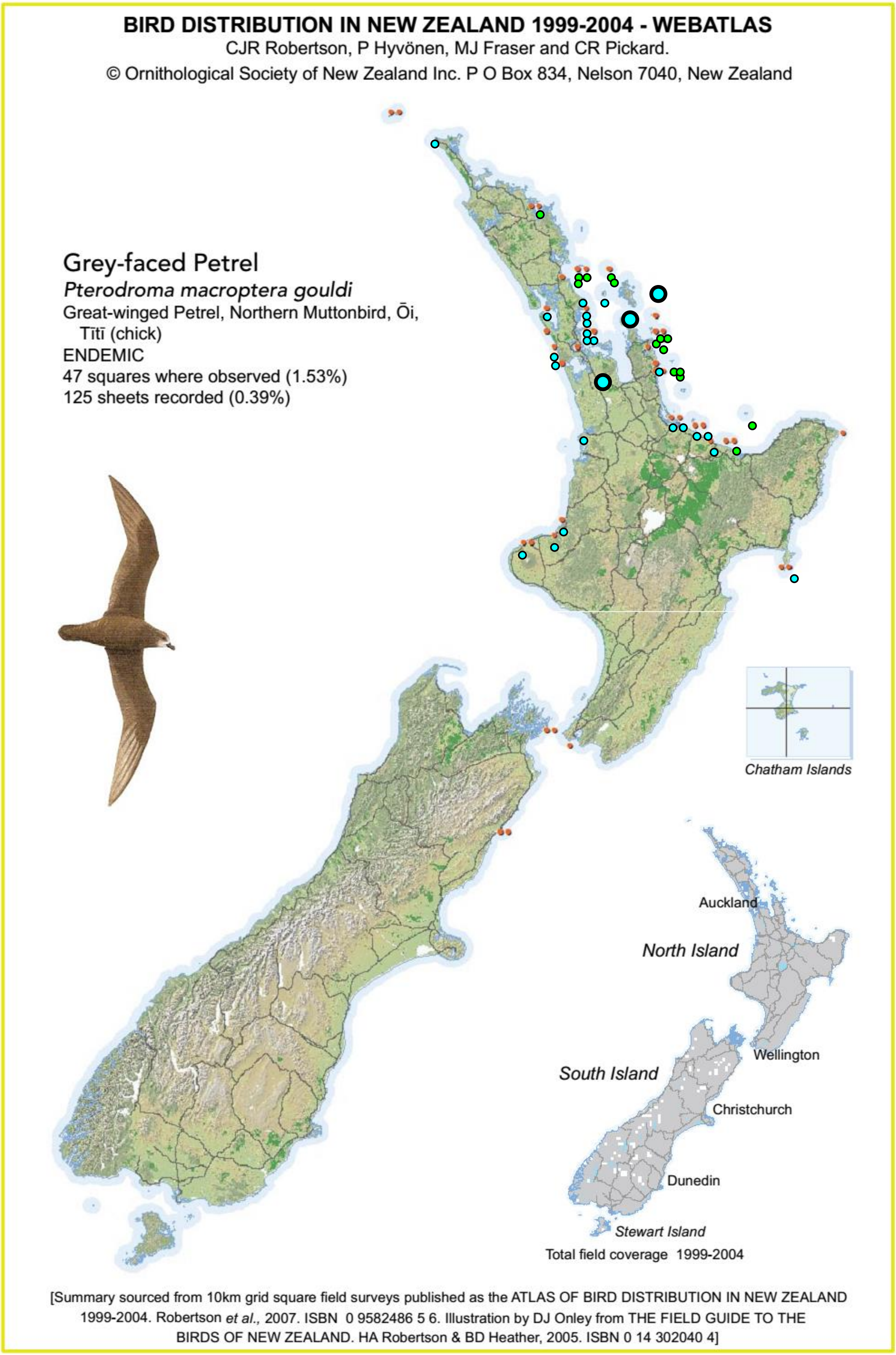
1.3.3 Conservation and Legal Status

The grey-faced petrel is recognised by the International Union for the Conservation of Nature's (IUCN) red list of threatened species as 'least concern' and New Zealand's own threat ranking system as 'not threatened' (IUCN, 2013; Miskelly et al., 2008; Taylor, 2000b). It is one of the few New Zealand *Pterodroma* species for which this is the case. The grey-faced petrel is protected in New Zealand under the 'Wildlife Act 1953' and its subsequent amendments. However, under 'Schedule Three' the grey-faced petrel may be hunted or killed subject to the Minister of Conservation's notification. This allows the continuation of the customary harvest of grey-faced petrel chicks in November from eight permitted islands/island groups by Māori iwi (tribe/s). This is detailed in the 'Grey-Faced Petrel (Northern Mutton-bird) Notice 1979 (SR 1979/237)'. This customary harvest serves to maintain mātauranga (Māori traditional knowledge) and tikanga (traditions and rituals) for Hauraki iwi (Lyver et al., 2008). An active interest among Hauraki iwi to reinstate a sustainable customary harvest of grey-faced petrels has resulted in a collaborative project between these iwi and Landcare Research. This project aims to understand and predict grey-faced petrel population trends, using both mātauranga and scientific methodology (Lyver et al., 2008).

1.3.4 Breeding Distribution and Population

The grey-faced petrel breeds exclusively in New Zealand and, like all Procellariiformes, is colonial during this time (Taylor, 2000b). Before the arrival of the first Polynesian settlers and the subsequent introduction of mammalian pest species, breeding colonies are expected to have been widely distributed throughout mainland and island sites. Though the grey-faced petrel persists as a large meta-population, today colonies are limited to islands, stacks and headlands free from, or inaccessible to, introduced mammalian predators (Taylor, 2000b). Over 100 colonies can be found from the Three Kings Islands in the north, to Omata, New Plymouth and a headland between Gisborne and Mahia Peninsula on the North Island’s west and east coasts, respectively (Taylor, 2000b; Taylor, 2013; map 1.1). The grey-faced petrel is one of New Zealand’s few Procellariiform species to have retained colonies at mainland locations, including Te Rerenga Wairau (Cape Reinga), Piha, Mount Karioi, Mount Maunganui and Rapanui Reserve. However, these colonies are small in size, supporting tens to hundreds of breeding pairs. The majority of colonies are found on islands scattered along the grey-faced petrel’s eastern breeding range and support fewer than 500 breeding pairs. The largest colonies are located on large offshore islands (more than 2 km from the mainland). At least 14 of these islands are expected to support more than 5,000 breeding pairs. These include Moutohora (Whale) and Hongiora Islands (Taylor, 2000b) both of which support an estimated 20,000 to 50,000 breeding pairs.

Recent estimates suggest an increasing population of 200,000 to 300,000 breeding pairs, indicating a total population in excess of one million birds (Taylor, 2000b). It is one of the few New Zealand seabird species for which populations are sustainable. This means the grey-faced petrel can be used as a suitable analogue species for developing management techniques for this and other, more vulnerable, *Pterodroma* species.



Map 1.1 Map of New Zealand with points showing the terrestrial distribution of grey-faced petrels (Robertson et al., 2007). Green points (●) represent known colonies supporting over 5,000 breeding pairs (Taylor, 2000b). Blue points (●) represent known colonies supporting fewer than 5,000 breeding pairs (Dunn, 2012; Rayner, 2009; pers. comm. C. Gaskin; pers. comm. J. C. Russell).

1.3.4 Breeding Biology

The grey-faced petrel is an austral winter breeder, along with its conspecific, the great-winged petrel (MacLeod et al., 2008). Prospecting birds begin returning to colonies to engage in courtship in February, with activity typically peaking in April (Imber, 1976a). Typically, males return prior to females to prepare burrows. Copulation is presumed to occur late in the courtship period after which females depart the colony.

Females remain absent for approximately two months before returning in June to July to lay a single egg, averaging 15.5% of the female's post-laying weight (Imber, 1976a). Incubation is subsequently shared by both parents who take alternating shifts. After an absence from the colony lasting an average of seven weeks, males return approximately four days after the egg has been laid to relieve the female. The male remains with the egg for approximately 17 days and, after an 18 day incubation stint by the female, 14 days (Johnstone and Davis, 1990). The female concludes incubation for approximately three days until hatching. This amounts to an average incubation length of 55 days. Common among the Procellariiformes, the egg is not replaced if lost.

Hatching occurs in August after which chicks are guarded for between five hours and three days before being left alone while parents forage (Imber, 1976a; Johnstone and Davis, 1990). Both parents contribute to chick provisioning for the remainder of the chick rearing period, which lasts an average of 118 to 120 days (Imber, 1976a; Taylor, 2013). Previous records suggest chicks are fed once every four days on average, suggesting trip durations for each parent of seven to eight days (Dunn, 2012; Imber, 1976a).

The first chicks fledge in early December, peaking in mid to late December, though some may not fledge until January (Dunn, 2012; Imber, 1976a). Observational data suggests that chicks raised on the west coast fledge considerably earlier than those raised on the east coast (pers. comm. G. A. Taylor). This delayed fledging observed in east coast chicks is thought to translate to a prolonged chick rearing period (Dunn, 2012). At fledging, the chick is independent of its parents and must learn to forage for itself. Fledglings begin returning to colonies as early as three years of age and can begin breeding as early as four (Jones et al., 2011). However, most delay breeding until they are eight to 10 years of age. Like other Procellariiformes, grey-faced petrels are philopatric in nature, with fledglings normally returning to their natal colony to breed (pers. comm. G. A. Taylor).

1.3.5 At Sea Distribution

Grey-faced petrels, along with all *Pterodroma* species, are highly pelagic. They return to land only to breed and are therefore rarely observed in inshore waters except near breeding grounds (Taylor, 2000b). Birds have generally been observed foraging from 25-50°S throughout the south-west Pacific Ocean and Tasman Sea. During July to October of 2006 and 2007, MacLeod et al. (2008) investigated the at sea distributions of failed and non-breeders captured from the Ruamaahua (Alderman) Islands. Birds were located almost exclusively over waters exceeding depths of 1,000 m throughout the south-western portion of the South Pacific subtropical gyre and the Tasman Sea (MacLeod et al., 2008). Given that 96% of the grey-faced petrels' diet consists of species living beyond the continental shelf, that birds were almost exclusively located over deep waters is not surprising (Imber, 1973). The distributions of birds over the two years was similar, with congregations observed in three general areas, termed 'hotspots' in reference to their presumed increased productivity and prey biomass (MacLeod et al., 2008). These were located near the Ruamaahua Islands, the Chatham Rise and the central Tasman Sea. Males tended to range further west and south while females tended to range further east and north, though both sexes congregated at observed hotspots.

No published data exist for the at sea distributions of successful breeders, both during and following the breeding season (K. Bourgeois unpub.). However, birds are thought to range further during the non-breeding season (Taylor, 2013). This is presumably because provisioning parents are limited in the distances they can travel given they are required to return to colonies to feed chicks. No data exist to date on the distribution of grey-faced petrels in the post-fledging period. This is likely due to a combination of reasons including: the increased mortality rates for birds during the post fledging period; the time required for fledglings to return to colonies and; the uncertainty that fledglings will return to their colony of origin (Jones et al., 2011; pers. comm. G. A. Taylor).

1.3.6 Diet and Foraging Behaviour

Prey items found in regurgitate samples collected from chicks raised on Moutohora Island close to fledging were investigated by Imber (1973). He found that, like other *Pterodroma* species, grey-faced petrels are cephalopod specialists, though fish and crustaceans also make up an important part of their diet. Ninety-six percent of prey items were found to be species that live beyond the continental shelf. A large proportion of prey items were also found to live between depths of 100 and 1,500 m by day. These species are known for their diurnal vertical migrations, ascending to the surface at dusk and descending to the depths at dawn. The grey-faced petrel is not renowned for the depths of their dives with the majority occurring within 5 m of the surface and only very occasionally to depths of up to 23 m (Taylor, 2008). They are therefore presumed to forage primarily at night. Greater than 90% of prey species contained light producing organs, suggesting grey-faced petrels make considerable use of such light sources in detecting prey at night (Imber, 1973). The grey-faced petrel's winter breeding habit is hypothesised as being an adaptation allowing adults to more effectively exploit diurnal vertically migrating prey. This would enable the grey-faced petrel to maximise its nocturnal foraging strategy. Day-time feeding is suggested as being mainly limited to scavenging dead squid at the ocean surface and is presumed to be aided by their well-developed sense of smell.

Given adaptations for prolonged, efficient flight among the *Pterodroma* and observations of the foraging behaviour of other *Pterodroma* species, Imber (1973), proposed that the grey-faced petrel detects prey while on the wing and captures it within 1 m of the ocean surface. Although the grey-faced petrel does not rely on deep dives to catch prey, Taylor (2008), found that breeding birds dived significantly deeper than their non-breeding counterparts. This is suggested as allowing breeding birds access to higher quality or more abundant prey and therefore promoting the rapid recovery of body condition essential for successful breeding.

Like all Procellariiformes, breeding grey-faced petrels are required to commute long distances between their colonies and foraging grounds, making them extreme central place foragers (Ballance et al., 2009; Davoren and Montevecchi, 2003). To allow them to exploit distant food resources while adequately providing for their chick, grey-faced petrels may employ a dual foraging strategy, as observed in a number of other Procellariiformes (Baduini and Hyrenbach, 2003; G. A. Taylor pers. comm.). In his study of chick provisioning rates, Dunn (2012), found a bimodal distribution in chick feeding frequency, along with large variances in meal sizes. Though methods in this study did not enable individual adults to be identified, these results suggest provisioning grey-faced petrel parents may adopt a dual foraging strategy.

1.3.7 Ecosystem Functioning

As providers of marine nutrients and the main contributors to natural disturbance regimes, Procellariiformes assume a crucial role in terrestrial ecosystem functioning throughout their breeding distributions (Bancroft et al., 2005; Bellingham et al., 2010; Fukami et al., 2006; Roberts et al., 2007). In these locations, nutrients from the sea are transported to land in substantial quantities by means of their guano, feathers, carcasses, eggs and food for their young (Fukami et al., 2006). Highlighted by significant reductions in the concentrations and availabilities of carbon, nitrogen (particularly δ^{15} N) and phosphorus from island soils in the absence of seabirds, this translates to a reduction in soil fertility and the corresponding primary productivity. These changes may also impact ecosystem processes by altering the below-ground community. Unfortunately, New Zealand seabirds are becoming increasingly limited to islands free of introduced mammalian predators (Bellingham et al., 2010; Towns and Ballantine, 1993). Due to its large meta-population, in New Zealand the grey-faced petrel is one of the few remaining species with abundant colonies undertaking this role. Though a few large and increasing colonies are supported on offshore islands (e.g. Moutohora and Hongiora Islands) most are small remnant colonies at risk of extinction. The risk of losing seabird colonies at many coastal locations is a cause for concern in maintaining their historic ecosystem functioning into the future.

1.3.8 Current Threats

On land grey-faced petrels have few natural predators. Before the introduction of mammalian predators, large breeding colonies of the grey-faced petrel are expected to have been widely distributed among mainland locations and inshore islands (Rayner et al., 2009). Today introduced mammalian predators present the greatest threat to the grey-faced petrel (Taylor, 2000b). The majority of colonies exist at locations inaccessible to, or managed for, such predators and supporting mere tens to hundreds of breeding pairs. Extensive colonies, supporting more than 5,000 breeding pairs, are currently only present on large off-shore islands, free of New Zealand’s more devastating introduced predators.

Feral cats (*Felis catus*) prey upon both adults attending colonies and chicks (Rayner et al., 2009). They are known to have contributed to the decline of grey-faced petrels on Hauturu (Little Barrier Island; Veitch, 2001). However, since their successful eradication from the majority of the grey-faced petrel’s range, cats are relatively unimportant presently. Mustelids and uncontrolled dogs can kill adults and chicks (Taylor, 2000b). Feral pigs (*Sus scrofa*) have the potential to kill adults and dig up burrows along with eggs and chicks. *Rattus* species, particularly Norway and ship rats (*Rattus norvegicus* and *Rattus rattus*, respectively) are common predators of unattended eggs and young, or weak, grey-faced petrel chicks (Imber et al., 2000). They have been known to severely reduce breeding success and even decimate entire colonies. Though Pacific rats (*Rattus exulans*) will take eggs and small chicks, their impact on breeding success is comparatively less severe (Taylor, 2000b). Mice have been shown to prey upon healthy Tristan and wandering albatross (*Diomedea dabbenena* and *Diomedea exulans*, respectively) chicks weighing up to 8 kg (Angel et al., 2008). Such findings suggest mice have the potential to be important predators of grey-faced petrel chicks especially in locations where they are the only introduced mammals (e.g. Moturekareka Island).

Grey-faced petrels may compete for burrows with rabbits (*Oryctolagus cuniculus*), possums (*Trichosurus vulpecula*), little blue penguins (*Eudyptula minor*) and flesh-footed shearwaters (*Puffinus carneipes*) where they co-exist (Dunn, 2012; Taylor, 2000b; G. A. Taylor pers. comm.). Competition for burrows with rabbits and possums, prior to their eradication from offshore islands, may have affected the grey-faced petrel’s breeding success (Taylor, 2000b).

Grey-faced petrels will scavenge behind fishing boats (Taylor, 2000b). Though occasionally birds will be caught on long-lines or in trawler fisheries, this is relatively uncommon, with only 39 reported killed between 1996 and 2005 (Conservation Services Programme, 2008). Comparatively, of the 44 species reported to have been killed between 1996 and 2005, six species accounted for 86% of the total birds. Direct competition with fisheries is unlikely a concern for the grey-faced petrel. The squid fishery in New Zealand consists of two species, both in the Ommastrephidae family (Ministry for Primary Industries, 2013). One of these species, *Nototodarus sloanii*, was found in regurgitate samples collected by Imber (1973), though only three of the 907 squid beaks he collected were from individuals of this species. However, the indirect impacts from fisheries are not known.

1.3.9 Current Management

Current management practices undertaken for the grey-faced petrel include: predator eradication from island colonies where possible and subsequent monitoring for reinvasions; predator control at mainland and inshore island colonies where eradication is not possible and; establishing new populations at sites from which they have been extirpated through chick translocations and acoustic attraction (Taylor, 2000b). Grey-faced petrels have greatly benefited from eradication of predators at locations that would have historically supported large colonies. Fortunately, colonies have been shown to recover quickly following the removal of introduced mammalian predators (Jones, 2010). Following the eradication of rats from Moutohora, the success of grey-faced petrels breeding there improved considerably (Imber et al., 2000). If allowed to continue, the predation of eggs and chicks by rats would likely have endangered this major grey-faced petrel colony. The eradication of all introduced mammals from Hauturu has since resulted in grey-faced petrels recolonising the island after a 60 year absence (Rayner et al., 2009).

Though colonies can, and do, recover naturally following eradication of mammalian predators, due to the philopatric nature of the grey-faced petrel this process can take time (Buxton et al., 2014a). Following the eradication of cats, presumed to be the primary predator of the grey-faced petrel, from Hauturu in 1980, it was close to 30 years till the species was next observed breeding on the island (Rayner et al., 2009). Therefore, it is often in the interest of restoration projects to establish new populations through chick translocations and acoustic attraction, in order to accelerate this process. Chick translocations to Matakohe (Limestone) Island have resulted in 152 successfully fledging over the five years of the project (Mitchell and Mitchell, 2009). Birds from the first cohort of translocations have since been observed returning to the island (pers. comm. C. Mitchell). Through the use of acoustic attraction and provision of burrows at suitable sites, grey-faced petrels are now successfully breeding at Tawharanui Regional Park (pers. comm. M. Friesen; plate 5.1).

As one of New Zealand’s few remaining seabird species with a large meta-population the continued management of the grey-faced petrel is important not only for maintaining their intrinsic value, but also maintaining their vital role in ecosystem functioning. More efficient management of populations will be possible with data determining effects of spatial and temporal variability on breeding success, particularly the impacts of introduced mammalian predators and provisioning parameters.

1.4 Thesis Outline

The grey-faced petrel has not been as detrimentally affected by the introduction of mammalian predators as have many other New Zealand Procellariidae and *Pterodroma* species (Imber et al., 2000; Taylor, 2000b). It persists as a large meta-population and is one of New Zealand’s few remaining seabirds to assume a crucial role in the functioning and health of the terrestrial ecosystems in which it breeds (Bellingham et al., 2010). The grey-faced petrel has even been found to have naturally recolonised historical breeding sites where introduced mammalian predators have been eradicated (Rayner at al., 2009; pers. comm. M. Friesen). These aspects of the grey-faced petrel’s biology make it a popular species for use within community led restoration projects, aiming to re-establish the role of seabirds in terrestrial ecosystems. They also make it suitable for use as an analogue species in developing management techniques for more vulnerable *Pterodroma* species, including the critically endangered Chatham Island taiko and the endangered Chatham Petrel (Lawrence et al., 2008; Miskelly et al., 2009; Rayner et al., 2012).

This study aims to characterise natural annual and geographical variations in grey-faced petrel chick growth rates, parental provisioning behaviours and annual variations in breeding success to allow for better planning in the management of this species into the future (Hutton and Priddel, 2002; Chapters Two, Three and Four). Understanding natural variations in chick growth rates and provisioning behaviours will hopefully inform the conservation of small grey-faced petrel colonies and translocation of chicks to sites from which they have been extirpated. Understanding annual variations in breeding success will hopefully provide insight into factors that may be detrimental to recruitment in the long term and in turn assist in the conservation of the many small grey-faced petrel colonies. Additionally, this understanding may be extrapolated to help conserve other *Pterodroma* species at more immediate risk of extinction for which intensive studies may be detrimental.

1.5 Thesis Structure

Chapter One: Introduction

The Procellariiformes, Procellariidae, *Pterodroma* and grey-faced petrel are introduced. A general overview of the current research concerning the grey-faced petrel is provided. The framework for this research is outlined and its significance discussed.

Chapter Two: Chick Growth in the Grey-Faced Petrel

The importance of monitoring Procellariiform chick growth rates is discussed. This chapter then presents growth rates obtained from chicks raised during the 2013-14 breeding season on west and east coast islands, Ihumoana and Te Hāwere-a-maki, respectively. This is the third consecutive breeding season the growth rates of chicks raised on Te Hāwere-a-maki have been monitored. Field methods and statistical analyses are outlined. Annual and geographical variations in grey-faced petrel chick growth rates are investigated. Geographical variations in chick growth rates, fledging times and durations of chick-rearing periods are pronounced and discussed in relation to possible reasons for the observed differences. Recommendations are given for the future study and management of this species.

Chapter Three: Parental Provisioning Behaviour in the Grey-Faced Petrel

The foraging strategies employed by Procellariiformes are discussed. This chapter then presents data on chick weight loss and parental provisioning for Te Hāwere-a-maki birds during the 2013-14 breeding season. Field methods and statistical analyses are outlined. Chick weight loss is investigated and discussed. Feeding frequencies and parental provisioning behaviours are investigated and discussed in reference to previous studies. Recommendations are given for future study and management of this species.

Chapter Four: Breeding Success and Population Dynamics in the Grey-Faced Petrel

The effects of variations in breeding success on Procellariiform populations and the importance of monitoring changes in breeding success are discussed. This chapter then presents data on breeding success of Te Hāwere-a-maki grey-faced petrels during the 2011, 2012, 2013, hypothetical good and bad breeding seasons. Field methods, modelling methods and statistical analyses are outlined. The impact of variations in breeding success on population dynamics are investigated and discussed in reference to future management practices for this species. The sensitivity of populations subjected to different breeding successes to changes in demographic parameters is explored. Realistic expectations of population growth are investigated by subjecting populations to a range of regimes where annual breeding success, within reasonable limits, was varied randomly. Recommendations are given for future study and management of this species.

Chapter Five: Conclusion

Summarises the results presented in Chapters Two, Three and Four. These are discussed in relation to conservation of the grey-faced petrel and other, more vulnerable, *Pterodroma* species. The scientific relevance, implications for management and recommendations for future research are summarised and discussed.

Chapter Two

Chick Growth in the Grey-Faced Petrel

Pterodroma macroptera gouldi

Plate 2.1 Teo, a beautiful chick from Te Hāwere-a-maki. Teo loved nothing more than to be scratched under the chin; it was almost a surprise to not hear Teo purring contentedly. Unfortunately Teo died in late November after months of surviving on very little food. It was not much bigger than a newly hatched chick at the time. Hopefully this research will be able to help beautiful chicks like Teo in the future.

2 Chick Growth in the Grey-Faced Petrel *Pterodroma macroptera gouldi*

Key words: Grey-faced petrel, *Pterodroma macroptera gouldi*, chick growth rate, annual variations, geographical variations

2.1 Introduction

Long-lived seabirds, including the Procellariiformes (albatrosses, petrels and shearwaters), are more sensitive to the loss of adults than they are chicks (Chastel et al., 1993; Jenouvrier et al., 2005). However, variations in chick growth rates and survivorship, due to changes in parental provisioning patterns or predation, can have long term implications for population dynamics, especially in terms of recruitment within a colony (Asmussen, 2006; Chapter Four). Chicks that fledge in reduced condition are less likely to survive the initial post-fledging period, as they are required to overcome a less than optimal start to life, while being faced with the challenges of patchy and scarce food resources (Asmussen, 2006). Reduced recruitment could be particularly detrimental where populations consist of numerous small colonies which, given the philopatric nature of Procellariiformes, could suffer from inbreeding depression (Brown and Brown, 1998). Understanding factors behind variations in chick growth rates (this chapter) and survivorship (Chapter Four) can help us to plan for the future management of at risk species (Pinet et al., 2009; Rayner et al., 2012; Weidinger, 1997).

Factors influencing the development of Procellariiform species during chick rearing can provide insights into patterns of annual and geographical variations (Weidinger, 1997). Sensitive to changes in their food supplies, Procellariiformes are often used as indicators of local ocean productivity (Cruz and Cruz, 1990a). Variables, such as adult condition, breeding success, feeding intervals, meal sizes and chick growth rates, are used as indirect indices for the availability of their prey species. Investigating annual variations in chick growth rates and survivorship can allow a better understanding of changes in conditions faced both at sea and within the colony (Tasker et al., 2000). Geographical variations in chick development can allow an understanding of the feeding conditions experienced by provisioning parents (Forero et al., 2002). Such insights are an essential element in planning for the long-term conservation of populations, species and/or the restoration of coastal and island ecosystems (Pinet et al., 2009; Rayner et al., 2012).

Inter-annual variations in chick growth rates can be indicative of annual changes in productivity at feeding grounds as a result of abnormally warm or cold sea surface temperatures (SST). A number of studies have demonstrated the detrimental effect increases in SST can have on aspects of seabird breeding biologies. Cruz and Cruz (1990) found that dark-rumped petrel chicks (*Pterodroma phaeopygia*) raised on the Galápagos Islands during the El Niño event of 1982-83 had reduced growth rates and fledged later than chicks raised during the other four breeding seasons of the study. El Niño describes the oceanic warming phase of the El Niño-Southern Oscillation (ENSO); its counterpart, the cooling phase, is the La Niña. Yellow-nosed albatross (*Diomedea chlororhynchos*) parents were able to make shorter foraging trips and provide larger meals when the SST near their breeding grounds was abnormally cold (Weimerskirch et al., 2001). In comparison to other years, when SST was warmer, both albatross adults and chicks were in better condition and chick growth rates were elevated. Understanding the effects such weather patterns have on chick growth and breeding success, can help us to predict how their increasing frequency or the general warming of oceans, both as the result of climate change, may affect breeding attempts of seabirds into the future.

Geographical variations in chick growth rates can be indicative of varying levels of both intra- and inter-specific competition for food at foraging grounds (G. A. Taylor pers. comm.). A reduction in the quality of offspring and the number that survive to fledge can be a consequence of high levels of competition at overlapping foraging grounds, resulting in the depletion of high quality food. This was shown in Magellanic penguins (*Spheniscus magellanicus*) breeding in Argentina (Forero et al., 2002). Chicks were fed lower quality diets as colony size and the density of conspecifics within a 100 km radius increased. As a consequence, chicks raised in larger colonies fledged at reduced size and with a reduced immune response.

Many marine fish populations have experienced depletions by 50 to 70%, with ecosystems displaying evidence of downward shifts in trophic levels as a result of fishing pressures (Wagner and Boersma, 2011). Such changes can have profound effects on the marine top predators that depend on them for food, including seabirds (Tasker et al., 2000). A shift in sardine distributions as a result of South African fisheries, culminated in a 45% drop in breeding adult African penguins (*Spheniscus demersus*) at colonies centred on the original distribution (Crawford et al., 2008). Concurrently, previously unknown colonies were established, centred on the new sardine distribution. Similar patterns were observed in breeding Cape gannets (*Morus capensis*), Cape cormorants (*Phalacrocorax capensis*) and swift terns (*Sterna bergii*) as the distribution of sardines shifted (Crawford et al., 2008).

Variations in chick growth rates may also be indicative of the effort required by parents to access food (G. A. Taylor pers. comm.). Breeding adults from different colonies are likely required to travel different distances to foraging grounds and face different local weather patterns. Both have the potential to drastically affect the energy expenditure and trip duration for each foraging trip. Trip range showed a strong positive relationship with foraging duration for provisioning Cook's petrels (*Pterodroma cookii*) breeding on Whenua Hou (Codfish Island), New Zealand (Rayner et al., 2010). In comparison, Cook's petrels breeding on Hauturu (Little Barrier Island), New Zealand, had generally shorter ranges that were unrelated to foraging duration. This discrepancy was attributed to greater wind velocities surrounding Whenua Hou which improved flight efficiency and consequently allowed adults to travel further in less time. As the foraging trip ranges increased, so too did provisioning mass. Therefore, for trips of similar durations, Whenua Hou chicks would be expected to receive more food from parents than those on Hauturu. Annual variations in chick growth may be similarly affected if foraging grounds shift or local weather conditions change.

The grey-faced petrel (*Pterodroma macroptera gouldi*) is a medium sized Procellariiform, endemic to New Zealand (Onley and Scofield, 2007). Adult birds captured on Auckland's west coast (Ihumoana and Kauwahaia Islands) and islands in the Hauraki Gulf (Motuora, Te Hāwere-a-maki and Tiritiri Matangi) have weighed 550 g on average, with average bill depths at the nares, bill, maximum tarsus and wing lengths of 13.2 mm, 36.4 mm, 51.6 mm and 320 mm, respectively (Taylor, 2013; G. A. Taylor pers. comm.; pers. obs.). The grey-faced petrel is an austral winter breeder with chicks hatching in August to September, after an average incubation of 55 days (Dunn, 2012; Imber, 1976a). Chicks are guarded for up to three days after hatching, before being left alone while parents forage. Both parents contribute to incubation and subsequent chick rearing which lasts 115 days, on average (Imber, 1976a). Chicks fledge in mid-to-late December though sometimes as late as January (Dunn, 2012; Imber, 1976a). Observational data suggests that chicks raised on the west coast fledge considerably earlier (two to three weeks) than those raised on the east coast (G. A. Taylor pers. comm.). However, no study has reported on variations in growth rates of grey-faced petrel chicks between west and east coast colonies.

Insights into factors causing variations in chick growth rates among breeding seasons may enable small colonies of grey-faced petrels to be conserved more efficiently. The population dynamics and breeding success of two grey-faced petrel populations on Auckland’s west coast (Ihumoana and Kauwahaia Islands, Te Henga) have been studied since 1989 (Taylor, 2000b). However, understanding annual variations in chick growth and breeding success of grey-faced petrel’s breeding on the east coast, is also important given that the majority of the meta-population consists of small, east coast colonies. This is particularly so given the indication of disparate chick growth rates between east and west coast colonies and may enhance their management.

This study sought to investigate the differences in grey-faced petrel chick growth rates between east and west coast colonies: Te Hāwere-a-maki, an island situated in the inner Hauraki Gulf and Ihumoana, an island situated on Te Henga in West Auckland. Additionally, this study sought to further inter-annual data on Te Hāwere-a-maki chick growth rates collected in the 2011-12 and 2012-13 breeding seasons (henceforth 2011 and 2012, respectively; Dunn, 2012; Russell, 2013). This research is critical to better understand trends in populations, monitor changes in oceanic conditions experienced by parents, and inform grey-faced petrel management.

2.2 Aims

There were two main aims for this study:

1. To compare geographical variations in growth rates of naturally reared chicks between Te Hāwere-a-maki (east coast) and Ihumoana (west coast) colonies across the 2013-14 (henceforth 2013) breeding season.
2. To compare annual variations in growth rates of naturally reared Te Hāwere-a-maki chicks among the 2011, 2012 and 2013 breeding seasons.

2.3 Methods

2.3.1 Study sites

This study was carried out on two islands located within the Auckland region of New Zealand during the 2013 breeding season.

Te Hāwere-a-maki (also known as Motu Hāwere and Goat Island; 36° 16’ S, 174° 47’ E) is a 9.3 ha island. It is situated within the Cape Rodney to Okakari Point Scientific Marine

Reserve, Leigh, which forms a part of the Hauraki Gulf Marine Park (map 2.1 top). Occurring along the coastal margins and exposed sea cliffs is a single, widespread grey-faced petrel colony that supports a breeding population of approximately 40-50 pairs (Dunn, 2012). The area of greatest burrow density can be found along the southern landward coast. Ihumoana (36° 53’ S, 174° 26’ E) is a small island of approximately 1.3 ha situated in the intertidal zone at the northern end of Te Henga (Bethells Beach; map 2.1 bottom). The island supports a single, large grey faced petrel colony of approximately 120 pairs (G. A. Taylor pers. comm.).

The naturally regenerating vegetation on Te Hāwere-a-maki consists of 95 species, though from a lack of active management, approximately a third of these are introduced (Gordon and Ballantine, 1976). The abundance of introduced species has reduced as native vegetation continues to develop. Pohutukawa (*Metrosideros excelsa*) forest is found along the coastal margins of the island with an understory of houpara (*Pseudopanax lessonii*), karo (*Pittosporum crassifolium*), tarangarara (*Gahnia lacera*) and a multitude of ferns. The coastal broadleaf forest, covering the inner island, is dominated by mapou (*Myrsine australis*) with houpara, karamu (*Coprosma robusta*), mahoe (*Melicytus ramiflorus*), kohekohe (*Dysoxylum spectabile*) and manuka (*Leptospermum scoparium*). Due to the much smaller size of Ihumoana, pohutukawa dominated forest extends from the margins of the island towards the centre (Rattenbury, 1989). The understory consists largely of houpara and kawakawa (*Macropiper excelsum*).

The close proximity of both islands to the mainland allows for continued reinfestation of introduced mammalian pests. Rats (*Rattus* spp.) are more than capable of traversing the 50 metre wide channel to reach Te Hāwere-a-maki (Russell et al., 2005). Recorded rat densities are highly stochastic, from 12-20 ha^{-1} in 1977 dropping through 3.2 ha^{-1} in 2005 to 1.3 ha^{-1} in 2011 and rising again to 4.3 ha^{-1} in 2012 (Dunn, 2012; Russell et al., 2009; Russell, 2013). Ihumoana’s connection to the mainland during low tide each day means it is similarly affected by introduced mammalian pests, with annual incursions of rats and occasionally mustelids (J. Lusk pers. comm.; G. A. Taylor pers. comm.).

Map 2.1 The study islands. Top: Map of Te Hāwere-a-maki, an island located at the centre of the Cape Rodney to Okakari Point Scientific Marine Reserve, Leigh in the Hauraki Gulf; Bottom: Map of Ihumoana, an intertidal island located at the northern end of Te Henga (Bethells Beach) and its surrounds.

2.3.2 Field Methods

To allow for comparison with results obtained from Te Hāwere-a-maki in the 2011 and 2012 breeding seasons, evaluation of chick growth rates throughout the 2013 breeding season was carried out using the same methodology employed by these studies (Dunn, 2012; Russell, 2013).

Upon the return of adults to their colonies in June and July 2013, burrows were inspected weekly by hand for easily accessible adults incubating eggs. Any adults found were removed, weighed, identified and if not already, banded with a metal band. Study lids, enabling easy access to nest chambers, were installed in suitable burrows that did not already have them. The location of each burrow was recorded and uniquely labelled. Twenty-two burrows were selected from Te Hāwere-a-maki and 23 from Ihumoana.

Te Hāwere-a-maki burrows were checked more regularly than Ihumoana (every three to four days and five to nine days, respectively) around hatching (late August). At each visit, eggs were inspected for changes (e.g. pipping) which, with a combination of the morphometric measurements taken upon the first encounter of a newly hatched chick, allowed for more accurate estimates of hatching dates. Hatching dates for Ihumoana chicks were estimated based on a combination of observation, egg development during incubation (by candling; G. A. Taylor pers. comm.) and initial measurements of newly hatched chicks.

When first found, newly hatched chicks were weighed in a dark cotton breathable bag using either a 600 g or 1000 g Pesola spring scale (as appropriate), to the nearest 5 g. The weight of the bag was subtracted from this measurement to give the weight of the chick. Using vernier callipers, bill culmen lengths, bill depths at the nares and maximum (or false) tarsus lengths were measured to the nearest 0.5 mm (see plate 2.2). Wing lengths, taken as the

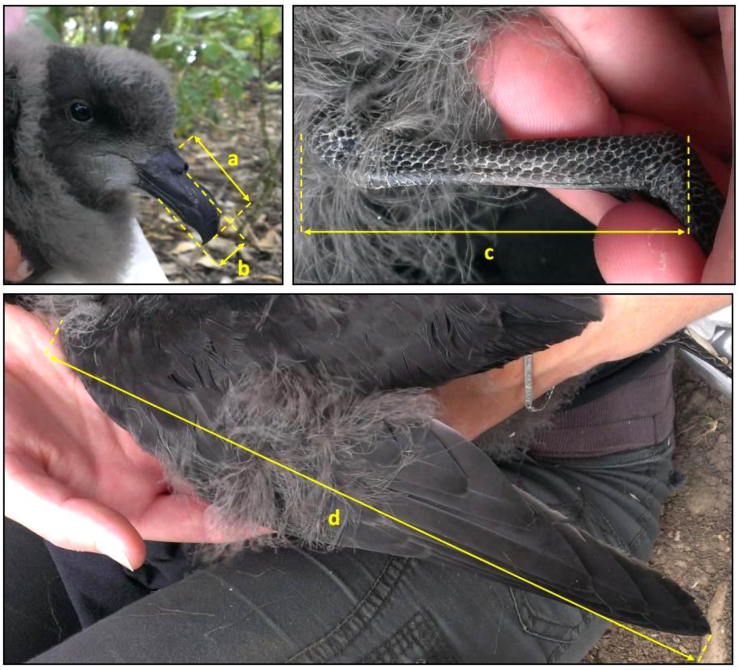


Plate 2.2 Pictures showing the measurements taken from grey-faced petrel chicks (a: bill culmen length; b: bill depth at nares; c: maximum tarsus length; d: wing length).

maximum flattened chord, were measured to the nearest 0.5 mm using a steel butt-stopped rule (see plate 2.2). From the end of the hatching period, burrows on both islands were revisited and chicks measured weekly (± two days). In addition to this, chicks from Te Hāwere-a-maki were handled daily between the 3rd and the 22nd of October to determine patterns of hourly weight loss and ascertain meal sizes (Chapter Three). When chicks regurgitated the regurgitate was collected, weighed and examined for identifiable prey items (K. Bourgeois unpub.). When regurgitate consisted of proventricular oil alone it was not able to be collected and weighed.

Burrows on both islands were frequented every three to four days over the fledging period (December to late-January) to more accurately estimate dates of fledging. Chicks no longer found inside their burrows, if when last observed were fully feathered with approximate adult dimensions, were considered to have fledged the previous night.

2.3.3 Control Group

To assess the effects of repeated handling on the growth of chicks, accessible chicks from other burrows on Te Hāwere-a-maki were measured along with the surviving study chicks on the 18th of December, prior to fledging. These burrows were inspected every three to four days over the fledging period, along with the study burrows, to determine if the chick was still present. If a chick was found absent it was presumed to have fledged the previous night.

2.3.4 Statistical Analysis

Differences in chick growth between Te Hāwere-a-maki and Ihumoana in the 2013 breeding season were investigated using a linear mixed model with the fixed effects of: chick age (expressed as days since hatching; DSH), island (Te Hāwere-a-maki and Ihumoana) and the interaction between chick age and breeding season. Bird identity was included in the model as a random factor to control for repeated observations of the same individual. Differences in chick growth on Te Hāwere-a-maki among breeding seasons were investigated similarly but using breeding season (2011, 2012 and 2013) as opposed to island. In order to satisfy the assumption of linearity for their use in normal linear regressions, different transformations on the response variables (weight, tarsus length, bill culmen length, bill depth and wing length) were trialled for their effect on the residual plot (Dunn, 2012; Tabachnick and Fidell, 2007). The most appropriate transformation chosen. Linear mixed models were chosen as opposed to non-linear models, due to difficulties that can arise in testing differences in fixed effects within non-linear growth curves (Hart and Chute, 2009). Unless otherwise stated, chick age is given in days since hatching (DSH) with mean values quoted with ± standard deviation. These analyses were carried out using the nlme package in R version 3.0.2 (Pinheiro et al., 2014; R Core Team, 2013).

To compare chick morphometric measurements between the Te Hāwere-a-maki control and study groups, measurements taken from control and study groups in the 2011, 2012 and 2013 breeding seasons were grouped. T-tests for independent samples were performed for each of the morphometric measurements. For this comparison, chick age was expressed as days before fledging (DBF) as exact hatching dates of control chicks were unknown. A t-test for independent samples was also performed on the DBF. For chicks that died before fledging, the mean fledging date was used. As part of another study conducted on Te Hāwere-a-maki during the 2013 breeding season, seven study chicks had one of their parents equipped with a GPS device (K. Bourgeois unpub.). To ensure that this had no effect on chick growth, the morphometric measurements taken on the 18th December 2013 were compared between chicks that had neither parent equipped with a GPS and chicks that had one parent equipped with a GPS.

2.4 Results

2.4.1 Overview

Twenty-three burrows were intensively monitored on Ihumoana throughout the 2013 breeding season all of which produced a chick in late-August to early-September (mean = 26th August 2013 ± 7 days; range: 15th August to 8th September). All 23 chicks survived to fledge in December to early-January (average = 20th December ± 10 days; range: 1st December 2013 to 9th January 2014) at an average age of 116 days ± 7 days (range: 105 and 131 days). There were 107 other active burrows on Ihumoana at the start of the breeding season (G. A. Taylor pers. comm.). It is unknown how many of these produced a chick, but 62 chicks survived to fledge, a peak for the island’s 25 monitored years.

Twenty-two burrows were intensively monitored on Te Hāwere-a-maki throughout the 2013 breeding season 15 of which produced a chick in late-August to early-September (mean = 26th August 2013 ± 6 days; range: 16th August to 7th September). Ten of these 15 chicks survived to fledge in January 2014 (mean = 14th January 2014 ± 10 days; range: 1st January to 29th January) at an average age of 139 days ± 9 days (range: 128 to 157 days). Post-mortem examination of the five chicks that died prior to fledging suggested that starvation was the cause of death. There were at least 44 other active burrows on Te Hāwere-a-maki. Twenty-eight of these produced a chick, of which 25 survived to fledge (K. Bourgeois pers. comm.).

Twenty-two burrows were intensively monitored on Te Hāwere-a-maki throughout both the 2011 and 2012 breeding seasons. In the 2011 breeding season, 19 burrows produced a chick, eight of which survived to fledge at an average age of 136 days ± 10 days (range: 126 to 153 days; Dunn, 2012). Eight of the 22 burrows monitored on Te Hāwere-a-maki throughout the 2013 breeding season were also monitored throughout the 2011 breeding season. Six of these burrows had at least one of the same adults. In the 2012 breeding season 18 burrows produced a chick, nine of which survived to fledge at an average age of 133 days (Russell, 2013). Nine of the 22 burrows monitored during the 2013 breeding season were also monitored throughout the 2012 breeding season. Six of these burrows had at least one of the same adults breeding inside them. Nine burrows were monitored in both the 2011 and 2012 breeding seasons seven of which had at least one of the same adults breeding inside them. There were only two occasions in which a chick was successfully raised by an adult breeding in successive years.

2.4.2 Weight

The growth curves for weight for chicks raised on Te Hāwere-a-maki and Ihumoana in the 2013 breeding season is shown in figure 2.1. The growth curves for chick weight on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons is shown in figure 2.2. As is typical for Procellariiformes, chicks experienced periods of rapid weight gain, associated with feeding events, punctuated by relatively longer periods of weight loss (see Chapter Three). For analyses of weight, chick age, expressed as days since hatching (DSH), was square rooted to make the data linear for use in the linear mixed model regressions. The regression equations, investigating the differences between islands in the 2013 breeding season (table 2.1) and among Te Hāwere-a-maki breeding seasons (table 2.2), both follow the growth curves well.

The results from the linear mixed regression investigating the differences in chick growth rates between islands in the 2013 breeding season, suggest that there is evidence for weight at hatching being larger for chicks raised on Te Hāwere-a-maki compared to chicks raised on Ihumoana (*ISLANDTE.HĀWERE*: value = 47.498, p-value = 0.068; table 2.1). This is obviously not the case as the intercept for chicks raised on Ihumoana is below zero (intercept: value = -2.052, p-value = 0.900; table 2.1). However, the curve for this model, where the square root of DSH is used as a predictor, follows the data well and so the model was chosen despite this apparent error in the estimate of intercepts. The average weight at hatching, recorded for two Te Hāwere-a-maki chicks was 54 g (range: 50 to 58 g). No chicks from Ihumoana were measured at hatching. However, the average weight at one DSH, recorded for three chicks from Ihumoana was 80 g ± 2.1 g (range: 78 to 82 g), similar to the average weight recorded for five chicks from Te Hāwere-a-maki at one DSH (97 g ± 20.2 g; range: 79 to 132). There is very strong evidence that chicks raised on Ihumoana gained weight at an elevated rate than chicks raised on Te Hāwere-a-maki (*Sqrt(DSH):ISLANDTE.HĀWERE*: value = -28.698, p-value < 0.001; table 2.1).

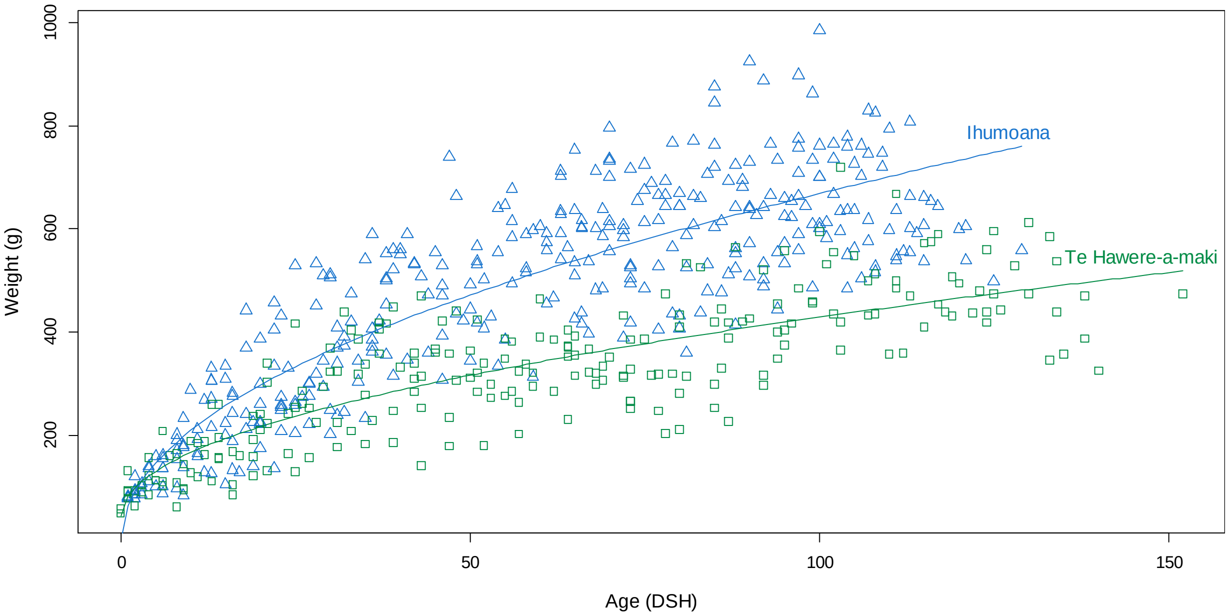


Figure 2.1 Weight (g) of grey-faced petrel chicks raised over the 2013 breeding season (n = 33) on Te Hāwere-a-maki (□) and Ihumoana (△) as a function of age, expressed as days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for weight with square root DSH displayed in Table 2.1.

As is common in growing Procellariiformes, some chicks were observed to have attained a weight greater than that of adults or fledglings. During the 2013 breeding season all of the 23 study chicks raised on Ihumoana attained a weight equal to or greater than the average adult weight of 550 g. Comparatively six of the 15 chicks from Te Hāwere-a-maki (60%) attained a weight equal to or greater than 550 g. Fifteen of the chicks from Ihumoana (65%) also attained a weight considerably greater than the average adult (> 750 g) while none of the Te Hāwere-a-maki chicks attained such a weight. There is very strong evidence for a difference in the peak weight attained between islands with chicks raised on Ihumoana having a larger peak weight (p-value < 0.001). The average peak weight attained for chicks raised on Ihumoana was 761 g ± 92 g (range: 557 to 985 g; n = 23) while for chicks raised on Te

Hāwere-a-maki peak was 561 g ± 79 g (range: 443 to 720 g; n = 10).Additionally, There is very strong evidence for a difference in the age at which peak weight was attained between islands with chicks raised on Ihumoana being considerably younger (p-value < 0.001). The average age at which peak weight was attained for chicks raised on Ihumoana was 96 DSH ± 13 DSH (range: 70 to 113 DSH; n = 23) while or chicks raised on Te Hāwere-a-maki was 120 DSH ± 13 DSH (range: 100 to 133 DSH; n = 10).

In the two weeks prior to fledging, 17 chicks from Ihumoana lost an average of 149 g ± 114 g (range: 2 to 378 g) while six chicks gained an average of 84 g ± 68 g (range: 8 to 171 g). With 95% confidence, the proportion of chicks that lost weight is somewhere between 0.442 and 0.514 higher than the proportion of chicks that gained weight. In the two weeks prior to fledging six chicks from Te Hāwere-a-maki lost an average of 113 g ± 75 g (range: 31 to 225 g) while four chicks gained an average of 26 g ± 39 g (range: 3 to 84 g). With 95% confidence, the proportion of chicks that lost weight is somewhere between 0.139 and 0.261 higher than the proportion of chicks that gained weight. This suggests that for chicks raised in the 2013 breeding season there is a pattern of weight recession prior to fledging on both islands though this was more pronounced on Ihumoana. Interestingly, on both islands there was no difference in the fledging weight between the chicks that lost weight and those that gained weight prior to fledging (p-values = 0.101 and 0.060 respectively).

There is very strong evidence for a difference in weight at fledging between islands in the 2013 breeding season (p-value < 0.001). The average weight for Ihumoana chicks at the last measurement before fledging was 607 g ± 82 g (range: 484 to 825 g; n = 23). This was significantly higher than the average weight for Te Hāwere-a-maki chicks at the last measurement before fledging (average = 451 g ± 82 g; range: 326 to 585 g; n = 10). On average Ihumoana chicks were heavier than the average adult at fledging while Te Hāwere-a-maki chicks were lighter.

Table 2.1 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for weight (g) of grey-faced petrel chicks raised over the 2013 breeding season on Te Hāwere-a-maki and Ihumoana, investigating the terms: days since hatching (DSH) and island (ISLANDTE.HĀWERE) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	-2.052	16.273	549	-0.126	0.900
Sqrt(DSH)	67.094	1.678	549	39.992	$<0.001^{***}$
ISLANDTE.HĀWERE	47.498	25.199	36	1.885	0.068
Sqrt(DSH):ISLANDTE.HĀWERE	-28.698	2.574	549	-11.148	$<0.001^{***}$

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	2283.999	47.791	24.8
Residual	6913.999	83.148	75.2
Total	9197.596		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

The difference in weight at hatching for chicks raised on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons is almost negligible (*YEAR2012*: value = 80.394, p-value = 0.053; *YEAR2013*: value = 22.228, p-value = 0.485; table 2.2). The average weight at hatching, recorded for five chicks over the past three breeding seasons (two from both 2011 and 2013 and one from 2012), was 56 g ± 5.2 g (range: 50 to 60 g). The average weight at one DSH, recorded for nine chicks (three from 2011, one from 2012 and five from 2013) was 84 g ± 22.6 g (range: 55 to 132 g). There is no evidence for a difference in the rate at which chicks gained weight among breeding seasons (*Sqrt(DSH):YEAR2012*: value = -2.202, p-value = 0.556; *Sqrt(DSH):YEAR2013*: value = -0.514, p-value = 0.842; table 2.2).

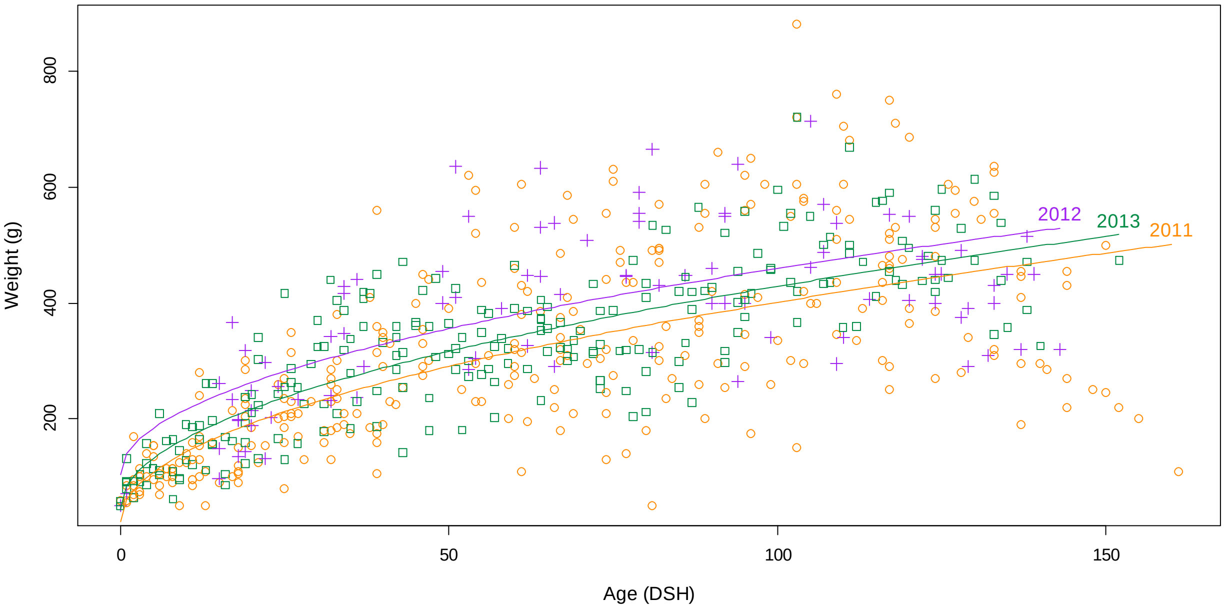


Figure 2.2 Weight (g) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the 2011 (○) 2012 (+) and 2013 (□) breeding seasons (n = 27) as a function of age, expressed in days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for weight with square root DSH displayed in Table 2.2.

Taken together, 75% of the chicks raised on Te Hāwere-a-maki over the past three breeding seasons (2011, 2012 and 2013), have attained a weight equal to or greater than the average adult weight of 550 g; this is made up of eight chicks from the 2011 breeding season and six from both the 2012 and 2013 breeding seasons. Only two chicks from Te Hāwere-a-maki have attained a peak weight considerably greater (> 750 g) both of which were raised in the 2011 breeding season. There is weak evidence for a difference in the age at which peak weight was attained among the breeding seasons. This is likely due to the difference between the 2012 and 2013 breeding seasons (p-values = 0.064, 0.069 respectively). The average age at which peak weight was attained for the 2011 breeding season was 115 DSH ± 13 DSH (range: 103 to 133 DSH; n = 8) and for the 2012 breeding season was 97 DSH ± 32 DSH (range: 51 to 139 DSH; n = 9) compared to 120 DSH for the 2013 breeding season. The reason peak weight was apparently attained at a much younger age in the 2012 breeding season is probably attributable to the two weeks ± 2 day interval between measurements as opposed to the shorter interval used in 2011 and 2013. There is evidence for a difference in the peak weight attained among breeding seasons which is likely due to the differences between the 2011 and 2012/2013 breeding seasons (p-values = 0.021, 0.035 and 0.020 respectively). The average peak weight attained during the 2011 breeding seasons was 679 g ± 104 g (range: 560 to 880 g; n = 8) and for the 2012 breeding season was 569 g ± 88 g (range: 450 to 713 g; n = 9) compared to 561 for the 2013 breeding season.

Over the past three breeding seasons, in the two weeks prior to fledging, 15 chicks surviving to fledge on Te Hāwere-a-maki (control chicks not included) lost an average of 121 g ± 62 g (range: 13 to 225 g) while 10 chicks gained an average of 60 g ± 62 g (range: 3 to 190 g). With 95% confidence, the proportion of chicks that lost weight is somewhere between 0.163 and 0.238 higher than the proportion of chicks that gained weight. This suggests that there is a general pattern of weight recession prior to fledging in chicks raised on Te Hāwere-a-maki. There is no evidence for a difference in the fledging weight between chicks that lost weight and chicks that gained weight (p-value = 0.434).

There is no evidence for a difference in weight at fledging among breeding seasons (p-value = 0.182). The average weight at fledging for chicks raised during the 2011 breeding season was 518 g ± 62 g (range: 430 to 625 g; n = 8) and during the 2012 breeding season was 481 g ± 73 g (range: 320 to 552 g; n = 9). Over the past three breeding seasons, Te Hāwere-a-maki chicks have been lighter than the average adult (550g) at fledging. The average weight at fledging for all three breeding seasons combined was 481 g ± 76 g (range: 320 to 625 g; n = 27).

Table 2.2 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for weight (g) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the past three breeding seasons (2011, 2012 and 2013), investigating the terms: days since hatching (DSH) and year (YEAR2012 and YEAR2013) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	23.833	20.562	566	1.159	0.247
Sqrt(DSH)	37.741	1.681	566	22.452	<0.001***
YEAR2012	80.394	40.599	49	1.980	0.053
YEAR2013	22.228	31.611	49	0.703	0.485
Sqrt(DSH):YEAR2012	-2.202	3.736	566	-0.589	0.556
Sqrt(DSH):YEAR2013	-0.514	2.679	566	-0.199	0.842

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	5394.997	73.451	44.1
Residual	6846.067	82.741	55.9
Total	12241.060		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

2.4.3 Wing Length

The growth curves for wing length for chicks raised on Te Hāwere-a-maki and Ihumoana in the 2013 breeding season is shown in figure 2.3. The growth curves for chick wing length on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons is shown in figure 2.4. The average wing length at zero to one DSH, recorded for 12 chicks (two and seven from Te Hāwere-a-maki 2011 and 2013 breeding seasons, respectively, and three from Ihumoana) was 25.6 mm ± 3.0 mm (range: 21 to 33 mm). As is typical of wing growth in Procellariiformes, wings grew slowly initially, but as primaries started growing, at around 50 DSH, wings increased more rapidly in length (figures 2.3 and 2.4). To make the data linear for use in the linear mixed model regressions the natural log of wing length was used. The regression equations investigating the differences between islands in the 2013 breeding season (table 2.3) and among Te Hāwere-a-maki breeding seasons (table 2.4) both follow the growth curves well although they do not logically flatten out prior to fledging.

For chicks raised in the 2013 breeding season, there is no evidence of a difference in wing length at hatching between Te Hāwere-a-maki and Ihumoana (*ISLANDTE.HĀWERE*: value = 0.015, p-value = 0.722; table 2.3). However, there is very strong evidence for a difference in the rate at which wing length increased over the breeding season between islands. Wing lengths of chicks raised on Ihumoana grew significantly faster than those of chicks raised on Te Hāwere-a-maki (*DSH:ISLAND TEHĀWERE*: value = -0.006, p-value < 0.001; table 2.3).

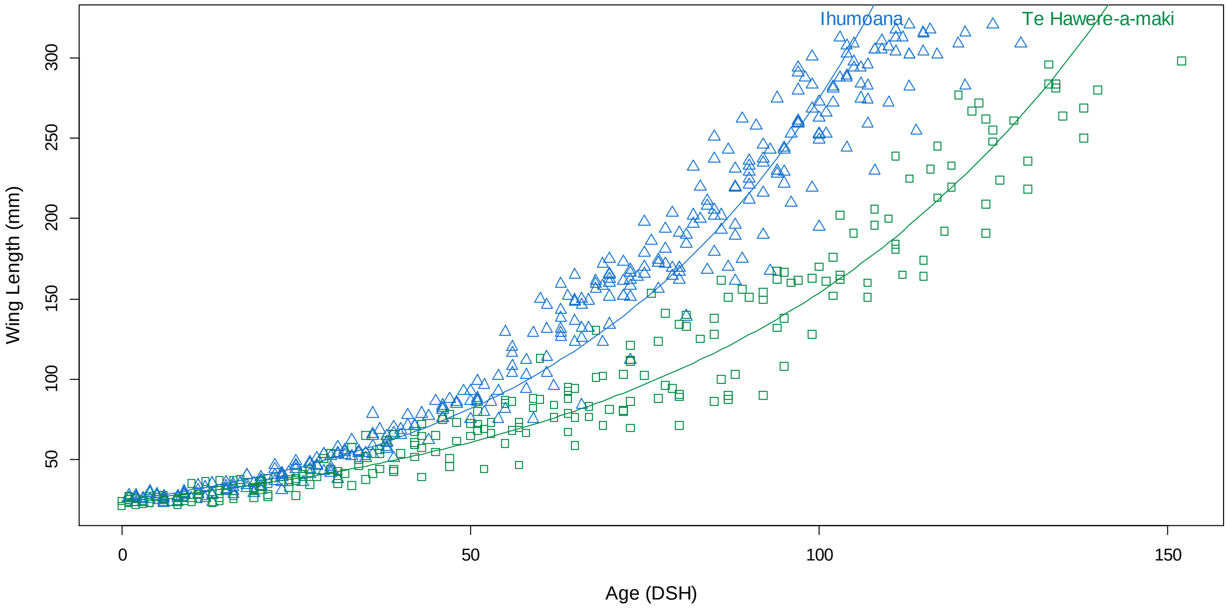


Figure 2.3 Wing length (mm) of grey-faced petrel chicks raised over the 2013 breeding season (n = 33) on Te Hāwere-a-maki (□) and Ihumoana (△) as a function of age, expressed as days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for log(wing length) displayed in Table 2.3.

There is very strong evidence for a difference in wing length at fledging between islands in the 2013 breeding season (p-value < 0.001). The average wing length for Ihumoana chicks at the last measurement before fledging was 310.2 mm ± 6.5 mm (range: 298 to 321 mm; n = 23). This was significantly higher than the average wing length for Hāwere-a-maki chicks at the last measurement before fledging of 280.9 mm ± 10.4 mm (range: 267 to 298 mm; n = 10). Ihumoana chicks fledged with a wing length close to that of an average adult (320 mm). Te Hāwere-a-maki chicks have had a significantly shorter wing length at fledging than that of an average adult.

Table 2.3 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for log(wing length) (mm) of grey-faced petrel chicks raised over the 2013 breeding season from Te Hāwere-a-maki and Ihumoana, investigating the terms: days since hatching (DSH), survivorship class (FLEDGEDYES) and island (ISLANDTE.HĀWERE) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.189	0.026	549	121.314	<0.001***
DSH	0.024	0.000	549	131.558	<0.001***
ISLANDTE.HĀWERE	0.015	0.041	36	-0.358	0.722
DSH:ISLANDTE.HĀWERE	-0.006	0.000	549	-20.224	<0.001***

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	0.012	0.121	44.4
Residual	0.015	0.129	55.6
Total	0.027		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

There was no evidence for a difference in wing length at hatching between chicks raised on Te Hāwere-a-maki in the 2011 and 2012 breeding seasons (*YEAR2012*: value = -0.010, p-value = 0.893; table 2.4). There is, however, evidence for wing length at hatching being slightly lower for chicks raised during the 2013 breeding season (*YEAR2013*: value = -0.163, p-value = 0.010; table 2.4). There is very strong evidence of a difference in the rate at which wings grew among breeding seasons, though the difference is likely small enough to be negligible. The wings of chicks raised during the 2012 breeding season grew faster than those of chicks raised during the 2013 breeding season which in turn, grew faster than those of chicks raised during the 2013 breeding season (*DSH:YEAR2012*: value = 0.003, p-value < 0.001; *DSH:YEAR2013*: value = 0.002, p-value < 0.001; table 2.4).

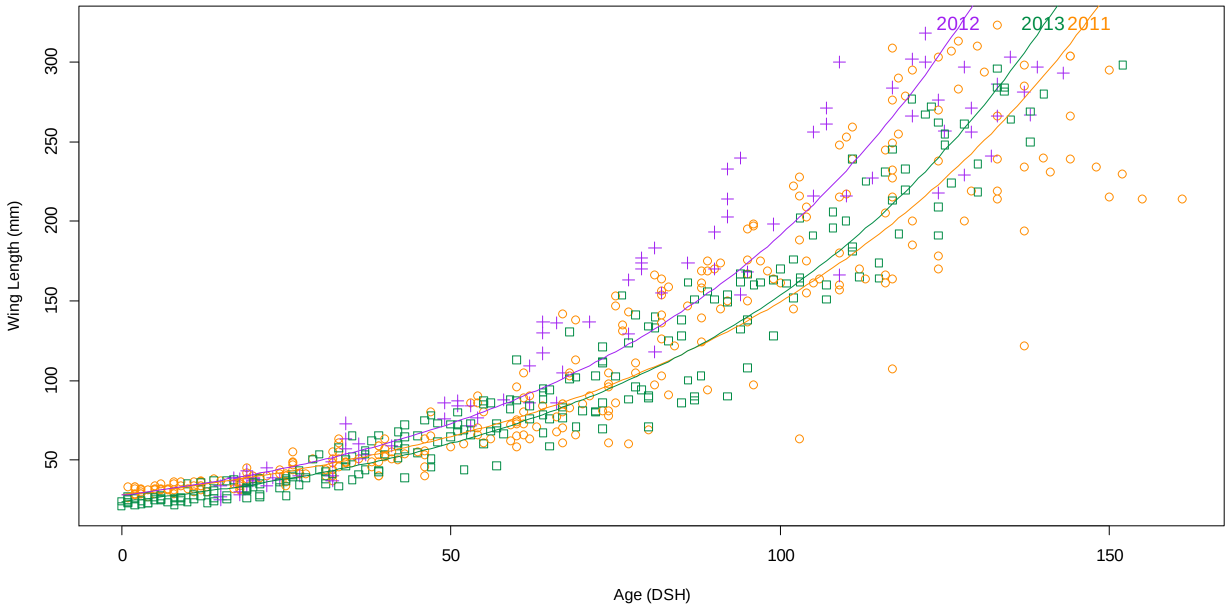


Figure 2.4 Wing length (mm) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the 2011 (○) 2012 (+) and 2013 (□) breeding seasons (n = 27) as a function of age, expressed in days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for log(wing length) displayed in Table 2.4.

There is no evidence for a difference in wing length at fledging among breeding seasons (p-value = 0.513). The average wing length at fledging for chicks raised in the 2011 breeding season was 284.4 mm ± 50.4 mm (range: 164 to 323 mm; n = 8), in the 2012 breeding season was 296 mm ± 14.1 mm (range: 267 to 318 mm; n = 9), and in the 2013 breeding season was 280.9 mm. However, over the past three breeding seasons, Te Hāwere-a-maki chicks have fledged with much smaller wing lengths than that of the average adult (320 mm). The average wing length at fledging for all three breeding seasons combined was 289 mm ± 28.8 mm (range: 164 to 323 mm; n = 27).

Bird identity accounts for 52.8% of the total variance in the regression investigating differences in Te Hāwere-a-maki chick growth among breeding seasons (table 2.4). This implies that the variance in wing length was greater among measurements taken from the same chick than among chicks. This indicates that wings experienced spurts in growth over the chick rearing period. Bird identity accounts for 42.3% of the total variance in the regression investigating differences in chick growth between islands in the 2013 breeding season (table 2.3). This implies that the variance in wing length was greater among chicks than among measurements taken from the same chick. However, wings are still expected to have grown in spurts and this lower variance for bird identity is probably due to the pronounced difference in the rate of wing growth between islands.

Table 2.4 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for log(wing length) (mm) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the past three breeding seasons (2011, 2012 and 2013), investigating the terms: days since hatching (DSH) and year (YEAR2012 and YEAR2013) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.337	0.039	561	85.758	<0.001***
DSH	0.017	0.000	561	79.284	<0.001***
YEAR2012	-0.010	0.073	48	-0.135	0.893
YEAR2013	-0.163	0.061	48	-2.668	0.010*
DSH:YEAR2012	0.003	0.000	561	5.822	<0.001***
DSH:YEAR2013	0.002	0.000	561	5.870	<0.001***

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	0.029	0.170	59.2
Residual	0.020	0.140	40.8
Total	0.049		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

2.4.4 Maximum Tarsus Length

The growth curves for the maximum (false) tarsus length for chicks raised on Te Hāwere-a-maki and Ihumoana in the 2013 breeding season is shown in figure 2.5. The growth curves for the maximum tarsus length for chicks raised on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons is shown in figure 2.6. As is typical of tarsus growth in Procellariiformes, the tarsus grew more rapidly in length at the beginning of the chick rearing period, reaching an asymptote relatively early compared to measurements for the bill culmen length and bill depth at the nares (sections 2.4.5 and 2.4.6, respectively). For analyses of tarsus length, DSH was logged as this transformation had the best influence on the residual plots. Though the assumption of linearity is still not satisfied the regression equations investigating the differences between islands during the 2013 breeding season (table 2.5) and among years on Te Hāwere-a-maki (table 2.6), generally follow the growth curves. They are therefore able to give an idea of the differences in growth rates and allow testing for significant differences.

For chicks raised in the 2013 breeding season, there is weak evidence of a difference in tarsus length at hatching between Te Hāwere-a-maki and Ihumoana (*ISLANDTE.HĀWERE*: value = 1.920, p-value = 0.058; table 2.5). There is however, a significant difference in the rate at which length increased over the breeding season between islands. The tarsus lengths of chicks raised on Ihumoana grew significantly faster than those of chicks raised on Te Hāwere-a-maki (*log(DSH):ISLANDTEHĀWERE*: value = -1.443, p-value < 0.001; table 2.5).

Ihumoana chicks reached an asymptote in their tarsus at approximately 50 to 60 DSH while Te Hāwere-a-maki chicks reached an asymptote at 90 to 100 DSH (figure 2.5).

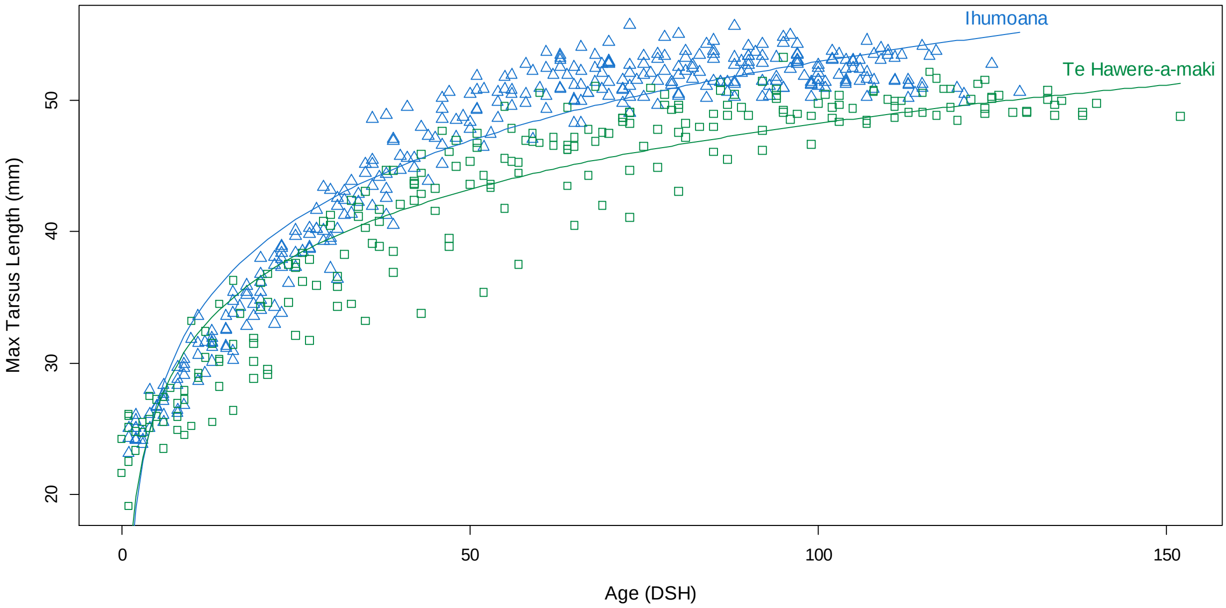


Figure 2.5 Maximum tarsus length (mm) of grey-faced petrel chicks raised over the 2013 breeding season (n = 33) on Te Hāwere-a-maki (□) and Ihumoana (△) as a function of age, expressed as days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for bill culmen length displayed in Table 2.5.

There is very strong evidence of a difference in the tarsus length at fledging between islands in the 2013 breeding season (p-value < 0.001). The average tarsus length at the last measurement before fledging for chicks raised on Ihumoana was 52.1 mm ± 1.3 mm (range: 49.9 to 54.2 mm; n = 23) and for Te Hāwere-a-maki chicks was 49.7 mm ± 0.9 mm (range: 48.5 to 51.3 mm; n = 10). Ihumoana chicks fledged with a tarsus length essentially equal to that of an average adult (51.6 mm). In comparison, Te Hāwere-a-maki chicks had a significantly smaller tarsus at fledging.

Table 2.5 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for maximum tarsus length (mm) of grey-faced petrel chicks raised over the 2013 breeding season on Te Hāwere-a-maki and Ihumoana, investigating the terms: log of days since hatching (DSH) and island (ISLANDTE.HĀWERE) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	12.888	0.633	547	20.354	<0.001***
log(DSH)	8.708	0.145	547	60.161	<0.001***
ISLANDTE.HĀWERE	1.920	0.982	36	1.955	0.058
log(DSH):ISLANDTE.HĀWERE	-1.443	0.224	547	-6.429	<0.001***

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	1.959	1.400	21.0
Residual	7.370	2.715	79.0
Total	9.329		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Tarsus length at hatching for chicks raised on Te Hāwere-a-maki was highest in 2013 and higher in 2011 than 2012 (*YEAR2012*: value = -5.452, p-value = 0.012; *YEAR2013*: value = 3.532, p-value = 0.005; table 2.6). There is strong evidence of a difference in the rate at which tarsus length grew among breeding seasons. The tarsus lengths of chicks raised in both the 2011 and the 2013 breeding seasons grew slower than those of chicks raised in the 2012 breeding season (*log(DSH):YEAR2012*: value = 1.923, p-value < 0.001; *log(DSH): YEAR2013*: value = -0.707, p-value = 0.003; table 2.6). In all three Te Hāwere-a-maki breeding seasons, chicks appeared to reach an asymptote in their tarsus lengths at a similar age (approximately 90 to 100 DSH; figure 2.6).

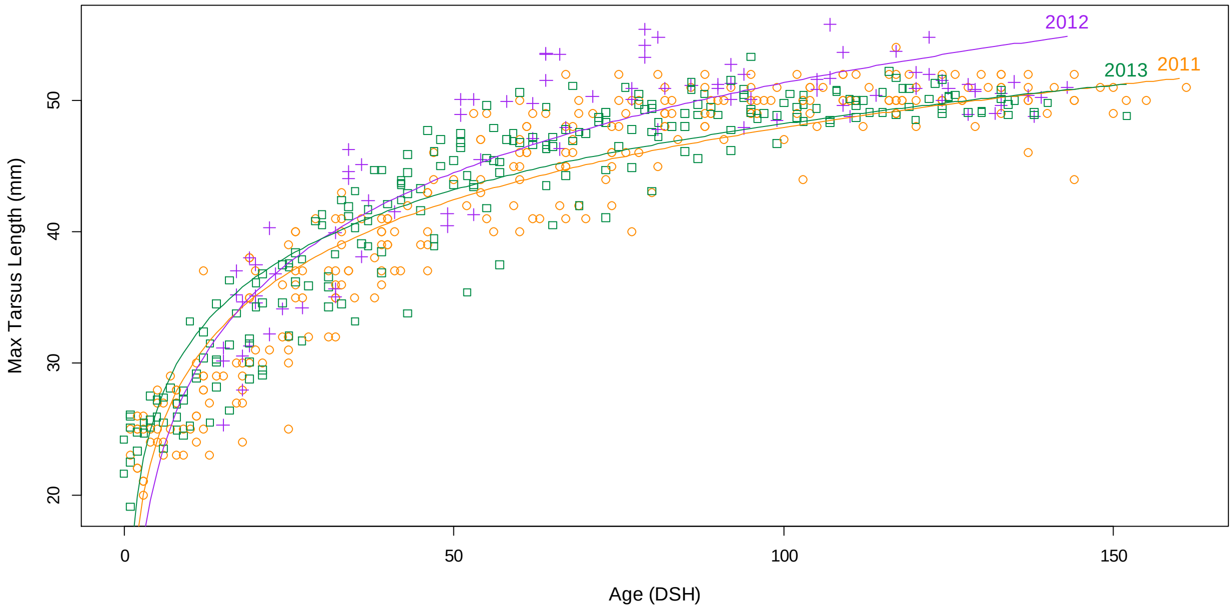


Figure 2.6 Maximum tarsus length (mm) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the 2011 (○) 2012 (+) and 2013 (□) breeding seasons (n = 27) as a function of age, expressed in days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for bill culmen length with log DSH displayed in Table 2.6.

There is strong evidence for a difference in tarsus length at fledging among breeding seasons. This is likely due to the difference between the 2011 and 2013 breeding seasons and the 2012 and 2013 breeding seasons (p-value = 0.009 and 0.011 respectively). The average tarsus length at fledging for chicks raised in the 2011 breeding season was 51.0 mm ± 0.9 mm (range: 50 to 52 mm; n = 8), in the 2012 breeding season was 51.8 mm ± 1.9 mm (range: 48.8 to 54.8 mm; n = 9), and in the 2013 breeding season was 49.7 mm. However, over the past three breeding seasons, Te Hāwere-a-maki chicks have fledged with tarsus lengths similar in size to the average adult (51.6 mm). The average tarsus length at fledging for all three breeding seasons combined was 50.8 mm ± 1.6 mm (range: 48.5 to 54.8 mm; n = 27).

Table 2.6 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for maximum tarsus length (mm) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the past three breeding seasons (2011, 2012 and 2013), investigating the terms: log of days since hatching (DSH) and year (YEAR2012 and YEAR2013) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	11.324	0.790	557	14.334	<0.001***
log(DSH)	7.950	0.162	557	48.996	<0.001***
YEAR2012	-5.452	2.081	48	-2.619	0.012*
YEAR2013	3.532	1.184	48	2.983	0.005**
log(DSH):YEAR2012	1.923	0.467	557	3.116	<0.001***
log(DSH):YEAR2013	-0.707	0.239	557	-2.960	0.003**

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	4.921	2.218	39.2
Residual	7.624	2.761	60.8
Total	12.545		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

2.4.5 Bill Culmen Length

The growth curves for the bill length for chicks raised on Te Hāwere-a-maki and Ihumoana in the 2013 breeding season is shown in figure 2.7. The growth curves for the bill length of chicks raised on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons is shown in figure 2.8. As is typical of bill growth in Procellariiformes, bills grew more rapidly in length at the beginning of the chick rearing period before reaching an asymptote. For analyses of bill length, DSH was square rooted as this transformation had the best influence on the residual plots. The assumption of linearity is, however, not completely satisfied. The regression equations investigating the differences between islands in the 2013 breeding season (table 2.7) and among Te Hāwere-a-maki breeding seasons (table 2.8) model their corresponding growth curves well, up until bill length reaches its asymptote, and allow testing for significant differences.

For chicks raised in the 2013 breeding season, there is strong evidence of a difference in bill length at hatching between Te Hāwere-a-maki and Ihumoana (*ISLANDTE.HĀWERE*: value = 1.338, p-value = 0.001; table 2.7). There is also a significant difference in the rate at which bill length increased over the breeding season between islands. The bill lengths of chicks raised on Ihumoana grew significantly faster than those of chicks raised on Te Hāwere-a-maki (*sqrt(DSH): ISLANDTEHĀWERE*: value = -0.474, p-value < 0.001; table 2.7). Ihumoana chicks reached an asymptote in bill length at a much younger age (approximately 70 to 80 DSH) than Te Hāwere-a-maki chicks (approximately 120 to 130 DSH; figure 2.7).

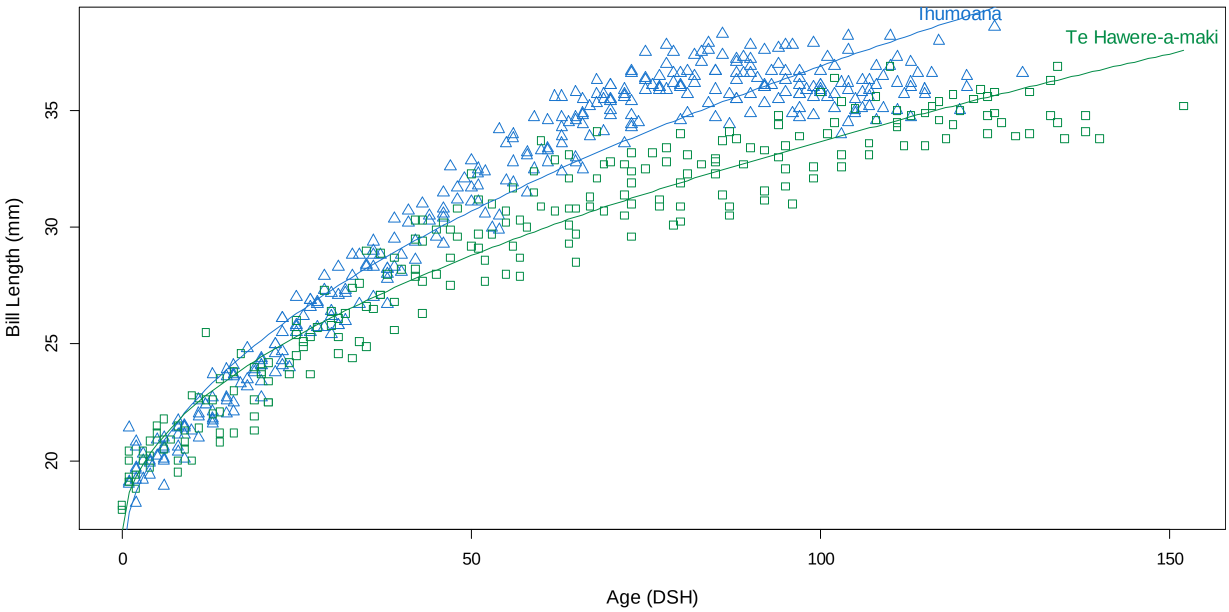


Figure 2.7 Bill culmen length (mm) of grey-faced petrel chicks raised over the 2013 breeding season (n = 33) on Te Hāwere-a-maki (□) and Ihumoana (△) as a function of age, expressed as days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for bill culmen length displayed in Table 2.7.

There is evidence for a difference in the bill length at fledging between islands in the 2013 breeding season (p-value = 0.041). The average bill length at the last measurement before fledging for chicks raised on Ihumoana was 36.0 mm ± 1.0 mm (range: 34.6 to 38.6 mm; n = 23) and for chicks raised on Te Hāwere-a-maki was 35.2 mm ± 1.0 mm (range: 33.8 to 36.9 mm; n = 10). Ihumoana chicks fledged with a bill length essentially equal to that of an average adult (36.4 mm). The Hāwere-a-maki chicks fledged with a bill length significantly shorter than an average adult.

Table 2.7 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for bill culmen length (mm) of grey-faced petrel chicks raised over the 2013 breeding season on Te Hāwere-a-maki and Ihumoana, investigating the terms: square root of days since hatching (DSH) and island (ISLANDTE.HĀWERE) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	15.637	0.241	547	64.857	$<0.001^{***}$
Sqrt(DSH)	2.144	0.027	547	80.729	$<0.001^{***}$
ISLANDTE.HĀWERE	1.338	0.371	36	3.605	0.001^{**}
Sqrt(DSH):ISLANDTE.HĀWERE	-0.474	0.041	547	-11.658	$<0.001^{***}$

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	0.384	0.620	18.181
Residual	1.728	1.315	81.818
Total	2.112		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Bill length at hatching for chicks raised on Te Hāwere-a-maki was highest in 2012 and slightly higher in 2013 than 2011 (*YEAR2012*: value = 2.707, p-value = 0.001; *YEAR2013*: value = 1.937, p-value = 0.001; table 2.8). There is some evidence of a difference in the rate at which bill length grew among breeding seasons. The bill lengths of chicks raised in both the 2012 and 2013 breeding seasons grew slower than those of chicks raised in 2011 (*sqrt(DSH):YEAR2012*: value = -0.170, p-value = 0.004; *sqrt(DSH):YEAR2013*: value = -0.229, p-value < 0.001; table 2.8). In all three breeding seasons chick raised on Te Hāwere-a-maki have reached an asymptote their bill lengths at a similar age (approximately 120 to 130 DSH; figure 2.8).

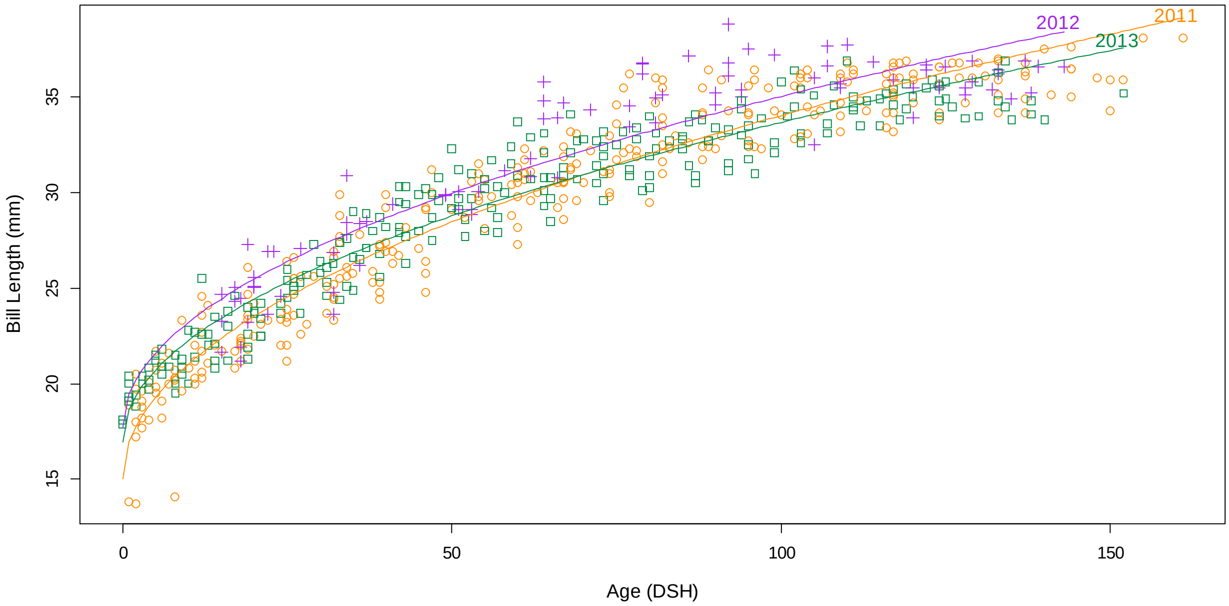


Figure 2.8 Bill culmen length (mm) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the 2011 (○) 2012 (+) and 2013 (□) breeding seasons (n = 27) as a function of age, expressed in days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for bill culmen length with square root DSH displayed in Table 2.8.

There is evidence for a difference in bill length at fledging among breeding seasons. This is likely due to the difference between the 2011 and the 2013 breeding seasons (p-value = 0.020). The average bill length at fledging for chicks raised in 2011 was 36.3 mm ± 0.9 mm (range: 34.3 to 36.9 mm; n = 8), in 2012 was 35.7 mm ± 1.0 mm (range: 33.9 to 36.7 mm; n = 9) and in 2013 was 35.2 mm. Over the past three breeding seasons, Te Hāwere-a-maki chicks have fledged with bill lengths similar in size to the average adult (36.4 mm). The average bill length at fledging for all three breeding seasons combined was 35.7 mm ± 1.0 mm (range: 33.8 to 36.9 mm; n = 27).

Table 2.8 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for bill culmen length (mm) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the past three breeding seasons (2011, 2012 and 2013), investigating the terms: square root of days since hatching (DSH) and year (YEAR2012 and YEAR2013) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	15.034	0.307	559	48.960	<0.001***
Sqrt(DSH)	1.900	0.026	559	73.024	<0.001***
YEAR2012	2.707	0.638	48	4.242	0.001**
YEAR2013	1.937	0.466	48	4.156	0.001**
Sqrt(DSH):YEAR2012	-0.170	0.059	559	-2.860	0.004**
Sqrt(DSH):YEAR2013	-0.229	0.039	559	-5.868	<0.001***

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	1.127	1.061	42.7
Residual	1.510	1.229	57.3
Total	2.637		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

2.4.6 Bill Depth at the Nares

The growth curve for the bill depth of chicks raised on Te Hāwere-a-maki and Ihumoana in the 2013 breeding season is shown in figure 2.9. The growth curve for the bill depth of chicks raised on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons is shown in figure 2.10. As is typical of bill growth in Procellariiformes, bills grew more rapidly in depth at the beginning of the chick rearing period before reaching an asymptote. For analyses of bill depth, DSH was square rooted as this transformation had the best influence on the residual plots. The assumption of linearity is, however, not completely satisfied. This is particularly so for the regression investigating the differences between islands in the 2013 breeding season (table 2.9). This regression equation models the corresponding growth curve well up until bill depth reaches its asymptote but still allows testing for significant differences. The regression equation investigating the differences among Te Hāwere-a-maki breeding seasons (table 2.10) models the corresponding growth curve well.

For chicks raised in the 2013 breeding season there is no evidence of a difference in bill depth at hatching between islands (*ISLANDTE.HĀWERE*: value = 0.095, p-value = 0.580; table 2.9). There is however, a significant difference in the rate at which bill depth increased over the breeding season between islands. The bill depths of chicks raised on Ihumoana grew significantly faster than those of chicks raised on Te Hāwere-a-maki (*sqrt(DSH): ISLANDTEHĀWERE*: value = -0.101, p-value < 0.001; table 2.9). Ihumoana chicks reached an asymptote in their bill depth at approximately 70 to 80 DSH while Te Hāwere-a-maki chicks appear to not have reached an asymptote at fledging (figure 2.9).

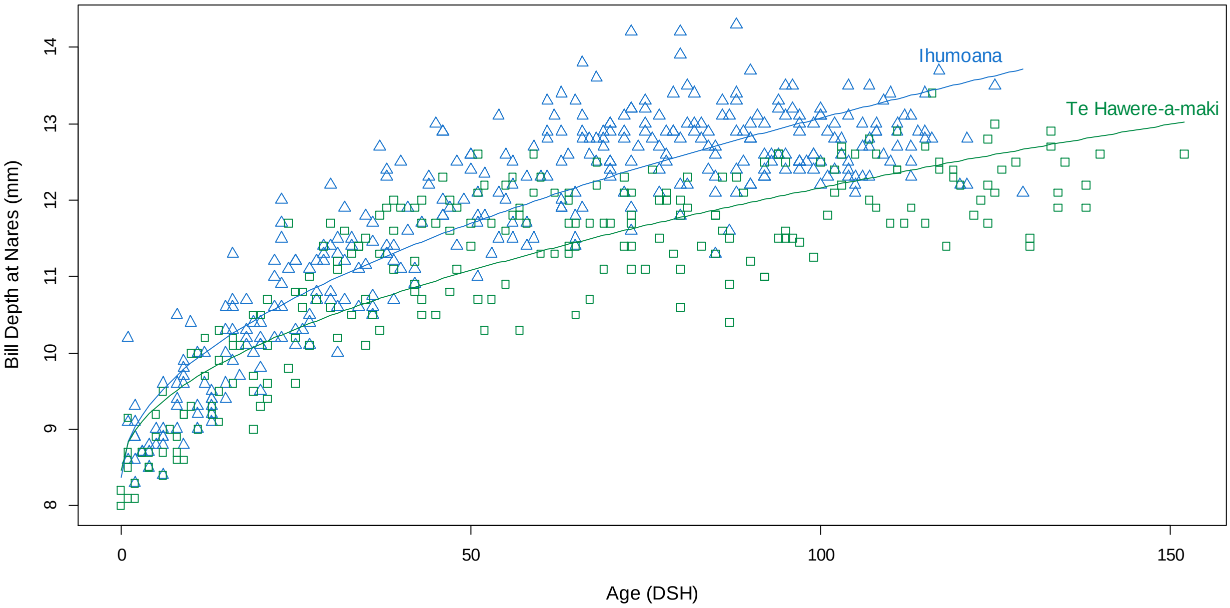


Figure 2.9 Bill depth at nares (mm) of grey-faced petrel chicks raised over the 2013 breeding season (n = 33) on Te Hāwere-a-maki (□) and Ihumoana (△) as a function of age, expressed as days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for bill culmen length with square root displayed in Table 2.9.

There is strong evidence of a difference in bill depth at fledging between islands in the 2013 breeding season (p-value = 0.003). The average bill depth at the last measurement before fledging for chicks raised on Ihumoana was 12.8 mm ± 0.4 mm (range: 12.1 to 13.5 mm; n = 23) and for chicks raised on Te Hāwere-a-maki was 12.3 mm ± 0.4 mm (range: 11.8 to 12.9 mm; n = 10). Ihumoana chicks fledged with a bill depth essentially equal to that of the average adult (13.2 mm). In comparison, Te Hāwere-a-maki chicks fledged with a bill length significantly smaller than the average adult.

Table 2.9 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for bill depth at nares (mm) of grey-faced petrel chicks raised over the 2013 breeding season on Te Hāwere-a-maki and Ihumoana, investigating the terms: square root of days since hatching (DSH) and island (ISLANDTE.HĀWERE) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	8.370	0.109	547	76.988	<0.001***
Sqrt(DSH)	0.471	0.010	547	45.570	<0.001***
ISLANDTE.HĀWERE	0.095	0.169	36	0.580	0.580
Sqrt(DSH):ISLANDTE.HĀWERE	-0.101	0.016	547	-6.353	<0.001***

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	0.128	0.358	32.9
Residual	0.261	0.511	67.1
Total	0.389		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Bill depth at hatching for chicks raised on Te Hāwere-a-maki was highest in the 2012 breeding season and slightly higher in 2013 than in 2011 (*YEAR2012*: value = 1.362, p-value < 0.001; *YEAR2013*: value = 0.238, p-value = 0.155; table 2.10). The reason for bill depth at hatching being so much higher in the 2012 breeding season is probably due to the lack of measurements in the first 15 days after hatching. There is some evidence of a difference in the rate at which bill depth grew among the breeding seasons. The bill depths of chicks raised in both the 2012 and the 2013 breeding seasons grew slower than those of chicks raised in the 2011 breeding season (*sqrt(DSH):YEAR2012*: value = -0.080, p-value = 0.002; *sqrt(DSH): YEAR2013*: value = -0.031, p-value = 0.062; table 2.10). For all three breeding seasons on Te Hāwere-a-maki, chick bill depth appeared to not yet have reached an asymptote at fledging (figure 2.10).

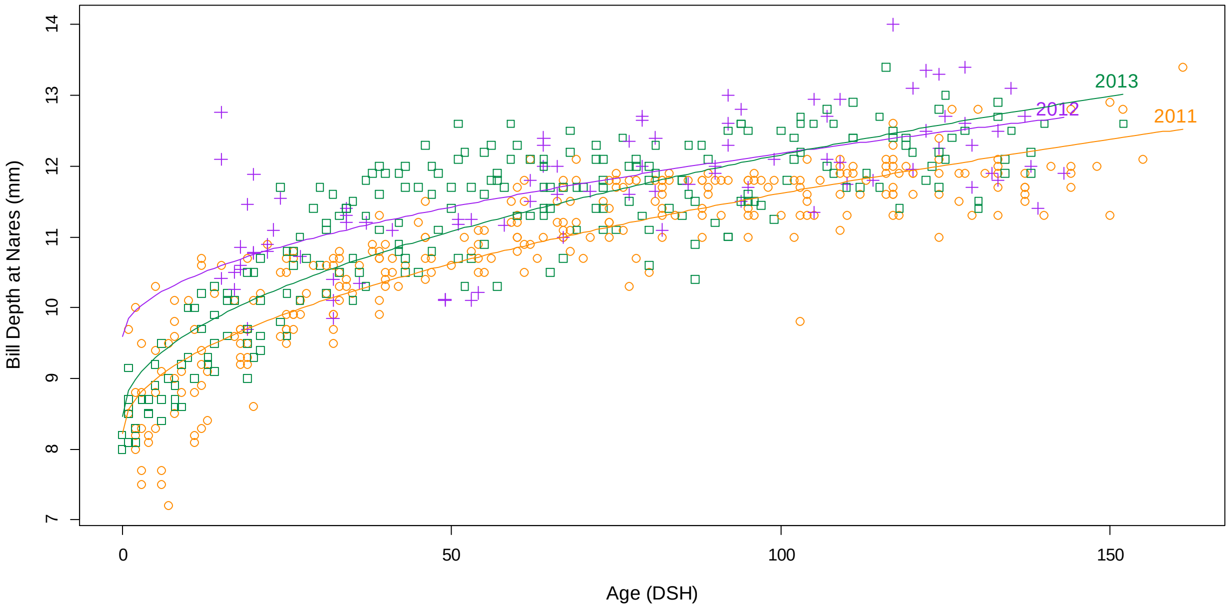


Figure 2.10 Bill depth at nares (mm) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the 2011 (○) 2012 (+) and 2013 (□) breeding seasons (n = 27) as a function of age, expressed in days since hatching (DSH). Slopes and intercepts of the lines of best fit were calculated using the parameter estimates obtained from the linear mixed effects model for bill culmen length with square root DSH displayed in Table 2.10.

There is no evidence for a difference in bill depth at fledging among breeding seasons (p-value = 0.082). The average bill depth at fledging for chicks raised in 2011 was 11.88 mm ± 0.6 mm (range: 11 to 12.9 mm; n = 8), in 2012 was 12.6 mm ± 0.8 mm (range: 11.4 to 14.0 mm; n = 9), and in 2013 was 12.3 mm. However, over the past three breeding seasons, Te Hāwere-a-maki chicks have fledged with bill depths similar in size to the average adult bill depth (13.2 mm). The average bill depth at fledging for all three breeding seasons combined was 12.3 mm ± 0.7 mm (range: 11 to 14 mm; n = 27).

Table 2.10 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects model for bill depth at nares (mm) of grey-faced petrel chicks raised on Te Hāwere-a-maki over the past three breeding seasons (2011, 2012 and 2013), investigating the terms: square root of days since hatching (DSH) and year (YEAR2012 and YEAR2013) with BIRD.ID included as a random factor.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	8.227	0.110	557	74.638	<0.001***
Sqrt(DSH)	0.339	0.011	557	31.138	<0.001***
YEAR2012	1.362	0.241	48	5.657	<0.001***
YEAR2013	0.238	0.165	48	1.444	0.155
Sqrt(DSH):YEAR2012	-0.080	0.025	557	-3.186	0.002**
Sqrt(DSH):YEAR2013	-0.031	0.016	557	1.870	0.062

Variance component estimates

Source	Variance	Std.Dev	Percentage
BIRD.ID	0.097	0.312	26.3
Residual	0.272	0.521	73.7
Total	0.369		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

2.4.7 Summary

Table 2.11 summarises the main findings of the linear mixed effects models for each of the morphological measurements. Chicks raised on Ihumoana in the 2013 breeding season had consistently elevated growth rates compared to chicks raised on Te Hāwere-a-maki in the same breeding season. Chick growth rates were not consistently higher for any one breeding season on Te Hāwere-a-maki (2011, 2012 and 2013).

Table 2.11 Table comparing the intercepts and growth rates obtained from the linear mixed effects models of differences in morphological measurements between islands (Te Hāwere-a-maki and Ihumoana) for grey-faced petrel chicks raised in the 2013 breeding season and among breeding seasons (2011, 2012 and 2013) for chicks raised on Te Hāwere-a-maki. Significance is denoted by italics.

	Measurement	2013 Breeding Season	Te Hāwere-a-maki
Intercept	Weight	Te Hāwere-a-maki > Ihumoana	2012 > 2013 > 2011
	Wing Length	Te Hāwere-a-maki > Ihumoana	2011 > 2012 > *2013*
	Tarsus Length	Te Hāwere-a-maki > Ihumoana	*2013* > *2011* > 2012
	Bill Length	*Te Hāwere-a-maki* > Ihumoana	*2012* > *2013* > 2011
	Bill Depth	Te Hāwere-a-maki > Ihumoana	*2012* > 2013 > 2011
Rate	Weight	Ihumoana > *Te Hāwere-a-maki*	2011 > 2013 > 2012
	Wing Length	Ihumoana > *Te Hāwere-a-maki*	*2012* = *2013* > 2011
	Tarsus Length	Ihumoana > *Te Hāwere-a-maki*	2012 > *2011* > *2013*
	Bill Length	Ihumoana > *Te Hāwere-a-maki*	2011 > *2012* > *2013*
	Bill Depth	Ihumoana > *Te Hāwere-a-maki*	2011 > 2013 > *2012*

2.4.8 Regurgitate

Regurgitate was collected from chicks raised during the 2013 breeding season that expelled their stomach contents when handled. On 11 occasions during the study, nine of the original 15 study chicks to hatch on Te Hāwere-a-maki regurgitated (range: 1 to 2 times). On seven of these occasions (64%) regurgitate consisted primarily of proventricular oil (< 2 g solids) that was dark orange-brown in colour. This was not weighed due to the difficulty in collecting it. The average weight of regurgitate on the other four occasions was 12.5 g ± 9.6 g (range: 1 to 24 g). On 69 occasions during the study, 19 of the 23 study chicks to hatch on Ihumoana regurgitated (range: 1 to 7 times). On 26 of these occasions (38%) regurgitate consisted primarily of proventricular oil (< 2 g solids) the majority of which was dark orange-brown in colour though a pale yellow on two occasions. The average weight of regurgitate on the other 43 occasions was 15 g ± 15.4 g (range: 1 to 67 g). There is strong evidence for a difference in the age at which chicks stopped vomiting between islands (p-value = 0.001). On average chicks on Te Hāwere-a-maki stopped regurgitating when handled at a younger age (24 DSH ± 9 DSH; range: 12 to 37 DSH) compared to chicks from Ihumoana (47 DSH ± 16 DSH; range: 5 to 74 DSH).

2.4.9 Control Group

Morphometric measurements taken from the 18 control and 30 study chicks raised on Te Hāwere-a-maki in the past 2011, 2012 and 2013 breeding seasons are presented in table 2.12. There are been no differences between the control and study groups in the DBF that these data on morphometric measurements were gathered (p-value = 0.192). There are also no differences between the control and study groups in any of the morphometric measurements taken ($\text{p-value}_{\text{Weight}} = 0.619$; $\text{p-value}_{\text{Wing Length}} = 0.776$; $\text{p-value}_{\text{max. Tarsus Length}} = 0.154$; $\text{p-value}_{\text{Bill Length}} = 0.717$; $\text{p-value}_{\text{Bill Depth}} = 0.917$).

Table 2.12 The average morphometric measurements ± standard deviation for control (n = 18) and study (n = 30) group grey-faced petrel chicks raised on Te Hāwere-a-maki over the 2011, 2012 and 2013 breeding seasons.

Treatment		DBF	Weight (g)	Wing Length (mm)	Tarsus Length (mm)	Bill Length (mm)	Bill depth (mm)
Control	Mean	19 ± 8	465 ± 94	234.4 ± 53.4	49.8 ± 2.3	35.6 ± 1.3	12.3 ± 0.5
	Range	5 to 35	250 to 610	107 to 309	43 to 54	33.2 to 37.5	11.3 to 13.1
Study	Mean	25 ± 11	481 ± 118	238.8 ± 48.7	50.7 ± 1.5	35.4 ± 1.1	12.3 ± 0.6
	Range	14 to 41	270 to 750	152 to 318	48 to 54.8	33.1 to 36.9	11.3 to 14

Morphometric measurements taken from the ten chicks raised in the 2013 breeding season whose parents were not equipped with a GPS (seven control chicks and three study chicks) and the seven whose parents were equipped with a GPS, are presented in table 2.13. There is no evidence of a difference between chicks that did not have a parent with a GPS and chicks that did in the DBF that the measurements were taken (0.116). Similarly, there is no evidence of differences in any of the morphometric measurements taken ($\text{p-value}_{\text{Weight}} = 0.514$; $\text{p-value}_{\text{Wing Length}} = 0.167$; $\text{p-value}_{\text{max. Tarsus Length}} = 0.778$; $\text{p-value}_{\text{Bill Length}} = 0.453$; $\text{p-value}_{\text{Bill Depth}} = 0.988$). Sixty percent of the five study chicks that died during the chick rearing period had parents with a GPS. Given the low percentage of chicks whose parents had GPS's that died, and the fact greater numbers of chicks died in the 2011 and 2012 breeding seasons (11 and seven respectively), it would appear that this is just random variation.

Table 2.13 The average morphometric measurements ± standard deviation for grey-faced petrel chicks reared during the 2013 breeding season whose parents were not equipped with a GPS device (n = 10) and who had one parent equipped with a device (n = 7).

Treatment		DBF	Weight (g)	Wing Length (mm)	Tarsus Length (mm)	Bill Length (mm)	Bill depth (mm)
No GPS Parents	Mean	19 ± 8	465 ± 52	229.1 ± 45.7	50.3 ± 1.2	35.5 ± 1.5	12.5 ± 0.4
	Range	5 to 35	400 to 583	166 to 295	49 to 52.5	33.2 to 37.5	11.7 to 13.1
GPS Parent	Mean	25 ± 11	496 ± 114	197.9 ± 41.7	50.2 ± 0.8	34.9 ± 1.1	12.5 ± 0.4
	Range	14 to 41	358 to 668	152 to 262	49.1 to 51.6	33.1 to 36.9	11.7 to 12.8

2.5 Discussion

2.5.1 Summary

During the 2013 breeding season growth characteristics were obtained for 15 grey-faced petrel chicks raised on Te Hāwere-a-maki and 23 chicks raised on Ihumoana. These data allow an understanding of geographical variations in chick growth between east and west coast colonies. Chick growth characteristics have also been obtained from Te Hāwere-a-maki for 19 chicks raised in the 2011 breeding season and 15 raised in the 2012 breeding season (Dunn, 2012; Russell, 2013). Comparison of Te Hāwere-a-maki chick growth over these three breeding seasons allow a better understanding of temporal variations for this small, inshore colony on Auckland’s east coast.

The chick rearing period on Ihumoana lasted, on average, 116 days ± 7 days (range: 105 to 131 days, n = 22), similar to previous records for this species which estimate a chick rearing period of between 118 and 120 days (Imber, 1976a; Taylor, 2013). The chick rearing period on Te Hāwere-a-maki in all three breeding seasons was longer than expected for this species, lasting, on average, 138 days ± 9 days (range: 127 to 157 days; n = 19). The average fledging date for chicks raised on Ihumoana was the 20th of December 2013 ± 10 days (range: 1st December 2013 to 9th January 2014). The average fledging date for chicks raised on Te Hāwere-a-maki raised in the 2013 breeding season was the 14th of January 2014 ± 10 days (range: 1st January to 29th January; n = 10), five days later than the 2011 breeding season (average: 9th January 2012) and ten days later than the 2012 breeding season (average: 4th January). Chicks raised on Ihumoana during the 2013 breeding season fledged, on average, three weeks earlier than chicks raised on Te Hāwere-a-maki during the same season. Data on annual variations in breeding success are presented in Chapter Four.

2.5.2 Control

There were no differences in any of the morphometric measurements, or DBF these were taken, between the control and study chicks raised on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons. Similarly, there were no differences between chicks raised in the 2013 breeding season that had one parent equipped with a GPS and chicks that had neither of their parents equipped with a GPS. Hence, there is no evidence to suggest that frequent handling of the chicks or, inadvertently manipulating the behaviour and weight of their parents, has affected chick growth in this study. Other studies have similarly reported that frequent handling does not affect chick growth in Procellariiformes (Gangloff and Wilson, 2004; O'Dwyer et al., 2006; Saffer et al., 2000). Other studies have also found that attaching tracking devices to parents provisioning chicks does not affect their foraging trip durations, the frequency with which they are able to provide for chicks or chick growth rates (Phillips et al., 2003; Rayner et al., 2008). However, too few studies have reported on the effects of frequent handling on chick growth rates, which are unlikely to be uniform among Procellariiform species (Carey, 2009). Indeed, there have been studies that have reported a disturbance to Procellariiform chick growth with regular handling (Weidinger, 1997).

It would seem that there is a high potential for frequent handling of grey-faced petrel chicks to reduce growth given a number of chicks regurgitated their stomach contents when handled. If this behaviour is on-going it would have the potential to directly impact growth, as each time it occurs the chick loses part of a, or a whole, meal (Carey, 2009). Regurgitation as a defence mechanism has been shown to come with a growth cost in the juveniles of other animals: the more regurgitate produced over the growth period the smaller they were upon reaching maturity (Higginson et al., 2011). No studies were found that have quantified the effect of regurgitation on growth rate in Procellariiformes. However, one chick from Ihumoana that continued to regurgitate into November 2013, appeared to have slightly stunted growth and was one of the last chicks to fledge from the island on the 9th of January 2014. However, such reduced growth was not observed in any other chicks that regurgitated over the course of the study. Some chicks were also particularly aggressive when handled throughout the chick rearing period. Such behaviour could have the potential to indirectly impact growth by directing energy obtained from food to defence as opposed to growth (Mangel and Stamps, 2001). This study did not determine if frequent handling had a metabolic or hormonal impact on chicks, though other studies on Procellariiformes have shown increased heart rates and energy expenditure (Carey, 2009). However, because no detectable differences in the morphometric measurements were observed between Te Hāwere-a-maki control and study chicks, the results presented here are considered representative of the grey-faced petrel. Reasons other than frequent handling are thought to have contributed to the patterns in growth presented here.

2.5.3 Chick Growth

Chicks raised on Ihumoana during the 2013 breeding season had much faster growth rates in all morphological measurements and fledged in better condition than chicks raised on Te Hāwere-a-maki during the same breeding season. Among the 2011, 2012 and 2013 breeding seasons, chicks raised on Te Hāwere-a-maki appear to have had similar growth rates in all morphometric measurements. Despite the disparity observed between islands, chick morphological development in all breeding seasons has conformed to the general pattern of growth reported for chicks of other *Pterodroma* and Procellariiform species (Booth et al., 2000; Cruz and Cruz, 1990b; Cuthbert, 2005; Gangloff and Wilson, 2004; Petit et al., 1984; Quillfeldt and Peter, 2000; Saffer et al., 2000; Zotier, 1990). Wing length grew in spurts of growth as shown by the larger variance within measurements for each chick than between chicks, a pattern presumably associated with recent provisioning.(Dunn, 2012). Though growing slowly initially, wings grew more rapidly as primaries started growing, at approximately 50 DSH for Ihumoana chicks and 75 DSH for Te Hāwere-a-maki chicks. Wings were still growing at fledging. The earlier growth of primaries observed in chicks raised on Ihumoana is likely a result of their relatively heavier weights. This pattern has also been observed in wandering albatross (*Diomedea exulans*) chicks (Berrow et al., 1999). Comparatively, tarsus length, bill length and bill depth grew rapidly initially, reaching an asymptote some time before fledging. Chicks raised on Ihumoana reached an asymptote in all measurements, at a younger age than chicks raised on Te Hāwere-a-maki. All measurements were significantly larger at fledging for chicks raised on Ihumoana, so it is possible that Te Hāwere-a-maki chicks were still growing at fledging.

There was a disparity in the pattern of weight gain between islands. Chick weight gain on Ihumoana was characteristic of other Procellariiformes (Cuthbert, 2005; Mauck and Ricklefs, 2005). Weight increased rapidly in the initial stages of growth until around 50 DSH, after which, it evened out. A peak weight, approximately 138% of average adult weight, was attained three to four weeks prior to fledging. Following this, most chicks went into a period of weight recession until fledging; however, some gained weight in the two weeks prior to fledging. Chicks ultimately fledged at similar weights whether they experienced weight losses or gains in the two weeks prior to fledging. Chick weight in other *Pterodroma* species has also been shown to decline from its peak for up to a month prior to fledging (Booth et al., 2000; Cuthbert, 2005; Mauck and Ricklefs, 2005; Teixeira et al., 2014). This is often due to a combination of parents reducing the amount they feed their chicks as they near fledging as well as chicks no longer accepting food from their parents (Teixeira et al., 2014; Weimerskirch and Lys, 2000; G. A. Taylor pers. comm.). In comparison, chick weight gain on Te Hāwere-a-maki increased slowly up until fledging. Averaged over all three Te Hāwere-a-maki breeding seasons, a peak weight, approximately 110% of the average adult weight, was attained three to four weeks prior to fledging. There is evidence of a pattern of weight recession in the two weeks prior to fledging though this was less noticeable than on Ihumoana. As on Ihumoana, chicks ultimately fledged at similar weights whether they experienced weight loss or gains in the two weeks prior to fledging. However, they were significantly lighter at fledging than chicks raised on Ihumoana.

Chicks nearing fledging appeared to be aiming to reach an optimal weight range that is likely balanced with their wing length (Mauck and Ricklefs, 2005). It would be in the interest of the chick to obtain the maximum reserves possible without limiting flight capability as this would increase their chances of survival in the initial post fledging period. On Ihumoana, where chicks were better provisioned, wings were able to grow to within the range of an average adult, meaning that they could support a much larger load and enabling chicks to be heavier at fledging. With better feeding conditions, chicks were able to attain weights well in excess of the average adult and so more were required to lose weight from their peak to their optimal weight range for fledging. In contrast, on Te Hāwere-a-maki chicks were poorly provisioned and the wings of many were much smaller than an average adult at fledging. Because few chicks raised on Te Hāwere-a-maki reached weights in excess of the average adult, many continued to gain weight up until fledging to reach their optimal weight range; still well below the weight of an average adult or fledgling from Ihumoana.

2.5.4 Geographical Variation

Chicks raised on Ihumoana in the 2013 breeding season, had much faster growth rates in all morphological measurements than chicks raised on Te Hāwere-a-maki during the same breeding season. They also fledged significantly earlier and with all measurements approximating those of an average adult. Ihumoana chicks reached an asymptote for tarsus length, bill length and bill depth relatively early in the chick rearing period, while Te Hāwere-a-maki chicks appeared to have reached their asymptote in these measurements at fledging, with some still growing. Irregular feedings and variable meal sizes have been shown to slow growth and development of other seabird chicks (Boersma et al., 1980). Given this, and that seabird chicks follow a pattern of growth whereby spurts in growth are related to the timing of a meal, weight gain should be of particular interest in determining the factors responsible for the observed difference between islands (Cook, 1995; Dunn, 2012). Ihumoana chicks gained weight at a much faster rate than Te Hāwere-a-maki chicks. Peak weight was attained significantly earlier for Ihumoana chicks (96 DSH on average compared to 120

DSH) and was greater (approximately 138% the weight of an average adult compared to 110%). A larger percentage of chicks on Ihumoana attained weights equal to or greater than the average adult weight of 550 g (100% compared to 60%) and weights considerably greater than the average adult weight (> 750 g; 65% compared to 0%). This lead to Ihumoana chicks displaying the pattern typically observed in Procellariiform chicks, of weight recession prior to fledging (Booth et al., 2000; Cuthbert, 2005; Mauck and Ricklefs, 2005; Teixeira et al., 2014). No such pattern was observed in Te Hāwere-a-maki chicks, many of which continued to gain weight up until fledging.

Also of interest, is that a greater proportion of chicks from Ihumoana regurgitated initially when handled. They also continued to do so further into the breeding season than chicks from Te Hāwere-a-maki, despite appearing to be at a similar level of distress when handled. Regurgitate from Ihumoana chicks was of a greater quantity on average and primarily consisted of largely undigested prey items including whole fish and squid eyes, squid beaks, fish and crustacean flesh. When chicks on Te Hāwere-a-maki did regurgitate it resulted in proventricular oil 64% of the time. Proventricular oil is a known by-product of digestion in Procellariiformes (Imber, 1976b). This could indicate that chicks raised on Te Hāwere-a-maki were either fed a greater quantity of oil by parents or had last been fed longer ago, but either way that food had been digesting (whether in the adults or chicks stomach) for a longer period of time. Regurgitation is used as a defence mechanism in Procellariiform adults and chicks (Imber, 1976b; Warham, 1977). If food was in abundance, it would be in the interest of chicks to regurgitate when they felt threatened as the act should not negatively impact growth while having the potential to influence their immediate survival (Mangel and Stamps, 2001). It would be in the interest of Te Hāwere-a-maki chicks, to become habituated to handling faster, as every time they regurgitated when handled they would have wasted a, comparatively, more valuable food resource, potentially risking their long-term survival.

Taken together, these results suggest that adults raising chicks on Ihumoana experienced better foraging conditions than those raising chicks on Te Hāwere-a-maki. The slow growth characteristic of Procellariiformes has been suggested as an adaptation to reduce the food requirements of the chick to a level that their parents can adequately provide for them, regardless of the distance parents are required to travel to obtain food (Dobson and Jouventin, 2007). Therefore, if food was in limited supply for Te Hāwere-a-maki chicks, slow growth would be selected for, reducing energy requirements and enabling chicks to survive the longer periods between meals required of them.

Breeding seabirds are required to commute long distances between their colonies and foraging grounds making them extreme central-place foragers (Ballance et al., 2009; Davoren and Montevecchi, 2003). Central-place foraging theory predicts that birds will have preference for prey items nearer the colony over prey items further away. As marine top predators, seabirds are known to concentrate their foraging efforts in areas where productivity is elevated or prey concentrated, often associated with specific oceanic features (Weimerskirch et al., 2005). If Ihumoana parents had access to better foraging conditions, closer to the colony, they would be able to increase the rate of delivery and quantity of food they were able to feed to their chicks compared to Te Hāwere-a-maki parents. Therefore, differences in chick growth rates between islands likely reflect a disparity in foraging distributions. There are a number of factors that could have led to this disparity between islands, including the distance to and food availability at reliable foraging grounds and local weather patterns.

The distance required to travel to feeding grounds would be expected to affect both the time taken for each foraging trip, as well as the energy required of parents. Consequently this would affect the amount of food they would be able to afford chicks. Similar disparities in chick growth have been observed in other seabirds where closely related species or conspecifics are required to travel different distances to forage. Hulsman and Smith (1988), found that black-naped tern (*Sterna sumutrana*) chicks had faster growth rates and consequently, fledged sooner after hatching, than bridled tern (*Sterna anaethetus*) chicks raised in the same area. The primary foraging grounds of black-naped tern parents were closer to the colony than those of bridled tern parents. Consequently, black-naped tern parents were able to provide food to their chicks well in excess of their energy requirements by feeding them a larger quantity at a higher frequency. The frequency at which adult common murres (*Uria aalge*) were able to provision their chicks differed between two major colonies; one located 45 km from the nearest aggregation of their preferred prey and the other within 5 km of the nearest aggregation (Davoren and Montevecchi, 2003). Adults from the colony closer to their preferred prey were able to feed their chicks at a higher frequency, translating to faster chick growth (weight and wing) and chicks fledging in better condition.

In a study conducted by Imber (1973) investigating the food of the grey-faced petrel, 96% of identifiable prey items found in regurgitate collected from chicks close to fledging and adults returning to provision chicks, were species which are only found beyond the continental shelf. He concluded that breeding grey-faced petrels forage primarily beyond the continental shelf. These results are supported by data collected from satellite tracked failed and non-breeding grey-faced petrels which were found to forage exclusively over offshore waters exceeding 1,000 m in depth (MacLeod et al., 2008). From Ihumoana, the shortest distance parents have to travel to reach waters over 1,000 m in depth is approximately 50 km (CANZ, 1997). Comparatively, the shortest distance from Te Hāwere-a-maki to waters over 1,000 m in depth is approximately 110 km, over double that from Ihumoana. This difference between Ihumoana and Te Hāwere-a-maki grey-faced petrels, in the distance to the nearest area they can potentially forage for their preferred prey, has the potential to affect the frequency at which parents are able to provision their chicks. This could have the potential to translate to the disparity in chick growth rates observed here.

Local weather patterns at breeding grounds or en route to feeding grounds, may influence the efficiency with which parents can travel and hence, the time taken per foraging trip. Increases in wind velocities are known to improve flight efficiency and speed in the Procellariiformes (Spear and Ainley, 1997). An improvement in the breeding success of wandering albatrosses has been observed with increases in wind intensity in the southern ocean (Weimerskirch et al., 2012). Decreases in foraging trip durations during breeding have been observed as a result of increases in flight speeds, allowing birds to travel greater distances per day and translating to an elevated probability of encountering prey. Concurrently, increases in body weight and therefore wing load, allow birds to exploit windier zones. Similarly, in a study conducted by Rayner et al. (2008), prevalent and consistent south-westerly winds around the Whenua Hou Cook’s petrel colony, meant adults breeding on the island were able to travel greater distances in less time, than adults breeding on Hauturu. As a result, chicks raised on Whenua Hou had increased growth rates and fledged in better condition. Predominantly west to south-westerly winds generated by Subantarctic weather systems, make the Tasman Sea more likely to experience consistent wind velocities compared to the Hauraki Gulf (Rayner et al., 2008). Average annual wind speeds are also higher for the coastline surrounding Ihumoana than they are for Te Hāwere-a-maki (NIWA, 2012). Therefore, adults from Ihumoana may be able to travel more efficiently and at a faster speed when leaving for and returning from foraging trips than adults from Hāwere-a-maki.

Food availability at the nearest foraging grounds also has the potential to influence the amount of work required of parents to attain enough food to sustain themselves and their chicks and the time required for each foraging trip. Food availability may be influenced by competition, both intra- and inter-specific. Balance et al. (2009) found that Adélie penguin (*Pygocelis adeliae*) parents from larger colonies had increased foraging trip durations and higher energy expenditures per trip. This was due to the depletion of prey items near the colony. Forero et al. (2002) found that Magellanic penguin chicks were fed lower quality diets as the density of conspecifics within a 100 km radius increased. Consequently, chicks had slower growth rates and fledged in reduced condition. It follows that chick growth rates should also be reduced at locations with higher densities of species specialising on the same food source (G. A. Taylor pers. comm.). The growth rates, fledging weights and breeding success of five species of seabirds coexisting on two islands, were all significantly reduced at the island supporting the greater number of birds (Hunt et al., 1986). Grey-faced petrels breed at approximately 46 locations within the Greater Hauraki Gulf Region (Gaskin and Rayner, 2013). One of these colonies is likely to have between 20,000 and 50,000 breeding pairs and ten are likely to have in excess of 5,000 breeding pairs (Taylor, 2000b). In comparison, grey-faced petrels are known to breed at only seven locations along the Auckland west coast, all of which would only support small colonies consisting of tens to hundreds of breeding pairs (Gaskin and Rayner, 2013; Taylor, 2000b; K. Bourgeois pers. comm.; pers. obs.). Te Hāwere-a-maki grey-faced petrels also share the Hauraki Gulf with ten other cephalopod specialising species, while Ihumoana grey-faced petrels share the Auckland west coast with only three other species (Gaskin and Rayner, 2013). Therefore, it is expected that adults provisioning chicks on Te Hāwere-a-maki experience more intense competition for food than adults provisioning chicks on Ihumoana. Consequently, this increased competition with conspecifics and other cephalopod specialists has the potential to deplete prey availability close to the Te Hāwere-a-maki colony and subsequently, detrimentally affect chick growth.

Though competition with fisheries has shown similar decreases in chick growth rates and breeding success in other seabirds, this is unlikely directly impact the grey-faced petrel (Crawford et al., 2008; Tasker et al., 2000). Imber (1973), found that grey-faced petrel diets comprise mainly of squid; the most abundantly eaten families including Spirulidae, Histiotheuthidae and Cranchiidae. The squid fishery in New Zealand consists of two species, both in the Ommastrephidae family (Ministry for Primary Industries, 2013). One of these, *Nototodarus sloanii*, was found in regurgitate samples collected by Imber (1973), though only three of the 907 squid beaks he collected were from individuals of this species.

Variations in SST have been shown to have profound influences on the availability of oceanic species (Wolff et al., 2012). This, in turn can similarly affect the amount of work required of parents to attain sufficient food to sustain themselves and their chicks (Weimerskirch et al., 2001). When the SST at foraging grounds close to the colony is abnormally high, parents have been shown to have trouble provisioning their chicks, whose development generally suffers as a result. Such deviations from the average SST are observed regularly with the ENSO. Studies undertaken by Abraham and Sydeman (2004), Cruz and Cruz (1990a), Schreiber (1994) and Smithers et al. (2003) provide evidence of reduced frequency of meals, meal sizes and chicks growth rates associated with El Niño events across a range of seabird taxa. Consequently, prolonged chick rearing periods are observed. Annual SST can fluctuate for reasons other than the ENSO. Yellow-nosed albatross parents were in better body condition and able to make shorter trips, while bringing larger meals, when the SST around their colony was abnormally cold (Weimerskirch et al., 2001). Consequently, their chicks had increased growth rates and were in good condition at fledging. However, when the SST around the colony was abnormally warm, chick growth rates and mass at fledging were reduced as a consequence of lower provisioning rates and meal sizes. Geographical variations in SST that are relatively consistent also exist. The study conducted by Schreiber (1994), found that birds from different islands were affected differently by the 1991 El Niño event, however, no studies were found that directly investigated the effect of geographical SST anomalies on breeding seabirds. However, given our understanding of how temporal anomalies in SST affect breeding seabirds, geographical anomalies would presumably have similar consequences on breeding efforts. In the neutral ENSO years of 1989 to 1991 the SST off the Auckland east coast was on average two degrees Celsius higher than off the west coast (Chiswell, 1994). Regions characterised by steep gradients in SST, known as oceanic fronts, are associated with high levels of productivity. The Tasman front, one of New Zealand’s major fronts, is located well within the foraging range of adults from Ihumoana, while there are no major fronts located close to Te Hāwere-a-maki. Therefore, in comparison to Te Hāwere-a-maki, adults from Ihumoana could be expected to be able to provision their chicks at an increased frequency as well as provide larger meals, resulting in increased growth rates of their chicks.

The possibility also exists that the reduced growth rates and longer chick rearing period experienced by Te Hāwere-a-maki chicks is the result of genetic differences between populations. Larger snow petrel adults (*Pagodroma nivea*) were presumed to raise larger chicks as a result of the larger and more frequent meals they fed to their chicks (Barbraud et al., 1999). However, after experimentally swapping young chicks among breeding adults of differing body sizes, Barbraud et al. (1999) found that at fledging chicks tended to be more similar in size to their biological parents. Therefore, Ihumoana chicks' elevated growth rates and larger sizes at fledging may be genetically predetermined.

2.5.5 Annual Variation

Chicks raised on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons have had similar growth rates in all morphological measurements. With the exception of tarsus length, which was highest for chicks raised in the 2012 breeding season, and bill length, highest for chicks raised in 2011, chicks fledged at similar sizes, albeit much smaller than an average adult. No breeding season stands out as being more successful for Te Hāwere-a-maki chicks than another. Despite this, Te Hāwere-a-maki chicks appear to have had reduced growth rates and have experienced a considerably longer chick rearing period than previously recorded for this species and indeed than chicks raised on Ihumoana in the 2013 breeding season.

The patterns of growth observed on Te Hāwere-a-maki in 2011, 2012 and 2013 breeding seasons do appear consistent with the patterns of growth observed in chicks during unfavourable ENSO conditions (Dunn, 2012). Chicks raised during unfavourable years, in often cases where water temperature is increased (i.e. during an El Niño event), have lower growth rates and longer chick rearing periods than they would otherwise (Abraham and Sydeman, 2004; Cruz and Cruz, 1990a; Schreiber, 1994; Smithers et al., 2003). However, the fact that growth patterns have not significantly changed despite shifts in the ENSO cycle, from La Nina conditions in 2011 to neutral conditions in 2012-14, suggest results observed here are relatively typical for this island and that there is another reason for the reduced growth of Te Hāwere-a-maki chicks. This is likely to be related to reasons affecting the disparity in chick growth between Ihumoana and Te Hāwere-a-maki (foraging effort, food availability, genetic differences). There is evidence for discrepancies in the effects the ENSO can have different colonies of other seabirds (Schreiber, 1994). Therefore, the results of this study do not necessarily mean that the breeding success of grey-faced petrels isn't affected by the ENSO.

2.6 Conclusions and Recommendations

This chapter presents chick growth rates for grey-faced petrel chicks raised on Te Hāwere-a-maki and Ihumoana in the 2013 breeding season. Growth rates obtained from Te Hāwere-a-maki were done so as a continuation of studies carried out on the island in the 2011 and 2012 breeding seasons (Dunn, 2012; Russell, 2013). Growth rates obtained from Ihumoana were done so with the hope of quantifying differences in chick morphological development between east and west coast sites which, up until now, has been anecdotal (Dunn, 2012; G. A. Taylor pers. comm.). The growth of all morphological measurements followed that of other Procellariiform species. However, the growth rate in all measurements was significantly greater for chicks raised on Ihumoana. In comparison, chick growth on Te Hāwere-a-maki was stunted during all three breeding seasons and as a consequence, chicks fledged in reduced condition approximately a month later than Ihumoana. The reduced condition at fledging is likely to negatively impact survival in the initial post-fledging period (Asmussen, 2006). This is because chicks are required to overcome a less then optimal start to life while being faced with the challenges of learning to forage for patchy and scarce food resources.

More research is required to determine what factors contribute to the pronounced difference in chick growth between Ihumoana and Te Hāwere-a-maki. Some factors have been suggested here as having the potential to lead to this disparity. The proximity to the continental shelf, as well as weather conditions around colonies and en route to foraging grounds, have the potential to directly influence the time taken and energy requirements of adults to reach foraging grounds. Competition and oceanic conditions at foraging grounds have the potential to directly influence the quantity of food at feeding grounds. Tracking provisioning parents throughout the chick rearing period could provide valuable insight into which factors may be more influential in determining the locations of feeding grounds (K. Bourgeois unpub.). By experimentally swapping chicks between islands it could be determined if there is a genetic basis underpinning the differences in chick growth rates.

Stunted growth and delayed fledging have also been observed for chicks raised on Motuora and Tiritiri Matangi in the 2011 breeding season and at Tawharanui Regional Park in the 2013 breeding season (Dunn, 2013; M. Friesen pers. comm.). By monitoring other west and east coast colonies it would be possible to determine the extent of these developmental differences. Along with Te Hāwere-a-maki, the inshore islands, Motuora and Tiritiri Matangi, as well as the mainland “island”, Tawharanui Regional Park, are located within the Auckland region of the Hauraki Gulf. Future comparisons of chick growth rates among these locations and offshore islands located on the east coast could help determine if proximity to the continental shelf and reduced competition are factors influencing chick growth rates. Study into differences in behaviours, such as provisioning rates and meal size, is warranted to determine if other aspects of the breeding biology is similarly affected by colony location.

If developmental differences extend to other west and east coast colonies, given the popularity of grey-faced petrels for translocating, this factor may be important in the long-term success of such projects (Miskelly et al., 2009). Before the arrival of the first Polynesian settlers and introduced mammalian species, the grey-faced petrel would have had a wider mainland distribution (Rayner et al., 2009). Projects focusing on restoration of seabird colonies may need to shift focus to the west rather than the east coast if they want to be more successful in establishing sustainable colonies. However, at mainland locations increased management in the form of predator control may be required at some point in the breeding season to reduce casualties through predation (Chapter Four). Alternatively, supplementary feeding of chicks in years when productivity is predicted to be low may reduce the number of casualties as a result of under-provisioning and give fledglings a better chance of survival (Chapter Three; Chapter Four).

Chapter Three

Parental Provisioning Behaviour in the Grey-Faced Petrel *Pterodroma macroptera gouldi*

Plate 3.1 A beautiful watercolour of a grey-faced petrel adult and its chick by Emma Scheltema.

3 Parental Provisioning Behaviour in the Grey-Faced Petrel *Pterodroma macroptera gouldi*

Key words: Grey-faced petrel, *Pterodroma macroptera gouldi*, foraging strategies, provisioning behaviour, foraging decisions

3.1 Introduction

The Procellariiformes (albatrosses, petrels and shearwaters) are well known for their extended chick rearing periods; lasting up to 278 days in some species (Dobson and Jouventin, 2007). This is presumed to be a consequence of the patchy and unpredictable marine food resources on which they rely. Despite foraging in distant areas, breeding adults manage to maintain frequent visits to breeding sites to provision their chicks during this period (Baduini, 2002). Being sensitive to changes in their food supplies, the quantity of food and frequency with which breeding Procellariiformes are able to provision their chicks, can provide valuable insight into the ease at which adults can find food (Cruz and Cruz, 1990a; Waugh et al., 2000). Further, these data can be extrapolated to aid in assessing changes in local ocean productivity (Cruz and Cruz, 1990a).

Studies on a wide range of Procellariiform species have revealed that provisioning parents adopt a dual foraging strategy, whereby they alternate between foraging trips of short and long durations (Chaurand and Weimerskirch, 1994; Congdon et al., 2005; Magalhães et al., 2008; Waugh et al., 2000; Weimerskirch, 1998). The primary function of a short foraging trip, lasting between one and five days, is to provide nourishment for the chick (Baduini and Hyrenbach, 2003). This comes at the expense of the adult, whose body condition deteriorates as a consequence of not adequately self-provisioning during short-trips (Congdon et al., 2005). Comparatively, the primary function of a long foraging trip, lasting between six and 29 days, is to allow the adult to restore its body condition by replacing lost reserves (Baduini and Hyrenbach, 2003; Congdon et al., 2005). However, a long trip results in lost opportunities to provision the chick, who receives significantly less food per day on average during the prolonged absence of at least one of its parents (Chaurand and Weimerskirch, 1994).

Chaurand and Weimerskirch (1994) were the first to describe such a strategy for a Procellariiform, the blue petrel (*Halobaena caerulea*). Foraging trips were able to be attributed to one of two distinct groupings: short foraging trips, lasting one to three days and long foraging trips, lasting five to ten days. Both sexes alternated between short foraging trips over the continental self and long foraging trips over oceanic waters. Short trips resulted in parental weight losses while long trips led to weight gains (Chaurand and Weimerskirch, 1994). Waugh et al. (2000) found that breeding black-browed albatrosses (*Diomedea melanophrys*), from Campbell Island, undertook either short foraging trips, lasting up to five days, or long foraging trips, lasting greater than five days. During short trips, adults foraged exclusively over the Campbell Plateau, in waters no greater than 1,000 metres in depth. Conversely, during long trips, adults foraged exclusively over waters 2,000 to 7,000 metres deep. Breeding Cory's shearwaters (*Calonectris diomedea*), were found to alternate between short trips, averaging one day in length, and long trips, averaging ten days (Magalhães et al., 2008). The number of consecutive preceding short trips was found to have a significant positive relationship with the duration of long trips. This is presumably because birds required a longer time to restore reserves that had been repeatedly depleted by each preceding short trip.

For a number of species, foraging strategies have been shown to vary both geographically and temporally (Baduini, 2002; Congdon et al., 2005; Weimerskirch and Lys, 2000). It has been hypothesised that this flexibility in foraging strategies is a consequence of geographical or temporal variations in the distribution and abundance of prey species (Baduini and Hyrenbach, 2003). Weimerskirch and Lys (2000), found that breeding wandering albatross (*Diomedea exulans*) adults adjusted their foraging strategy throughout a single chick rearing period as the requirements of the chick and their ability to find food changed. During the brooding period, adults exclusively undertook short foraging trips close to the colony, lasting up to six days. After the brooding period, adults alternated these short trips, with longer trips over pelagic waters, lasting six to 26 days. Initially adults undertook several consecutive short trips followed by one long trip. However, as prey availability close to the colony was depleted, adults were required to undertake a greater frequency of long trips in order to sustain themselves. Over two consecutive breeding seasons, Baduini (2002) investigated the foraging behaviour of adult wedge-tailed shearwaters (*Puffinus pacificus*) breeding at Tern Island, Hawai'i. Throughout the entire chick rearing period, breeding adults generally undertook short foraging trips, averaging one to two days in length. Adults were able to maintain their body condition despite infrequently undertaking long foraging trips of up to nine days. This behaviour suggests that reliable foraging grounds, at close proximity to the colony, allowed adults to easily provide for themselves and their chicks without the need to travel great distances. However, Congdon et al. (2005) found that a dual-foraging strategy was employed for the first month of the chick-rearing period by wedge-tailed shearwaters breeding at Heron Island, Australia. Adults generally undertook a number of consecutive short-trips, lasting one to four days, followed by a single long trip, lasting six to ten days. This behaviour suggests that high-productivity areas were located at-distance from the colony, requiring adults to employ a dual foraging strategy early on in the chick rearing period to access these areas and maintain their body condition.

Evidence of dual-foraging strategies contradicts the expectation that breeding adults would only undertake trips which prove energetically profitable for themselves (Chaurand and Weimerskirch, 1994). The purpose of such a strategy has been hypothesised to allow adequate provisioning for chicks while adults also maintain their own body condition (Baduini and Hyrenbach, 2003). In their decision to undertake a short or a long foraging trip, breeding adults must consider their own energy requirements as well as that of their chick (Baduini, 2002; Baduini and Hyrenbach, 2003). This represents a key trade-off where adults must prioritise either their own health or that of their chick. There is evidence that parents take their chick's body condition into account in their decision whether to make a short or long foraging trip (Granadeiro et al., 1999; Ochi et al., 2010; Phillips and Croxall, 2003; Tveraa et al., 1998). However, a parent's ability to respond to their chick's needs is constrained by their own body condition and the need to ensure their own survival.

The grey-faced petrel (*P. macroptera gouldi*) is a medium sized Procellariiform, endemic to New Zealand (Onley and Scofield, 2007). Recognised by the IUCN as 'least concern', the grey-faced petrel persists as a large meta-population, comprising of over 100 colonies ranging in size from tens to thousands of breeding pairs (IUCN, 2013; Taylor, 2000b; Taylor, 2013). Its large meta-population makes the grey-faced petrel one of New Zealand's few remaining seabirds to assume a crucial role in the functioning and health of the terrestrial ecosystems in which breeds (Bellingham et al., 2010).

The grey-faced petrel is an austral winter breeder with chicks hatching in mid-August to early-September (Dunn, 2012; Imber, 1976a). After hatching, chicks are guarded for up to three days before being left alone while parents forage. Both parents contribute to chick provisioning for the remainder of the chick rearing period which lasts an average of 115 days (Imber, 1976a). Chicks fledge in mid-to-late December though sometimes as late as January.

Chicks raised on Ihumoana, an island located on Auckland’s West Coast, during the 2013 breeding season fledged approximately three weeks earlier than chicks raised on Te Hāwere-a-maki, an island located on Auckland’s east coast (Chapter Two). There is evidence that suggests this pattern extends to other west and east coast colonies (Dunn, 2012; M. Friesen pers. comm.; G. A. Taylor pers. comm.).

Anecdotal evidence suggests that grey-faced petrels breeding along Auckland’s west coast (Ihumoana and Kauwahaia Islands, Te Henga) adopt a dual-foraging strategy (G. A. Taylor pers. comm.). This study sought to analyse the foraging strategy and provisioning behaviour of grey-faced petrels breeding on Te Hāwere-a-maki. Pronounced differences in chick growth rates and survivorship during the 2013-14 (henceforth 2013) breeding season were observed between Ihumoana and Te Hāwere-a-maki (Chapter Two; Chapter Four). Ihumoana chicks grew significantly faster in all measurements, with a larger proportion surviving to fledge, approximately three weeks earlier than Te Hāwere-a-maki chicks. Investigations into the foraging strategies and provisioning behaviours of breeding adults from Te Hāwere-a-maki may provide insight into why this discrepancy in chick growth and survivorship between islands exists. It may also shed light on flexibility in the foraging strategies employed by provisioning grey-faced petrels, with respect to environmental variability and climate change.

3.2 Aims

There were two main aims for this study:

1. To examine the pattern of weight loss after feeding in grey-faced petrel chicks.
2. To investigate patterns in parental provisioning behaviour and the role of adult and chick condition in foraging decisions.

3.3 Methods

3.3.1 Study site

This study was carried out on Te Hāwere-a-maki (also known as Motu Hāwere or Goat Island; 36° 16’ S, 174° 47’ E) during October 2013. Te Hāwere-a-maki is a 9.3 ha island situated within the Cape Rodney to Okakari Point Scientific Marine Reserve, Leigh, which forms a part of the Hauraki Gulf Marine Park (map 2.1 top). Occurring along the coastal margins and exposed sea cliffs is a single, widespread grey-faced petrel colony that supports a breeding population of approximately 40-50 pairs (Dunn, 2012). The area of greatest burrow density can be found along the southern landward coast.

The naturally regenerating vegetation on Te Hāwere-a-maki consists of 95 species though, from a lack of active management, approximately a third of these are introduced (Gordon and Ballantine, 1976). However, the abundance of introduced species has reduced as native vegetation continues to develop. Pohutukawa (*Metrosideros excelsa*) forest is found along the coastal margins of the island with an understory of houpara (*Pseudopanax lessonii*), karo (*Pittosporum crassifolium*), tarangarara (*Gahnia lacera*) and a multitude of ferns. The coastal broadleaf forest, covering the inner island, is dominated by mapou (*Myrsine australis*) with houpara, karamu (*Coprosma robusta*), mahoe (*Melicytus ramiflorus*), kohekohe (*Dysoxylum spectabile*) and manuka (*Leptospermum scoparium*).

Reinfestation of introduced mammalian pests is common because of the island's close proximity to the mainland. Rats (*Rattus* spp) are more than capable of traversing the 50 m wide channel to reach Te Hāwere-a-maki (Russell et al., 2005). Recorded rat densities are highly stochastic, from 12-20 ha^{-1} in 1977 dropping through 3.2 ha^{-1} in 2005 to 1.3 ha^{-1} in 2011, rising again in 2012 to 4.3 ha^{-1} (Dunn, 2012; Russell et al., 2009; Russell, 2013).

3.3.2 Field Methods

During the incubation period of the 2013 breeding season (June to July), it was ensured that breeding grey-faced petrels from the Te Hāwere-a-maki study colony were banded with individually numbered metal bands, to allow their easy identification throughout this study.

The provisioning behaviour of pairs of breeding adults in 14 study burrows was monitored from the 3rd to the 22nd of October 2013, using methods similar to those detailed by Chaurand and Weimerskirch (1994) and Baduini (2002). Breeding grey-faced petrels are nocturnally active at the colony (Taylor, 2013). In preparation for each evening, stick gates were constructed in the entrance to the burrows. From dusk (approximately 20:00 hours) to sunrise (approximately 06:00 hours) sequential rounds of the burrows were made every 30 minutes, the minimum length of time adults remain in burrows (G. A. Taylor pers. comm.). The presence of an adult was determined by disturbance of the stick gate accompanied by the begging call of the chick and in some cases, visual observation. Once the presence of an adult was confirmed, the time was recorded and a rock placed in the burrow entrance to keep the adult inside. Burrows containing an adult were checked along with the remaining burrows during subsequent 30 minute rounds. If the adult was found at or near the burrow entrance, it was assumed that it had ceased feeding its chick. This was recorded as the time of intended departure, the rock was removed and the adult caught, identified, weighed and released back into the burrow. Stick gates were again placed in the entrance to determine the approximate time of actual departure. During this period, the second parent was never observed to return while the other parent was with the chick.

To ensure no feedings were missed, as well as allow for calculation of daily chick weight loss and meal size, chicks were weighed every 12 hours (at approximately 0600 hours and 1800 hours). This was done in a dark cotton breathable bag, using either a 600 g or 1,000 g Pesola spring scale (as appropriate), to the nearest 5 g. The weight of the bag was subtracted from this measurement to give the weight of the chick. Chicks were visited in the same sequence each morning and evening, with the exact time the weighing of each chick took place, recorded. No chicks regurgitated any food while being handled during this study. In addition to this, chicks were measured weekly from hatching (August 2013) to fledging (January 2014) to investigate their development throughout the chick rearing period (Chapter Two).

3.3.3 Control Group

To assess the effects of repeated handling of the chick on the provisioning behaviour of adults, pairs of breeding adults from 11 other burrows were also monitored. This involved placing stick gates outside burrows and recording times of parental arrival and departure.

3.3.4 Statistical Analysis

To calculate the hourly weight loss for a chick, the difference between a chick’s successive weights was divided by the time elapsed between measurements. The rate of weight loss was averaged across all chicks for the first, second, third and fourth day after a feeding event as well as greater than four days. Using a linear mixed model, a model building process was carried out to determine if the rate of weight loss was influenced by the fixed effects of: chick age (expressed as days since hatching; DSH), survivorship (fledged, died), time of day the weight loss corresponded to (night, day), days since last meal, chick’s pre-feed weight prior to last meal, size of the last meal and minimum duration of the last fast. Chick identity was included as a random factor to control for repeated observations of the same individual. The rate of weight loss was square root transformed to satisfy the assumption of linearity. A backwards elimination approach was used to determine which subset of variables was the best to use for the final model. Variables that were significant at the 10% level (the cut-off for weak evidence against the null hypothesis that the fixed effect has no influence on the hourly weight loss) were retained in the model.

The duration of a foraging trip was calculated as the time elapsed between successive recoveries of the same bird. Estimates for trips that started before the study commenced or ended after the study ceased, were calculated as the average length of known trips with a length greater than the unknown's minimum possible duration. Using a linear mixed model, a model building process was carried out to determine if trip length was influenced by the fixed effects of: chick age (DSH), last foraging trip duration, chick's pre-feed weight and adult's post-feed weight. The parent identity nested inside the chick identity was included in the model as a random effect to control for repeated observations of the same individuals. A backwards elimination approach was used to determine which subset of variables was the best to use for the final model with the same steps as for hourly chick weight loss.

The weight of a meal was calculated by subtracting the chick's estimated weight immediately after receiving a meal from its estimated weight immediately prior to receiving the meal. To estimate weight loss since last weighing, the hours elapsed were multiplied by the average hourly weight loss for the corresponding days since last feed (1, 2, 3, 4 or >4). To calculate immediate pre-feed weight this value was then subtracted from the previous weight. To estimate weight loss between the feed and subsequent weighing, the time elapsed was multiplied by the average hourly weight loss for the first day. This value was added to the subsequent weighing to calculate the immediate post-feed weight. Using a linear mixed model, a model building process was carried out to determine if meal size was influenced by the fixed effects of: chick age (DSH), chick's pre-feed weight, foraging trip duration and the adult's pre-feed weight. The parent identity nested inside the chick identity was included in the model as a random effect to control for repeated observations of the same individuals. A backwards elimination approach was used to determine which subset of variables was the best to use for the final model with the same steps as for hourly chick weight loss.

Linear mixed models were chosen as opposed to non-linear models due to difficulties that can arise in testing differences in fixed effects within non-linear growth curves (Hart and Chute, 2009). These analyses were carried out using the nlme package in R version 3.0.2 (Pinheiro et al., 2014; R Core Team, 2013). Unless otherwise stated mean values are quoted with ± standard deviation.

The number of adults returning on any given night was divided by the total number of adults from study burrows ($n_{adults} = 28$) to give the proportion of returned adults for the corresponding night. Using a linear model, a model building process was carried out to determine if the proportion of adults returning was influenced by: average and maximum wind velocities or minimum and maximum barometric pressures obtained for each day of the study and the moon illumination for the corresponding night. A backwards elimination approach was used to determine which subset of variables was the best to use for the final model with the same steps as for hourly chick weight loss. This was also carried out in R version 3.0.2 (R Core Team, 2013).

A t-test for independent samples was performed to compare the average duration of short and long foraging trips (days). To compare the adult weight (g) preceding, meal size (g) following and change in adult weight (g) following trips of short and long duration, t-tests for independent samples were also performed.

To compare the durations of complete forging trips between pairs of breeding adults from control and study burrows, t-tests for independent samples were performed. The number of times a chick received a meal over the course of this study was divided by the duration of the study (19 nights) to give the average time elapsed between meals. This was compared between chicks from control and study burrows using t-tests for independent samples.

3.4 Results

3.4.1 Overview

The foraging behaviour of provisioning grey-faced petrel pairs from 14 burrows (28 adults) was monitored over 19 nights from the 3rd to the 22nd of October 2013. During the course of this study adults returned to provision chicks on 40 occasions. However, on five of these occasions the returning adult was unable to be captured and identified due to severe weather preventing access to the colony on the nights of the 8th and 16th of October. Ten complete foraging trips were observed during the course of this study. Forty-seven partial foraging trips, beginning before this study commenced or ending after this study ceased, were observed. Apart from one, who returned after the studies completion, all parents returned at least once to provision their chicks during this study.

The average age of chicks at the start of this study was 35 days ± 7 days (range: 26 to 48 days) and at the end of this study was 54 days ± 7 days (range: 45 to 67 days). No chicks died during the course of this study. However, five chicks died subsequently, most likely as a result of starvation (Chapter Four).

3.4.2 Chick Weight Loss

The pattern of hourly weight loss with respect to the days since last meal for 26-67 day old grey-faced petrel chicks raised on Te Hāwere-a-maki in the 2013 breeding season is displayed in figure 3.1. Chicks lost, on average, 1.68 $g{\cdot}hr^{-1}$ ± 0.76 $g{\cdot}hr^{-1}$ (range: 0.67 to 3.58 $g{\cdot}hr^{-1}$) in the day following a feeding event. The average weight loss per hour declined thereafter to 1.03 $g{\cdot}hr^{-1}$ ± 0.44 $g{\cdot}hr^{-1}$ (range: 0.29 to 2.29 $g{\cdot}hr^{-1}$) in the second day, 0.85 $g{\cdot}hr^{-1}$ ± 0.40 $g{\cdot}hr^{-1}$ (range: 0.19 to 1.83 $g{\cdot}hr^{-1}$) in the third day and 0.82 $g{\cdot}hr^{-1}$ ± 0.41 $g{\cdot}hr^{-1}$ (range: 0.00 to 1.77 $g{\cdot}hr^{-1}$) in the fourth day following a feeding event. Greater than four days since a feeding event, chicks lost on average 0.42 $g{\cdot}hr^{-1}$ ± 0.42 $g{\cdot}hr^{-1}$ (range: 0.00 to 2.85 $g{\cdot}hr^{-1}$).

The most important predictors of hourly weight loss in grey-faced petrel chicks were: chick age (DSH), survivorship (fledged, died), days since last meal (DSLM), chick's pre-feed weight prior to last meal (WEIGHT.BLM) and size of the last meal (WEIGHT.LM; table 3.1). The time of the day the weight loss corresponded to (day or night) and the minimum duration of the last fast were not found to be important predictors of hourly weight loss and so were removed from the model. Hourly weight loss was found to decrease with both chick age and the time elapsed since the chick's last meal (DSH: value = -6.496e-03; DSLM: value = -5.815e-02; table 3.1). Conversely, hourly weight loss increased with both the size of the chick's last meal and with the chick's pre-feed weight prior to last meal (WEIGHT.LM: value = 3.003e-03; WEIGHT.BLM: value = 1.791e-03; table 3.1). Chicks surviving to fledge lost weight at a reduced rate compared to chicks that died (FLEDGEDYES: value = -1.258e-01; table 3.1). Chick identity was found to account for 0% of the total variance (table 3.1). This implies that the variance in hourly weight loss is almost non-existent among measurements taken from the same chick.

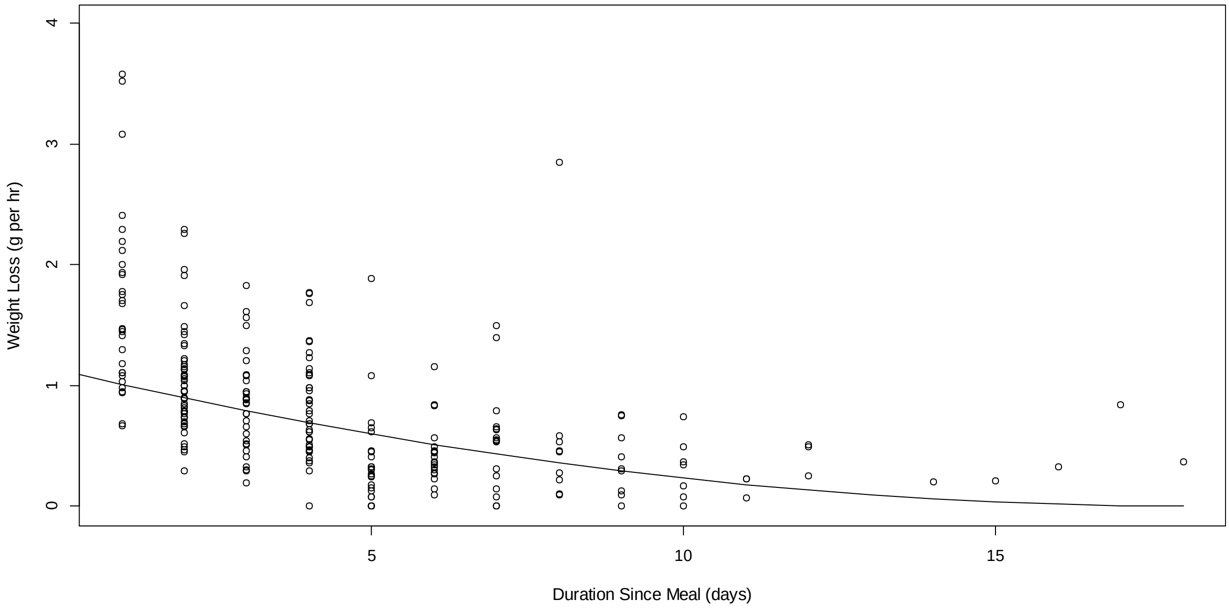


Figure 3.1 Weight loss (g·hr^{-1}) of 26-67 day old grey-faced petrel chicks raised on Te Hāwere-a-maki in the 2013 breeding season (n = 14) as a function of the time elapsed since LM (days). The slope and intercept of the line of best fit was calculated for chicks that survived to fledge (n = 10) using the parameter estimates obtained from the linear mixed effects model for chick weight loss (displayed in table 3.1), with the chick age (DSH), weight before least meal (g) and weight of last meal (g) held constant at their respective means for this data set (44 DSH, 307 g, 106 g).

Table 3.1 Parameter estimates and variance components (rounded to 3 d.p.) of the linear mixed effects models for sqrt(weight loss) (g·hr^{-1}) of 26-67 day old grey-faced petrel chicks raised on Te Hāwere-a-maki during the 2013 breeding season (n = 14) investigating the terms: days since hatching (DSH), survivorship class (FLEDGEDYES), days since last meal (DSLM), chick pre-feed weight (WEIGHT.BLM; g) and weight of last meal (WEIGHT.LM; g).

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	6.049e-01	1.826e-01	183	3.313	0.001**
DSH	-6.496e-03	3.200e-03	183	-2.030	0.044*
FLEDGEDYES	-1.258e-01	4.410e-02	11	-2.853	0.016*
DSLM	-5.815e-02	7.039-03	183	-8.262	<0.001***
WEIGHT.BLM	1.791e-03	3.474e-04	183	5.155	<0.001***
WEIGHT.LM	3.003e-03	9.610e-04	183	3.125	0.002**

Variance component estimates

Source	Variance	Std.Dev	Percentage
CHICK.ID	2.281e-10	1.510e-05	0.0
Residual	7.624e-02	2.761e-01	100.0
Total	7.624e-2		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

3.4.3 Colony Attendance

The 28 breeding adults from study burrows returned to provision chicks on 40 occasions throughout the course of this study. The number of adults visiting the colony each night varied from zero to five (figure 3.2). This represents, on average, 7.3% ± 4.8% (range: 0.0 to 17.9%) of adults returning each night to provision chicks. The proportion of adults returning to provision a chick on any particular night was not found to be related to measurements of the average wind speed (p-value = 0.736), maximum wind speed (p-value = 0.850), minimum barometric pressure (p-value = 0.465) or maximum barometric pressure (p-value = 0.415) relating to that day or the moon illumination (p-value = 0.202) for that night. Despite this, for the two cases in which no adults returned to the colony, the nights immediately following had the greatest (17.9%) and second greatest (14.3%) percentages of adults returning.

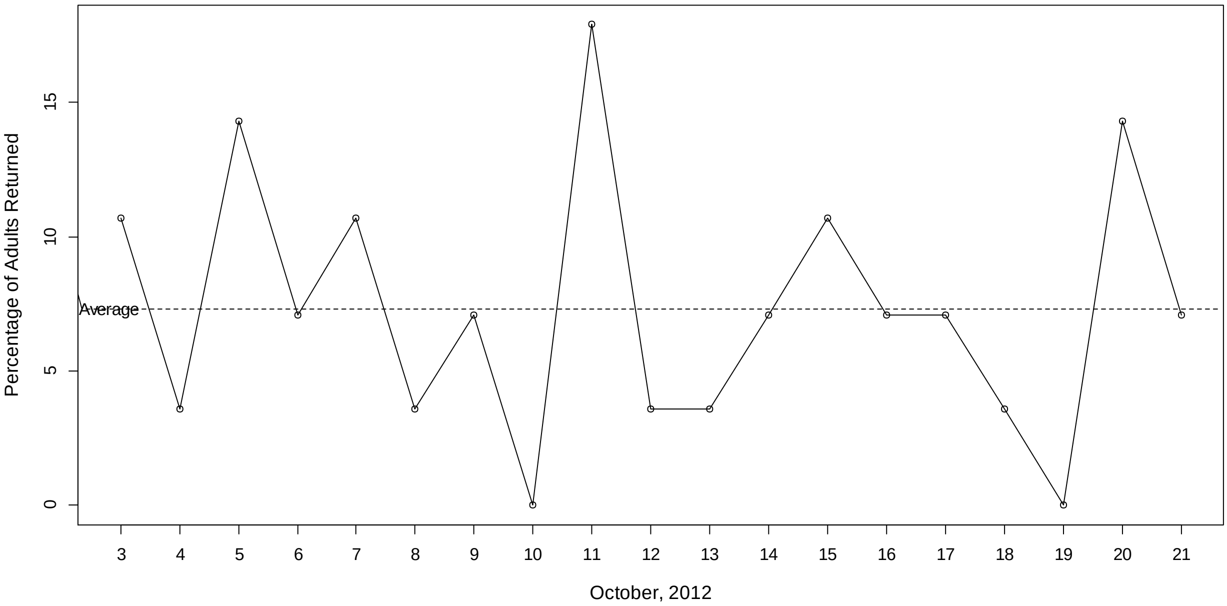


Figure 3.2 The percentage of the 28 breeding adults from 14 Te Hāwere-a-maki study burrows returning nightly from the 3rd to the 21st of October, 2013 to provision their chicks. The dotted line represents the average percentage of adults returning to provision chicks (7.3%).

The interval chicks were required to wait between successive meals ranged from two to greater than 16 days. Averaged across the study duration, chicks were fed at mean intervals of 7.7 days ± 2.2 days (range: 4.8 to 9.5 days). This suggests that each parent's average foraging trip length was approximately 15.4 days.

Breeding adults returned to the colony to provision their chicks in the hours between dusk (approximately 20:00 hours) and sunrise (approximately 06:00 hours). Returning adults arrived at the colony as early as 20:26 hours, with 65% of arrivals occurring between 22:00 hours and 01:00 hours. Adults arrived after 01:00 hours on only 12% of occasions. On two of these occasions (arrival times: 03:18 and 05:50 hours), the adults remained in the burrow with their chick for the day, leaving just after dusk that evening. Adults that left during the night in which they arrived, stayed with their chick an average of 104 minutes ± 68 minutes (range: 26 to 333 minutes) based on intended departure times (i.e. excluding additional handling time).

3.4.3 Foraging Trip Durations

Ten complete foraging trips were observed over the course of this study. The average trip duration for these complete foraging trips was 7.6 days ± 5.4 days (range: 2 to 16 days). This value is likely to be underestimated, as it is only half the predicted average foraging trip length of 15.4 days, calculated from the time elapsed between successive meals for each chick. Forty-seven incomplete foraging trips were observed for which the minimum possible duration was known. These trip durations were estimated using the average length of known trips with a length greater than the incomplete's minimum possible duration. Taken together this gave an average trip length of 11.4 days ± 3.9 days (range: 2 to 20 days). While this value is still likely to be underestimated, it is much closer to the predicted average foraging trip length above. This is probably due to the maximum duration of foraging trips being underestimated because of the comparatively short study period. One parent was not observed at the colony for the duration of this study (19 nights). Another parent was not observed at the colony for 18 nights and four others were not observed for 17 nights.

The frequency distribution of all foraging trips made by Te Hāwere-a-maki parents over the course of this study (n = 57) suggests trips can be divided into two categories: those of short duration and those of long duration (figure 3.2). Trips of short duration, lasted on average 3 days ± 1.4 days (range: 2 to 5 days) and accounted for 8.8% to 50% of foraging trips (n = 57 for all trips and 10 for complete trips). Trips of long duration, lasted on average 12.2 days ± 3.0 days (range: 8 to 20 days) and accounted for 50% to 91.2% of foraging trips. No foraging trips of six to seven days were observed during this study. There is very strong evidence that trips categorised as long foraging trips were of greater duration than trips categorised as short foraging trips, suggesting the two categories are distinct (p-value < 0.001; table 3.2).

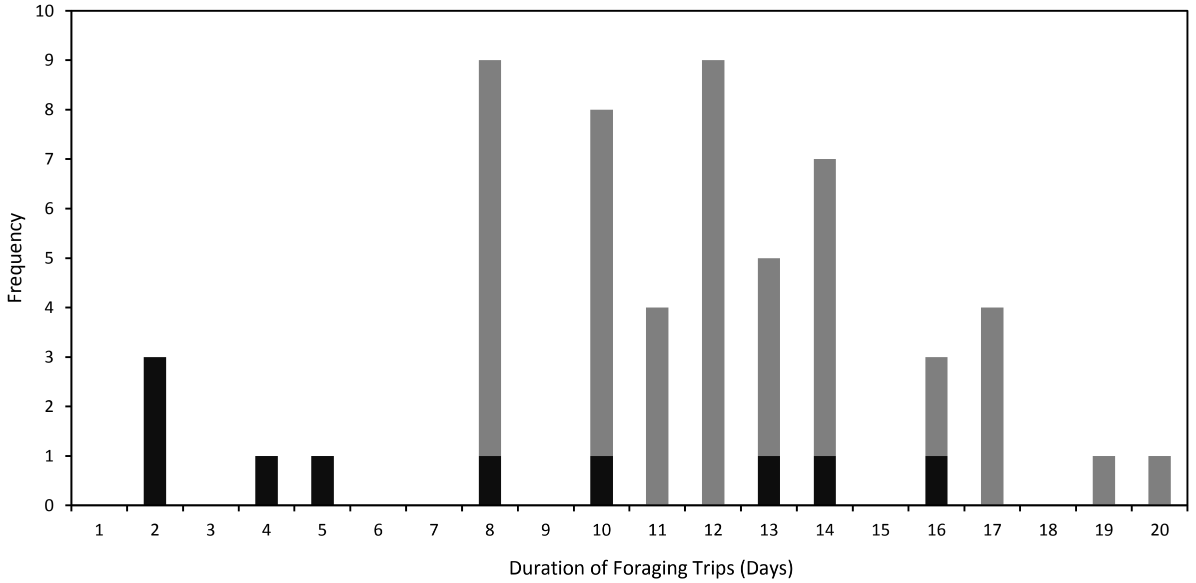


Figure 3.3 Distribution of complete (■ ; n = 10) and estimated incomplete (▨ ; n = 47) foraging trips undertaken from the 3rd to the 21st of October 2013, by the 14 pairs of adults from Te Hāwere-a-maki study burrows.

3.4.5 Provisioning Parameters

The average meal size delivered to chicks throughout this study was 108 g ± 29 g (range: 47 to 181 g). There is no evidence that meals delivered to chicks after parents returned from a long trip were heavier than meals delivered to chicks after returning from a short trip (p-value = 0.384; table 3.2).

The average weight of adults after provisioning their chicks was 473 g ± 27 g (range: 425 to 526 g). Though not statistically significant there was a trend towards adults starting a short trip being heavier than those starting a long trip (p-value = 0.137; table 3.2). All completed short trips resulted in parental weight loss, while in 50% of completed long trips, a parental weight gain was observed. Interestingly, the 50% of completed long trips that resulted in parental weight loss were the longest recorded. Though not statistically significant this suggests a trend towards adults returning from short trips being more likely to have lost weight than those returning from a long trip (p-value = 0.121; table 3.2).

Table 3.2 The average duration of (days), meal size following (g), adult weight preceding (g) and change in adult weight following (g) trips of short and long duration undertaken by Te Hāwere-a-maki parents (n = 28) from the 3rd to the 21st of October 2013 (± standard deviation).

Parameter		Short Trip	Long Trip	t-test p-value
Duration of Trip (days)	Average	3 ± 1.4 (n = 5)	12.2 ± 3.0 (n = 52)	<0.001***
	Range	2 to 5	8 to 10	
Meal Size (g)	Average	115 ± 29 (n = 5)	114 ± 34 (n = 16)	0.384
	Range	81 to 141	64 to 181	
Adult Weight Before Trip (g)	Average	488 ± 32 (n = 5)	470 ± 23 (n = 12)	0.137
	Range	445 to 519	435 to 515	
Change in Adult Weight (g)	Average	-17 ± 9 (n = 5)	6 ± 31 (n = 4)	0.121
	Range	-29 to -5	-26 to 36	

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

3.4.6 Influence of Chick and Adult Weight on Provisioning Behaviour

The most influential predictor of the duration of a Te Hāwere-a-maki adult's next trip between the 3rd and 21st of October 2013, was the time elapsed since its last visit. The duration of a foraging trip was found to decrease with the duration of the last foraging trip (DSLV: value = -0.499; table 3.3; figure 3.3). Chick age (p-value = 0.610), chick weight immediately after feeding (p-value = 0.542) and adult weight immediately after feeding (p-value = 0.302) were not found to be important predictors of the next trip's duration and so were excluded from the model.

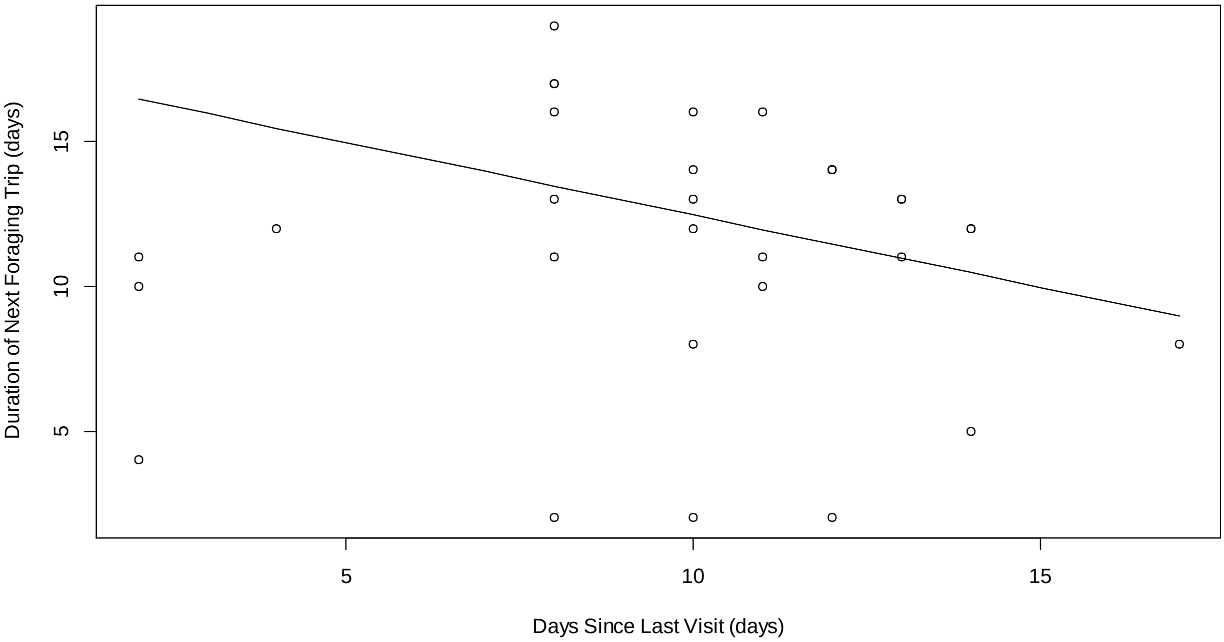


Figure 3.4 The duration of next foraging trip (days) made by 14 pairs of Te Hāwere-a-maki parents from the 3rd to the 21st of October, 2013, as a function of the days since last visit (days). The slope and intercept of the line of best fit was calculated using the parameter estimates obtained from the linear mixed effects model for the duration of next foraging trips, displayed in Table 3.3.

Chick identity and parent identity were found to account for similar percentages of the total random variance, suggesting that the duration of the next trip is relatively equally influenced by both the parent and the chick (39.2% and 49.4%, respectively; table 3.3). This implies that parents are in some way taking their particular chick into account when making decisions as to the duration of their next foraging trips. Chick age and chick weight immediately after feeding were not found to be important predictors of the duration of the next trip. However, chicks may be conveying some other signal to parents that is influencing the duration of the next trip that was not measured in this study.

Table 3.3 Parameter estimates and variance components (rounded 3 d.p.) of the linear mixed effects model for duration of the next foraging trips (days) made by 14 pairs of Te Hāwere-a-maki parents from the 3rd to the 21st of October 2013, investigating the term days since last visit.

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	17.448	2.370	12	7.363	<0.001**
DSLV	-0.499	0.209	5	-2.395	0.062

Variance component estimates

Source	Variance	Std.Dev	Percentage
CHICK.ID	2.378	1.542	39.2
PARENT.ID	10.223	3.197	49.4
Residual	8.108	2.847	39.1
Total	20.709		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

The most influential predictors of the size of a meal delivered to 26-67 day old grey-faced chicks raised on Te Hāwere-a-maki during the 2013 breeding season, were the time elapsed since the adult's last visit and the adult's pre-provisioning weight. The weight of a meal was found to increase with the adult's pre-provisioning weight (ADULT.WEIGHT.BEFORE: value = 0.545; table 3.4; figure 3.4). Conversely, the weight of a meal was found to decrease as the time elapsed since the adult's last visit increased (DSLV: value = -1.164; figure 3.4). Chick age (p-value = 0.942) and chick weight immediately prior to feeding (p-value = 0.901) were not found to be important predictors of meal size and so were excluded from the model.

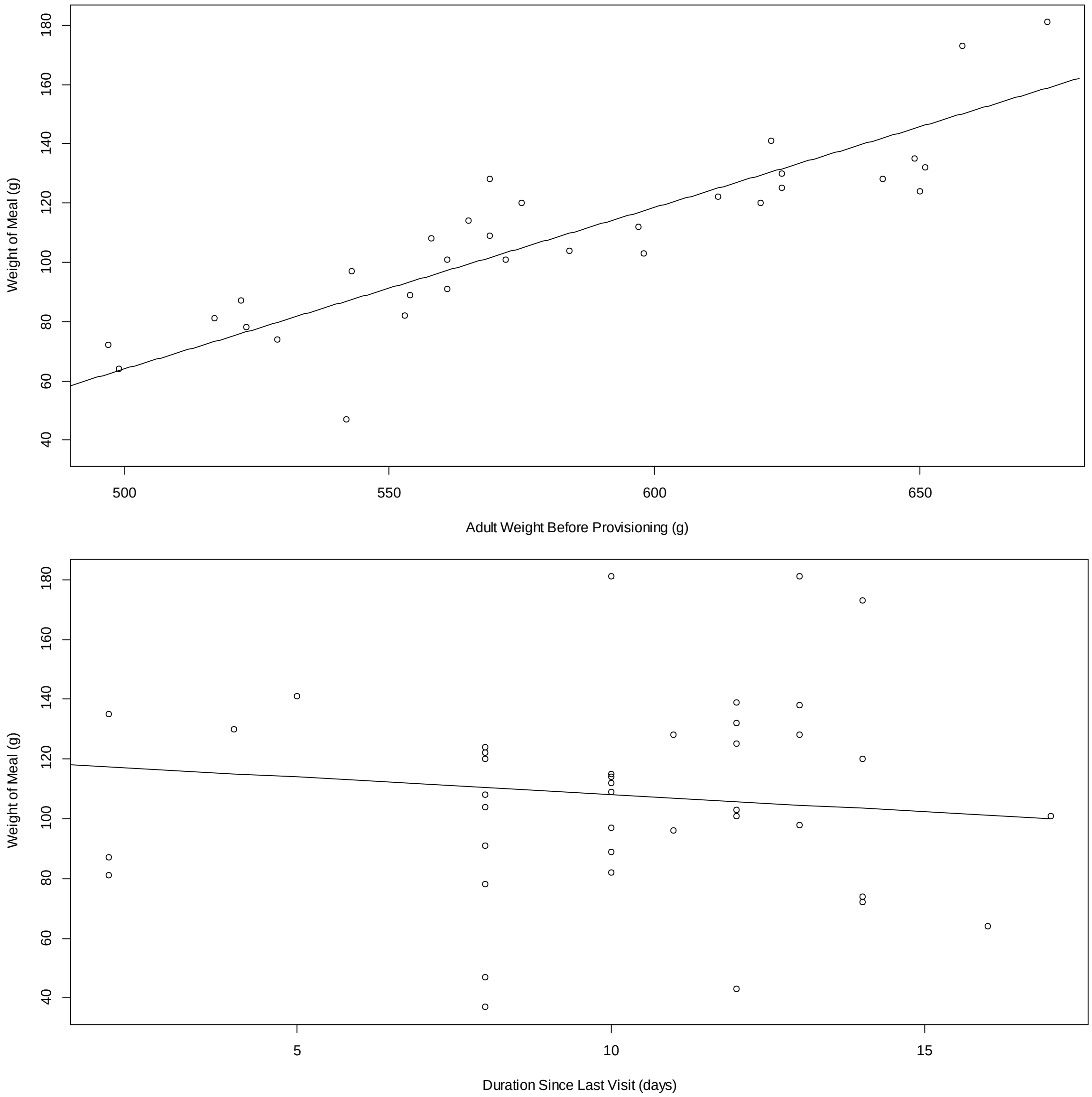


Figure 3.5 The weight of meals (g) delivered to 26-67 day old grey-faced chicks raised on Te Hāwere-a-maki during the 2013 breeding season (n = 14) as a function of the adult weight before provisioning (g; top) and the days since last visit (bottom). The slope and intercept of the line of best fits were calculated using the parameter estimates obtained from the linear mixed effects model for the weight of meals (displayed in table 3.4), with the time elapsed since last visit held constant at the mean for this data set of 10 days (top) and the weight of the adult pre-provisioning held constant at the mean for this data set of 482 g (bottom).

Parent identity was found to account for a much larger percentage of the total random variance than chick identity (74.2% and 12.3%, respectively; table 3.4). This implies that the size of a meal is almost entirely dependent on the parents and very little on the chick. This is suggested by the final model in which the most influential predictors of the size of a meal are the parent's pre-provisioning weight and the time elapsed since its last visit.

Table 3.4 Parameter estimates and variance components (rounded 3 d.p.) of the linear mixed effects model for the weight of meals delivered to 26-67 day old grey-faced chicks raised on Te Hāwere-a-maki during the 2013 breeding season investigating the term adult weight before feeding (g).

Parameter estimates

Source	Value	Std.Error	DF	t-value	p-value
(Intercept)	-196.978	33.805	12	-5.827	<0.001***
DSLV	-1.164	0.437	7	-2.664	0.032*
ADULT.WEIGHT.BEFORE	0.545	0.056	7	9.718	<0.001***

Variance component estimates

Source	Variance	Std.Dev	Percentage
CHICK.ID	32.338	5.687	12.3
PARENT.ID	190.573	13.805	72.4
Residual	40.301	6.348	15.3
Total	263.212		100

Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

3.4.7 Control Group

Data on the time elapsed between successive meals for chicks raised on Te Hāwere-a-maki during the 2013 breeding season from the 11 control and 14 study burrows are presented in table 3.5. There is no difference between chicks from control and study burrows in the time elapsed between successive meals (p-value = 0.523). Data on the duration of complete foraging trips undertaken by parents from the 11 control and 14 study burrows are also presented in table 3.5. There is no difference between parents from control and study burrows in the duration of individual foraging trips (p-value = 0.889).

Table 3.5 The average time between meals and duration of foraging trips ± standard deviations for chicks and adults, respectively, from Te Hāwere-a-maki 2013 control (n = 11) and study (n = 14) burrows

Treatment		Time Between Meals (Days)	Duration of Foraging Trips (Days)
Control	Average	8.7 ± 5.4	7.9 ± 5.1
	Range	3.8 to 19.0	2 to 15
Study	Average	7.7 ± 2.2	7.6 ± 5.4
	Range	4.8 to 9.5	2 to 16

3.5 Discussion

3.5.1 Summary

During October of the 2013 breeding season patterns in hourly weight loss following meals for 14 grey-faced petrel chicks aged 26 to 48 days raised on Te Hāwere-a-maki were obtained. Patterns in their parent’s provisioning behaviours were also obtained. These data are expected to allow a better understanding of the foraging strategies employed by grey-faced petrels. The chick rearing period on Te Hāwere-a-maki in the 2013 breeding season was unexpectedly long compared to other records for this species and to the chick rearing period on Ihumoana during the same breeding season (Chapter Two). These data are also expected to provide some insight into reasons for the unexpectedly long chick rearing period observed on Te Hāwere-a-maki and why this discrepancy in chick growth between Ihumoana and Te Hāwere-a-maki may have existed throughout the 2013 breeding season (Chapter Two).

3.5.2 Control

There were no differences in the time chicks were required to wait between successive meals or the duration of parent’s individual foraging trips between control and study groups on Te Hāwere-a-maki during October 2013. Hence, there is no evidence to suggest than frequent handling of chicks and parents from study burrows throughout the course of this study affected parental provisioning behaviour. Chick growth in the grey-faced petrel has also been found to be unaffected by frequent handling of chicks and so is unlikely to have been affected during this study (Chapter Two).

Other studies have similarly reported that frequent handling of chicks and parents had no effect on the duration of the parent’s foraging trips (Granadeiro et al., 1999; Phillips et al., 2003; Quillfeldt and Masello, 2004; Rayner et al., 2008). However, too few studies have reported on the effects of frequent handling of chicks and adults on parental provisioning behaviour, which are unlikely to be uniform among Procellariiformes (Carey, 2009). Despite this, because no detectable differences in the time chicks were required to wait between successive meals or the duration of parent’s individual foraging trips were observed between control and study burrows, the results presented here are considered representative of this species. Therefore, reasons other than frequent handling are thought to have contributed to the patterns in chick weight loss and parental provisioning behaviour, presented here.

3.5.3 Chick Weight Loss

Patterns of weight loss through respiration and excretion, observed for 26 to 48 day old grey-faced petrel chicks raised on Te Hāwere-a-maki followed similar patterns to those previously recorded for grey-faced petrel chicks and for chicks of other *Pterodroma* species (Bester et al., 2002; Chaurand and Weimerskirch, 1994; Dunn, 2012; Imber, 1976a). Hourly chick weight loss was greatest in the first day following a meal. Thereafter, hourly weight loss declined with the days elapsed since the chick's last meal, until reaching an asymptote at greater than four days. As found by Imber (1976a) in his study on grey-faced petrel chicks raised on Motuhora Island during the 1969 breeding season, hourly chick weight loss was also dependent on the weight of the chick immediately preceding its last meal. However, unlike Imber's study, the weight of the chick's last meal and whether the chick ultimately survived to fledge or died, also proved important variables in determining the hourly chick weight loss.

It would appear that chicks are in some way able to adjust their metabolic rate: lowering it as the reserves gained from their last meal were depleted, their body condition deteriorated or the size of received meals decreased. The ability of chicks' to adjust their metabolic rate, as a consequence of variable provisioning and meal sizes, has been observed in other Procellariiform species (Boersma et al., 1980; Schultz and Klomp, 2000; Teixeira et al., 2014). For grey-faced petrel chicks in this study, it appears that when food became more limited, as adults struggled to keep up with the increasing demands of their chick, chicks unable to quickly adjust their metabolic rate in response, were at greater risk of not surviving to receive their next meal. The ability of chicks' to adjust their metabolic rate is likely an adaptation allowing for variable provisioning and it has been suggested that this ability is in some way related to a chick's prior experience (Boersma et al., 1980; Teixeira et al., 2014; Warham, 1990). Of the five chicks that died after the completion of this study, three were consistently among the heaviest and fastest growing of the 15 chicks regularly measured on Te Hāwere-a-maki (Chapter Two). This is presumably a consequence of receiving relatively more frequent visits from their parents. For these chicks, from hatching, food was in apparent abundance and their metabolism appeared to reflect this in their relatively high growth rates. As soon as these chicks faced periods of food limitation, they did not have the capabilities to respond by lowering their metabolic rates fast enough. Their body conditions therefore deteriorated faster following a meal and they were unable to survive for as long between successive meals. This is in comparison to chicks for whom food was less abundant and whose hourly weight loss was lower, making them more likely to survive to receive their next meal.

Conversely, the ability of chicks' to adjust their metabolic rates may be a consequence of genetics, assuming their parents were raised in better conditions and were not required to be able to quickly adjust their metabolic rates in order to survive. However, for two of these chicks their parents have successfully raised a chick in the 2011 breeding season. Chicks raised in the 2011 and 2013 breeding seasons had similarly reduced growth rates so conditions are likely to have been similar between seasons (Chapter Two). However, there is evidence that the feeding frequency may have been slightly higher for chicks raised in the 2011 breeding season (Dunn, 2012).

3.5.4 Feeding Frequency

Over the 19 night period that parental provisioning behaviour on Te Hāwere-a-maki was monitored, parents from the 14 study burrows visited the colony to provision chicks infrequently. The average duration chicks were required to wait between successive meals, of 7.7 days, was higher than reported elsewhere for grey-faced petrel chicks (Dunn, 2012; Imber, 1976a). Both Dunn (2012) and Imber (1976a) estimated an average duration between successive meals of close to 4 days. From this value both authors estimated an average trip length of between 7 and 8 days, compared to the average trip length estimated here of 15.4 days. However, chicks raised on Te Hāwere-a-maki in the 2011 breeding season (Dunn, 2012) had similar growth rates to chicks raised in the 2013 breeding season (Chapter Two). The times of fledging were indistinguishable between years as were the measurements at fledging. This suggests that the feeding frequencies experienced by chicks raised during these two breeding seasons should be more similar.

A number of factors could be responsible for this difference. Dunn's study spanned 49 nights, over double the length of this study, while Imber's spanned 13 nights. Short studies of foraging behaviour, such as this one or Imber's, could coincide with the large majority of parents undertaking only one type of trip: trips of either long or short duration (Schultz and Klomp, 2000). This may explain the low feeding frequency recorded here or, conversely, the high feeding frequency recorded by Imber. Though shorter, Imber's study was carried out slightly earlier in the chick rearing period, taking place at the end of September. A wide range of Procellariiform parents begin the chick rearing period undertaking short foraging trips, which generally increase in duration as chicks age (Boersma et al., 1980; Weimerskirch and

Lys, 2000). This could also explain the higher feeding frequency recorded by Imber. Better foraging conditions are also likely to have been experienced by adults in Imber's study which theoretically, could result in adults undertaking shorter trips. This is reflected in the reduced chick rearing period (120 days compared to 139 days).

However, the maximum duration chicks were required to wait between successive meals was found to be much greater in this study (> 16 days), than observed by Dunn (13 days) or Imber (ten days). Additionally, a number of observed foraging trips lasted longer than the 15 day maximum previously observed for grey-faced petrel adults raising chicks on Ihumoana and Kauwahaia (G. A. Taylor pers. comm.). One parent did not return to the colony for the duration of this study (19 nights), though was observed returning later in the chick rearing period. Another parent was not observed for 18 nights, four others were not observed for 17 and three others were not observed for 16. This suggests that the greater duration chicks were required to wait between meals and the estimated average foraging trip lengths observed in this study, are the result of factors additional to differences in study duration or time of year. For instance, geographical and/or annual variability in foraging conditions could have negatively impacted the ability of Te Hāwere-a-maki adults raising chicks during the 2013 breeding season to obtain food. However, because the methods employed in Dunn and Imber's studies were different to this one, such an interpretation must be applied with caution. This is because short studies of foraging behaviour may coincide with parents undertaking only one type of trip and parents adjust the lengths of their foraging trips throughout the chick-rearing period (Schultz and Klomp, 2000; Weimerskirch and Lys, 2000). Additionally, the similarities in chick growth rates observed in both the 2011 and 2013 breeding seasons suggest that parental provisioning parameters should be more similar (Dunn, 2012; Chapter Two). To determine genuine geographical or annual variations in feeding frequencies, longer studies, implementing identical methodologies, are required (Schultz and Klomp, 2000).

3.5.5 Parental Provisioning Behaviour

Foraging trips observed during this study appeared to be of two distinct types: trips of short duration, lasting two to five days and trips of long duration, lasting eight to greater than 19 days. Similar distinctions in trip lengths have also been observed in a wide range of other Procellariiform species including albatrosses, petrels and shearwaters (Chaurand and Weimerskirch, 1994; Congdon et al., 2005; Magalhães et al., 2008; Waugh et al., 2000;

Weimerskirch, 1998). Such a strategy has been hypothesised as being a way for adults to exploit distant food resources during the chick rearing period while adequately providing for their chicks (Baduini and Hyrenbach, 2003; Chaurand and Weimerskirch, 1994). The parental weight losses following short trips observed in other Procellariiformes, indicate that parents are not adequately self-provisioning during these trips (Congdon et al., 2005). The primary purpose of a short trip is therefore suggested as being to provide nourishment for the chick (Baduini and Hyrenbach, 2003). Comparatively, parental weight gains following trips of long durations, indicate that adults undertake such trips for the primary purpose of self-provisioning, to restore their reserves lost during preceding short trips (Baduini and Hyrenbach, 2003; Congdon et al., 2005). However, this results in lost opportunities to provision chicks who, though they generally receive larger meals following a parents return from a long trip, receive less food per day on average compared to when their parents undertake short trips (Chaurand and Weimerskirch, 1994).

Despite similar distinctions in trip lengths being observed for grey-faced petrels in this study as in other Procellariiform species, there were no significant differences observed in the weight of adults starting short as opposed to long trips. Additionally, there were no significant differences in the change in adult weight and the size of a meal delivered to chicks following short as opposed to long trips. Interestingly, throughout this study while grey-faced petrel adults had a tendency to lose weight during a short trip, they did not have a tendency to gain weight during a long trip. Contrary to findings in other Procellariiform species, adult weight losses were observed corresponding with complete foraging trips longer than 15 days in duration (Baduini and Hyrenbach, 2003; Chaurand and Weimerskirch, 1994; Congdon et al., 2005; Weimerskirch, 1998; Weimerskirch et al., 2003). Another unexpected finding, differing from patterns observed in other Procellariiform species, was that the size of a meal was negatively related to the time elapsed since the parent’s last visit (Chaurand and Weimerskirch, 1994; Granadeiro et al., 1999; Weimerskirch, 1998; Weimerskirch et al., 2003). This suggests that parents returning from longer trips would be expected to feed their chicks less. Parental pre-feed body weight was found to be the most influential variable affecting the meal size received by grey-faced petrel chicks. Therefore, this reduction of the size of a meal following trips of increasing duration could be a consequence of parental weight losses during very long trips.

In recent years a number of studies investigating parental provisioning behaviour have combined data gathered by continuously monitoring burrows during the chick rearing period, with tracking data obtained for individual foraging trips (Catard et al., 2000; Magalhães et al., 2008; Weimerskirch et al., 1997). Weimerskirch et al. (1997) found that adult wandering albatrosses (*Diomedea exulans*) provisioning chicks, travelled faster and more directly when moving away from and returning to the colony than during their time spent at sea between these two legs of foraging trips. Catard et al. (2000), along with Magalhães et al. (2008), observed similar behaviours in adult white-chinned petrels (*Procellaria aequinoctialis*) and Cory's shearwaters provisioning chicks. This suggests that in their commutes to and from reliable foraging grounds, adults of these species are spending most of their time in flight as opposed to foraging. If grey-faced petrel parents returning to the colony spend their time similarly, in flight as opposed to foraging, those returning from very long trips (> 15 days) could be expected to use up the reserves gained on their trip. Therefore, they may return to the colony having lost weight and consequently feed their chick less than they would otherwise.

Such long foraging trips could be a reflection of a combination of factors impacting the ease at which parents are able to find enough food to adequately provision themselves and their chicks (Chapter Two). The distance required to reach the continental shelf, over which grey-faced petrels spend the majority of their time foraging, along with weather conditions around the colony or en route to feeding grounds, have the potential to directly influence the time taken and energy requirements of adults to reach foraging grounds (Davoren and Montevecchi, 2003; MacLeod et al., 2008; Rayner et al., 2008). High levels of intra- or inter-specific competition, along with oceanic conditions at foraging grounds, have the potential to directly influence the quantity of food at feeding grounds and the time adults are required to spend foraging to find sufficient amounts of food for both themselves and their chicks (Forero et al., 2002; Weimerskirch et al., 2001).

Despite appearances that parents raising chicks on Te Hāwere-a-maki in the 2013 breeding season were struggling and, in some cases being unable to, keep up with the energetic demands of their chick, parents appear to be taking the needs of their chick into account when making foraging decisions. This is suggested by the similar variances that chick and parent identity account for in the mixed model investigating trip length (39.2% and 49.4%, respectively), implying that parents are taking their chick into account when making decisions as to trip length. However, how chicks are conveying their condition or requirements to parents remains unknown, though chick age and weight were found to have no influence on the duration of a foraging trip. Chicks could potentially be conveying information to parents as to their condition and food requirements through their begging calls. Cory’s shearwater chicks were able to honestly signal their reduced body condition to parents, by increasing the frequency of begging calls during provisioning (Quillfeldt and Masello, 2004). Adults respond to these increases in begging frequencies of their chicks by increasing the size of the meal delivered. It is possible that grey-faced petrel adults are also able to interpret changes in their chick’s begging calls in reference to their condition and food requirements. If this is the case it follows that they should be capable of responding by altering their provisioning behaviours, including the duration of foraging trips.

It is interesting that despite some parents being unable to keep up with the energetic demands of their chick, they did not readily abandon them. Parental behaviour following the death of a chick was observed on one occasion after the completion of this study, when one of the dead chick’s parents was observed returning to its burrow. For the other chicks that died after the completion of this study, stick gates placed in the entrance to their burrows were disturbed on a number of occasions between continued weekly visits to the island. Most of these disturbances were presumed to have been made by grey-faced petrels as they were often accompanied by fresh guano at the burrow entrance and therefore, were likely made by one of the deceased chick’s parents. Breeding Procellariiformes will invest in their own future maintenance over the survival of their offspring (Weimerskirch et al., 2001). However, as the time and energy invested into the rearing of a single chick increase, if adult survival was not compromised, it might be expected that parents would be more reluctant to abandon breeding attempts, in the off-chance that their chick did survive to fledge (Wojczulanis-Jakubas et al., 2013).

While the feeding frequencies presented here were much lower than previously recorded for the grey-faced petrel, the growth rates of chicks raised on Te Hāwere-a-maki have been similar among the 2011, 2012 and 2013 breeding seasons (Imber, 1976a; Chapter Two). Similar proportions of chicks survived to fledge at a similar time and were found to be indistinguishable in size prior to fledging (Chapter Two). This suggests that the provisioning behaviour displayed by parents in this study is unlikely to be unique to the 2013 breeding season. Less than optimal foraging conditions experienced by parents raising chicks on Te

Hāwere-a-maki, would have required them to travel further and spend more time searching to find sufficient food to provision both themselves, and their chicks. This would translate to parents provisioning chicks at lower frequencies and result in the prolonged chick rearing period observed on Te Hāwere-a-maki.

3.6 Conclusions and Recommendations

This chapter presents data on hourly chick weight losses following a meal and feeding frequencies experienced by fourteen 26 to 48 day old grey-faced petrel chicks raised on Te Hāwere-a-maki in the 2013 breeding season. Data on the provisioning behaviour of the parents of these 14 chicks are also presented. These data were obtained with the hope of better understanding reasons for the unexpectedly long chick rearing period observed on Te Hāwere-a-maki throughout the 2013 breeding season and the foraging strategies employed by grey-faced petrel parents.

Patterns of chick weight loss following a meal were similar to previous records for this species as well as other Procellariiform species. However, the feeding frequencies experienced by grey-faced petrel chicks throughout this study were much lower than previous records for this species (Dunn, 2012; Imber, 1976a). Parents appeared to employ a dual foraging strategy, alternating short, two to five day, trips with long, eight to greater than 19 day, trips. Though this type of foraging strategy is employed by other Procellariiform adults during chick rearing, many of the differences in provisioning parameters between trip lengths observed in other species were not observed during this study: adults were not consistently heavier starting a short trip as opposed to a long trip; adults did not consistently experience weight gains during long trips and weight losses during short trips and; chicks did not consistently receive larger meals from parents returning from long trips. This is suggested as the result of parents being required to travel particularly long distances from the colony to forage when embarking on a long trip and using up their reserves gained in the commute back to the colony. Though parents appeared to be struggling to find enough food to adequately provision both themselves and their chicks they appeared reluctant to abandon breeding attempts. They continued to provision chicks despite less than optimal foraging conditions, translating to a reduced feeding frequency and resulting in the prolonged chick rearing period.

The results from this study highlight a number of areas for continued research investigating grey-faced petrel parental provisioning behaviour. Longer studies, incorporating a number of colonies of varying size and employing consistent methodologies, may allow determination of the geographical and annual flexibility in the foraging strategy employed by grey-faced petrel parents. Integrating a tracking aspect to future studies may allow an understanding of foraging decisions made at sea and enable quantification of the distances travelled during individual foraging trips as well as the times spent in commute versus foraging (K. Bourgeois unpub.). Sex specific differences in foraging behaviour should also be investigated in future studies. These would have been investigated here, had time allowed for the results from blood samples taken from adults during this study to be obtained.

Although in their decisions as to the size of a meal delivered to chicks, adults did not appear to take their chicks condition into account, this could be a further consequence of parents struggling to find sufficient food to maintain both themselves and their chicks. They may therefore, be unable to take their chicks needs into account. By carrying out supplementary feeding experiments on Te Hāwere-a-maki in future breeding seasons, it may be possible to determine if adults are able to adjust their foraging decisions based on their chick’s condition, or if these decisions are constrained by marine conditions. Adults did appear to be taking their chick into account when making decisions as to trip length but how they are able to do this was not made clear by this study. Further study, investigating the relationship between acoustic qualities of begging calls and chick condition as well as the abilities of adults to adjust their provisioning behaviours in response to changes in their chick’s vocalisations, could provide insight into this mechanism.

Chapter Four

Breeding Success and Population Dynamics in the Grey-Faced Petrel *Pterodroma macroptera gouldi*

Plate 4.1 A grey-faced petrel adult prospecting on Te Hāwere-a-maki at the beginning of the 2013 breeding season. Photograph by Sylvain Dromzèe.

4 Breeding Success and Population Dynamics in the Grey-Faced Petrel *Pterodroma macroptera gouldi*

Key words: Grey-faced petrel, *Pterodroma macroptera gouldi*, demographic parameters, breeding success population dynamics

4.1 Introduction

Species persisting as a meta-population stand better chances of surviving into the future (Bonnaud et al., 2009; Buxton et al., 2014b; Hanski, 1998). This is because environmental stochasticity is less likely to detrimentally affect the entire meta-population, and migration among populations can rescue small ones from local extinction (Hanski, 1998). The same has been shown to be true for Procellariiform seabirds persisting as meta-populations, despite their philopatric nature. Immigration of breeding and prospecting birds can reverse the decline of populations subjected to predation pressures (Bonnaud et al., 2009). Passive recolonisation of Procellariiform species to sites from which they have been extirpated occurs faster when the species forms part of a stable or increasing metapopulation (Buxton et al., 2014b). Therefore, the importance of monitoring the dynamics of small Procellariiform populations within a meta-population context is well founded.

Predicting how variations in demographic parameters can affect population growth is a necessary means to this end. Decreases in adult survival have immediate effects on population dynamics, making long-lived Procellariiformes more sensitive to the loss of breeding adults than they are to chicks and juveniles (Asmussen, 2006; Jenouvrier et al., 2005). However, variations in breeding success and juvenile survival can also have long term implications for population dynamics, especially in terms of recruitment within a colony. With delays in reaching sexual maturity, it can be expected that the effects of decreases in adult fecundity, breeding success and juvenile survival on population dynamics will take years before becoming apparent (Jenouvrier et al., 2005; Thompson and Ollason, 2001a). If prolonged, decreases in these demographic parameters have the potential to profoundly impact the population in the future. Jenouvrier et al. (2005) found that strong fluctuations in the size of a southern fulmar (*Fulmarus glacialoides*) population were primarily driven by variations in the proportion of breeders and breeding success, as opposed to adult survival.

To improve Procellariiform population growth, active management can be undertaken in two places: at sea and at the colony (Carlile et al., 2003; Croxall et al., 2012; Taylor, 2000a). Management at the colony is often more economically and logistically feasible as well as being easier to monitor. The most serious threats to many Procellariiform populations are land based, and include pressures imposed by introduced predators as well as the loss of available breeding habitat (Taylor, 2000a). Therefore, management at the colony often yields positive results for populations. Given that the primary stage of a Procellariiform's lifecycle to occur at the colony is reproduction, understanding how variations in breeding success affect population growth may enable improved management planning for these seabirds.

Variations in breeding success have been shown to be caused by fluctuations in prey availability at sea. Breeding adults are more likely to abandon an egg or under-provision a chick in order to maintain their own body conditions, in years when prey availability near the colony is reduced (Jenouvrier et al., 2005). Oceanic conditions and competition at foraging grounds have the potential to directly influence the time parents are required to search for sufficient food to sustain both themselves and their chicks. Above average sea surface temperatures (SST), such as those experienced during El Niño years, correlate with a reduction in primary oceanic productivity and can consequently have detrimental effects on breeding seabirds (Smithers et al., 2003; Wolff et al., 2012). Smithers et al. (2003) found that above average SST was associated with wedge-tailed shearwaters (*Puffinus pacificus*) provisioning their chicks at a reduced frequency, resulting in increased chick mortality. The wedge-tailed shearwater population suffered an almost complete reproductive failure as a result. Impacts on parental foraging efficiency due to competition at foraging grounds can be both inter- and intra-specific. Magellanic penguins (*Spheniscus magellanicus*) breeding at high densities had increased levels of chick mortality as a consequence of depletion of high-quality food from the waters surrounding colonies by conspecifics (Forero et al., 2002). If poor prey availability can be predicted ahead of the breeding season, supplementary feeding of chicks, where required, could reduce the incidence of chick mortality.

Factors causing embryo and chick mortality may also include predation at the colony. An explosion in the rabbit population on Moutohora (Whale Island) subsequently caused an increase in the Norway rat (*Rattus norvegicus*) population due to the additional food supply (Imber et al., 2000). As a result of an increase in predation on grey-faced petrel (*Pterodroma macroptera gouldi*) eggs and chicks, breeding success was significantly reduced so that less than 7% of burrows produced a fledging annually. Comparatively, when predation by rats was considered negligible, 25% to 40% of burrows produced a fledging annually. If such high levels of predation had been allowed to continue, this major population of grey-faced petrels would have been at serious risk of extinction. Low breeding success has been observed for Gough Island colonies of the Atlantic petrel (*Pterodroma incerta*) as a consequence of predation by house mice (*Mus musculus*; Cuthbert, 2004). The highest incidence of mortality was found to occur during the chick rearing period, with apparently healthy chicks found dead and largely consumed at burrow entrances. If eradicating introduced predators altogether is not possible, insight into which stage of the breeding cycle is most affected by predation may help in planning cost effective predator control to increase breeding success (Russell et al., 2009).

The grey-faced petrel is a medium sized Procellariiform of the *Pterodroma* genus, found breeding exclusively in New Zealand (Taylor, 2000b). Once thought to have been widely distributed throughout mainland and island sites, today colonies are limited to islands, stacks and headlands free from, or inaccessible to, introduced mammalian predators. However, the grey-faced petrel still persists as a large meta-population with over 100 known colonies (Taylor, 2000b). It is one of New Zealand's few remaining Procellariiform species with abundant colonies, allowing them to fulfil the role of engineers within the terrestrial ecosystems in which they breed (Bancroft et al., 2005; Bellingham et al., 2010; Fukami et al., 2006). Though a few large and increasing colonies are supported on offshore islands (e.g. Moutohora and Hongiora Islands), most are small remnant colonies at risk of local extinction. Hence, it is important to understand how best to manage small grey-faced petrel populations, so they can continue to undertake this valuable role within the ecosystem. Long-term monitoring of small populations can provide information on factors resulting in variability in breeding success, informing future grey-faced petrel conservation measures as well as those for related, more endangered species.

In addition to being an important species in the ecosystem context, the grey-faced petrel has cultural significance among Hauraki Māori iwi who consider it as taonga (treasured; Lyver et al., 2008). An active interest to reinstate a sustainable customary harvest of grey-faced petrel chicks has resulted in a collaborative project between Hauraki iwi and Landcare Research. The project aims to understand and predict grey-faced petrel population trends, using both mātauranga (traditional knowledge) and scientific methodology. Understanding the effect of variations in breeding success on grey-faced petrel populations may provide a guideline estimate for sustainable harvest.

Over the 2011-12 and 2012-13 (henceforth 2011 and 2012, respectively) breeding seasons, research has been carried out investigating grey-faced petrel chick growth and breeding success on Te Hāwere-a-maki, an island located on Auckland's east coast (Dunn, 2012; Russell, 2013). By continuing this monitoring in the 2013-14 (henceforth 2013) breeding season, this study sought to analyse the effect variations in breeding success could have on the Te Hāwere-a-maki grey-faced petrel population into the future. This was done in the hope of being able to better inform management practices for this and other small grey-faced petrel populations.

4.2 Aims

There were two main aims for this study:

1. To examine the effects differences in breeding success have on the Te Hāwere-a-maki grey-faced petrel population.
2. To examine long-term population trends in the grey-faced petrel under variable estimates of breeding success.

4.3 Methods

4.3.1 Study site

This study was carried out on Te Hāwere-a-maki (formerly known as Motu Hāwere or Goat Island; 36° 16' S, 174° 47' E) during the 2013 breeding season. Te Hāwere-a-maki is a 9.3 ha island situated within the Cape Rodney to Okakari Point Scientific Marine Reserve, Leigh, which forms a part of the Hauraki Gulf Marine Park (map 2.1). Occurring along the coastal margins and exposed sea cliffs is a single, widespread grey-faced petrel colony that supports a breeding population of approximately 40-50 pairs (Dunn, 2012). The area of greatest burrow density can be found along the southern landward coast.

The naturally regenerating vegetation on Te Hāwere-a-maki consists of 95 species though, from a lack of active management, approximately a third of these were introduced (Gordon and Ballantine, 1976). However, the abundance of introduced species has reduced as native vegetation continues to develop. Pohutukawa (*Metrosideros excelsa*) forest is found along the coastal margins of the island with an understory of houpara (*Pseudopanax lessonii*), karo

(*Pittosporum crassifolium*), tarangarara (*Gahnia lacera*) and a multitude of ferns. The coastal broadleaf forest, covering the inner island, is dominated by mapou (*Myrsine australis*) with houpara, karamu (*Coprosma robusta*), mahoe (*Melicytus ramiflorus*), kohekohe (*Dysoxylum spectabile*) and manuka (*Leptospermum scoparium*).

Reinfestation of introduced mammalian pests is common because of the island's close proximity to the mainland. Rats (*Rattus* spp) are more than capable of traversing the 50 metre wide channel to reach Te Hāwere-a-maki (Russell et al., 2005). Recorded rat densities are highly stochastic, from 12-20 ha^{-1} in 1977 dropping through 3.2 ha^{-1} in 2005 to 1.3 ha^{-1} in 2011, rising again in 2012 to 4.3 ha^{-1} (Dunn, 2012; Russell et al., 2009; Russell, 2013).

4.3.2 Field Methods

To allow comparison with breeding success values calculated for the 2011 and 2012 breeding seasons, burrow monitoring during the 2013 season was carried out using the same methodology employed by these studies (Dunn, 2012; Russell, 2013). Upon adult birds' return to Te Hāwere-a-maki in June and July 2013, burrows were inspected weekly by hand for easily accessible adults incubating eggs. Any adults found were removed, weighed, identified and if not already, banded with a metal band. Study lids, enabling easy access to nest chambers, were installed in suitable burrows that did not already have them. The location of each burrow was recorded and uniquely labelled. Twenty-two burrows were selected for subsequent monitoring. These burrows were visited every three to four days in August 2013, until chicks hatched or un-hatched eggs were abandoned. Chicks that successfully hatched were measured weekly until they died or fledged, in January 2014, to investigate their development throughout the chick rearing period (Chapter Two). In addition to this, surviving chicks were handled daily between the 3rd and the 22nd of October to determine patterns of hourly weight loss and ascertain meal sizes (Chapter Three). In the event that the embryo or chick was found dead or missing, the egg, body or area was examined for evidence as to the cause of mortality.

4.3.3 Reproductive parameters.

For burrows monitored on Te Hāwere-a-maki during the 2011, 2012 and 2013 breeding seasons, hatching success, fledging success and breeding success were calculated (Dunn, 2012). Hatching success was calculated as the proportion of the 22 eggs that hatched each year. Fledging success was calculated as the proportion of hatched chicks to fledge each year. Breeding success was calculated as the number of eggs that produced fledglings. A hypothetical bad year was simulated by imposing the worst chances of hatching and fledging observed across the three breeding seasons on 22 burrows. Similarly, a hypothetical good year was simulated by imposing the best chances of hatching and fledging observed across the three breeding seasons on 22 burrows.

4.3.4 Population Viability Analysis

Considering the female population only, five three-class stage-structured (egg and chick, juvenile, adult) Lefkovitch population matrix models were constructed (Lefkovitch, 1965). Demographic data for the grey-faced petrel were used where available and where unavailable, for the conspecific great-winged petrel (*Pterodroma macroptera macroptera*). These data are summarised in table 4.1. The three-class stage-structured model representing the life cycle of the grey-faced petrel is depicted in figure 4.1.

Table 4.1 Estimates of the demographic parameters used in the population viability analyses obtained from grey-faced or great-winged petrels and the original source.

Demographic Parameter	Estimate (%)	Sub-species	Source
Adult Survival	89.0	Grey-faced petrel	Jones et al., 2011
Adult Fecundity	77.7	Great-winged petrel	Chastel, 1995
Juvenile Survival	20.0	Grey-faced petrel	Jones et al., 2011
Juvenile Maturity	45.7	Grey-faced petrel	Jones et al., 2011

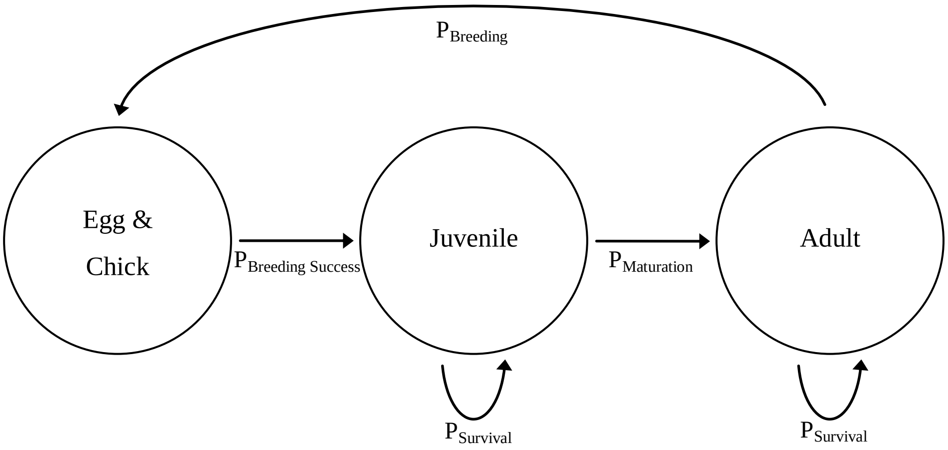


Figure 4.1 Diagrammatic representation of the three-class stage-structured Lefkovitch population model used to depict the life-cycle of the grey-faced petrel.

The constant parameters used in the matrix models are presented in tables 4.1 and 4.2. Jones et al. (2011) estimated that the probability of surviving juveniles having returned to their natal colony is 1.0 at six years of age. For simplicity this was assumed to be the age of first breeding, which gives a probability of remaining in the same class of 20.0%. The annual probability of juvenile survival in the first two years of age was presented by Jones et al.

(2011) as 85.5%. In the absence of data pertaining to the annual probability of survival from two years of age to maturity, this was assumed to remain at 85.5%. The probability of reaching maturity was therefore estimated to be 45.7% (0.855^5). The annual probability of adult survival, presented by Jones et al. (2011) as 89.0%, was used. In the absence of data pertaining to the breeding frequency of grey-paced petrels, Chastel's (1995) probability of successful great-winged petrels breeding in the subsequent season of 77.7% was used.

Table 4.2 The generic three-class stage structured population matrix model used in the population viability analyses. Probabilities for juvenile success (0.200), juvenile maturation (0.457), adult fecundity (0.777) and adult survival (0.890) were obtained from previous studies on the grey-faced or great-winged petrel. Breeding success was obtained from data collected from Te Hāwere-a-maki during the 2011, 2012 and 2013 breeding seasons and varied for each of these as well as hypothetical good and bad breeding years.

		From Class:		
		Egg + Chick	Juvenile	Adult
To Class:	Egg + Chick	0	0	0.777
	Juvenile	*Breeding Success*	0.200	0
	Adult	0	0.457	0.890

To allow the determination of the influence of breeding success on the Te Hāwere-a-maki grey-faced petrel population, five deterministic simulations, run for 50 years each, were carried out. For each simulation a different value of breeding success, calculated for the 2011, 2012 and 2013 breeding seasons as well as the hypothetical bad and good years, was used in the population matrix model. The simulations were run for 50 years as this was considered to be a reasonable time frame to determine population changes for informed strategic management planning (J. C. Russell pers. comm.). The initial age distribution for each simulation was set at 11 chicks and eggs, five juveniles and 22 adults. This approximated the size of the female population in the subset of 22 burrows selected for monitoring on Te Hāwere-a-maki in the 2013 breeding season, assuming an equal sex ratio. To assess the sensitivity of population growth (lambda, λ) under each population matrix model to changes in adult survival and fecundity, juvenile survival and maturation as well as breeding success, sensitivity coefficients were calculated by changing each parameter by ± 0.001 while holding everything else constant.

Ten stochastic simulations, run for 50 years each, were also carried out. Each of the five constructed population matrix models was assigned a number, one through five. For each stochastic simulation a randomly generated sequence of 50 numbers of equal possibility, between one and five, determined which population matrix model the population was subjected to at each time step (i.e. year).

4.3.5 Control Group

To assess the potential effects of repeated intrusion on egg and chick survival, all other known accessible burrows on Te Hāwere-a-maki were monitored intermittently throughout the 2013 breeding season. Using a burrowscope with an infrared camera, burrows were initially checked during incubation to ascertain the presence of an egg. Burrows were subsequently checked immediately after the hatching period and prior to the fledging period, to determine the presence of a chick. Chicks and eggs in control burrows were left undisturbed, with the exception of removing chicks from accessible burrows on the 18th of December, to take their morphometric measurements for comparison with study chicks (Chapter Two). Reproductive parameters, including hatching success, fledging success and overall breeding success, were calculated for control burrows.

4.3.6 Statistical Analysis

Chi-squared tests were used to compare reproductive parameters among breeding seasons, both real and hypothetical. Chi-square tests were also used to compare the time taken for starting populations to double in size, final population sizes and population growth rates for deterministic simulations. Population sizes were averaged and 95% confidence intervals determined for the ten 50 year stochastic simulations. To compare breeding success between control and study burrows, chi-squared tests were performed for each of the reproductive parameters calculated. All analyses were constructed using the PopTools add-in for Microsoft Excel.

4.4 Results

4.4.1 Overview

Of the 22 study burrows on Te Hāwere-a-maki found with adults incubating eggs at the beginning of the 2013 breeding season, 15 chicks successfully hatched in late-August to early-September 2013 (average: 26th August ± 6 days; range: 16th August to 7th September). There was no evidence of predation prior to the loss of the egg or abandonment by parents. Ten chicks survived to fledge in January 2014 (average: 14th January ± 10 days; range: 1st to 29th January). Post-mortem examination of the bodies of the five chicks that died prior to fledging and, in some cases, knowledge of the duration since their last meal, suggested all chicks died from starvation. Dates of death, estimated based on the state of decomposition of the bodies, averaged the 14th of November ± 20 days (range: 23rd October to 28th November).

Forty-four other active burrows were found on Te Hāwere-a-maki at the beginning of the 2013 breeding season. Twenty-eight of these produced a chick, of which 25 survived to fledge.

Of the 22 burrows found on Te Hāwere-a-maki with adults incubating eggs at the beginning of the 2011 and 2012 breeding seasons, 19 and 16 chicks hatched in late-August to early September of 2011 and 2012, respectively (Dunn, 2012; Russell, 2013). Similar to those observed in the 2013 breeding season, the average hatching dates in the 2011 and 2012 breeding seasons were the 26th and 25th of August 2011 and 2012, respectively. In the 2011 breeding season, eight chicks survived to fledge with an average fledging date of the 9th of January 2012. Starvation was hypothesised as the cause of death for all 11 chicks that died during the 2011 chick rearing period. In the 2012 breeding season nine chicks survived to fledge with an average fledging date of the 4th of January 2013. Predation was hypothesised as the cause of death for the seven chicks that died during the 2012 chick rearing period.

4.4.2 Reproductive Parameters

The number of eggs chicks and fledglings produced from Te Hāwere-a-maki study burrows in the 2011, 2012 and 2013 breeding seasons are presented in table 4.3, along with their corresponding hatching, fledging and breeding success rates. Of the 22 eggs laid in Te Hāwere-a-maki study burrows during July of the 2013 breeding season, 15 hatched within a four week window from the 15th of August 2013 to the 8th of September 2013. Ten of these chicks survived to fledge during January 2014. Though similar to the previous two breeding seasons, more chicks hatched in both 2011 and 2012 (19 and 16 respectively) though less survived to fledge (8 and 9 respectively). While the 2013 breeding season is associated with the lowest hatching success (68.2%), it is associated with the highest fledging success (66.7%). Conversely, the opposite is true for the 2011 breeding season in which the highest hatching success rate and the lowest fledging success rate were observed (86.4% and 42.1%, respectively). There is no evidence of differences in the hatching and overall breeding success among breeding seasons (hatching success: $\chi^2_4 = 2.371$, p-value = 0.305; breeding success: $\chi^2_4 = 1.012$, p-value = 0.603). There is however, weak evidence of a difference in the fledging success among breeding seasons ($\chi^2_4 = 2.372$, p-value = 0.063).

Table 4.3 The numbers of eggs, chicks and fledglings as well as the corresponding hatching, fledging and breeding success of grey-faced petrels from Te Hāwere-a-maki during the 2011, 2012 and 2013 breeding seasons. The hypothetical bad year was simulated using the worst hatching and fledging success rates observed over the 2011, 2012 and 2013 breeding seasons. Similarly, the hypothetical good year was simulated using the best hatching and fledging success rates.

Parameter	2011	2012	2013	Bad Year	Good Year
Eggs (n)	22	22	22	22	22
Chicks (n)	19	16	15	15	19
Fledglings (n)	8	9	10	7.1	12.7
Hatching Success (%)	86.4	72.7	68.2	68.2	86.4
Fledging Success (%)	42.1	56.3	66.7	42.1	66.7
Breeding Success (%)	36.4	40.9	45.5	28.7	57.6

4.4.3 Deterministic Simulations

Presented in table 4.4, below, are the findings from the deterministic simulations in which population matrix models incorporated the demographic estimates in table 4.2 with the varying values of breeding success in table 4.3. Grey-faced petrel populations experienced growth in all deterministic simulations, despite being subjected to different values of breeding success corresponding with the 2011, 2012, 2013, hypothetical good and bad breeding seasons. However, considerable variation in population growth existed.

Table 4.4 Breeding successes corresponding with the 2011, 2012, 2013, hypothetical good and bad breeding seasons used in the deterministic simulations with starting population sizes of 38.

Parameter	2011	2012	2013	Bad Year	Good Year
Breeding Success (%)	36.4	40.9	45.5	28.7	57.6
Time to Double in Size	16	12	10	44	7
Annual Percentage Increase	3.8	5.2	6.5	1.4	9.8

Differences in population growth under different values of breeding success are graphically depicted in figure 4.2. Population growth was found to be greatest for the hypothetical good breeding season followed by the 2013, 2012, 2011 and finally hypothetical bad breeding seasons. Despite breeding success calculated for a hypothetical good year (57.6%) only being double that of the hypothetical bad year (28.7%), this represented a seven-fold increase in the annual percentage growth of the population; 9.8% per annum as opposed to 1.4% per annum. There is very strong evidence of a difference in the time taken for the initial populations, of 38 individuals, to double in size among breeding seasons ($\chi^2_4 = 50.607$, p-value < 0.001).

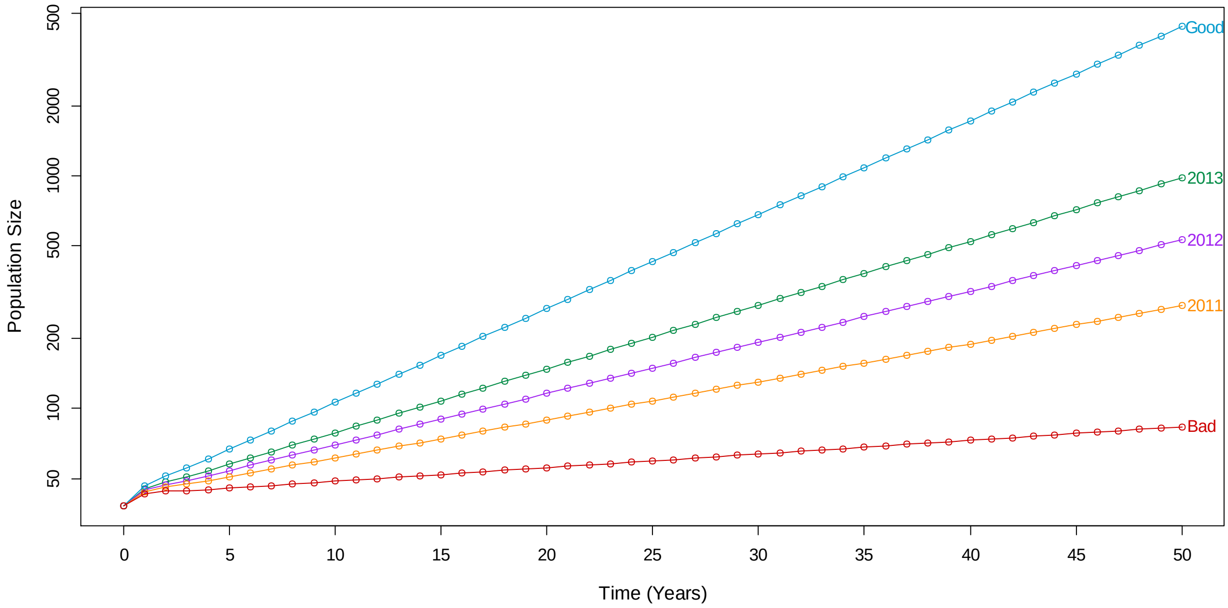


Figure 4.2 Variations in the size of the Te Hāwere-a-maki grey-faced petrel population originating from 22 burrows related to changes in breeding success corresponding with the 2011 (-o-), 2012 (-o-), 2013 (-o-), hypothetical good (-o-) and bad (-o-) breeding seasons expressed as a function of years into the future. Note the log scale used for population size.

Assuming all other values remain constant, population growth is predicted to become negative if breeding success fell 3.9% from that calculated for a hypothetical bad year to 24.8% (table 4.4). Using the average breeding success and keeping all other values constant, population growth is presumed to become negative following a 7.5% drop in adult survival to 81.5% or an 8.4% drop in juvenile maturation to 27.2%.

Table 4.5 The critical values determined separately for adult survival, fecundity, breeding success and juvenile maturation with everything else held constant and breeding success averaged across the 2011, 2012, 2013, hypothetical good and bad breeding seasons below which a negative population growth is expected.

Parameter	Original	Critical Level	Difference
Adult Survival	0.890	0.815	0.075
Adult Fecundity	0.777	0.461	0.316
Breeding Success	0.418	0.248	0.170
Juvenile Maturation	0.457	0.272	0.084

4.4.3 Sensitivity Analysis

The results for the sensitivity analyses performed on the five population matrix models used for the deterministic simulations are presented in table 4.6. With the highest sensitivity coefficients, changes in adult survival are most influential to the growth of the Te Hāwere-a-maki grey-faced petrel population for all five population matrix models. Adult survival appears to be more influential as the breeding success used in the population matrix model is worsened. Changes in breeding success and juvenile maturation are the next most influential to the growth of the population. However, their importance relative to one another is dependent on the average breeding success used in the population matrix model. Changes in breeding success are relatively more important when the average breeding success is worsened. Comparatively, changes in juvenile maturation are relatively more important when the unaltered breeding success is improved.

Table 4.6 Variations in the sensitivity of the Te Hāwere-a-maki grey-faced petrel population growth (measured by the dominant eigenvalue) to changes of ± 0.001 in each parameter for the five population matrix models with different breeding success rates corresponding to the 2011, 2012, 2013, hypothetical good and bad breeding seasons used for the deterministic simulations.

Parameter	2011	2012	2013	Bad Year	Good Year
Adult Survival	0.758	0.744	0.732	0.785	0.704
Adult Fecundity	0.115	0.155	0.165	0.125	0.188
Breeding Success	0.309	0.295	0.282	0.338	0.254
Juvenile Survival	0.134	0.141	0.148	0.119	0.163
Juvenile Maturation	0.246	0.264	0.280	0.212	0.320

4.4.4 Stochastic Simulations

The grey-faced petrel population experienced positive growth in all ten stochastic simulations. The average annual percentage increase of 5.7% ± 2.0% (range: 2.7% to 16.9%) fell between those observed for the deterministic simulations where the values of breeding success corresponded to the 2012 and 2013 breeding seasons (5.2% and 6.5%, respectively). The average time taken for the population to double from an original size of 38 individuals was 12.2 years ± 1.9 years (range: 9 to 15 years). This is very similar to the estimated 12 years for the population to double in size observed in the simulation using the value of breeding success from the 2012 breeding season. The average population size after 50 years was found to be 614 ± 92 individuals (range: 440 to 721 individuals), falling between the deterministic simulations using values of breeding success corresponding with the 2012 and 2013 breeding seasons (531 and 984 individuals, respectively).

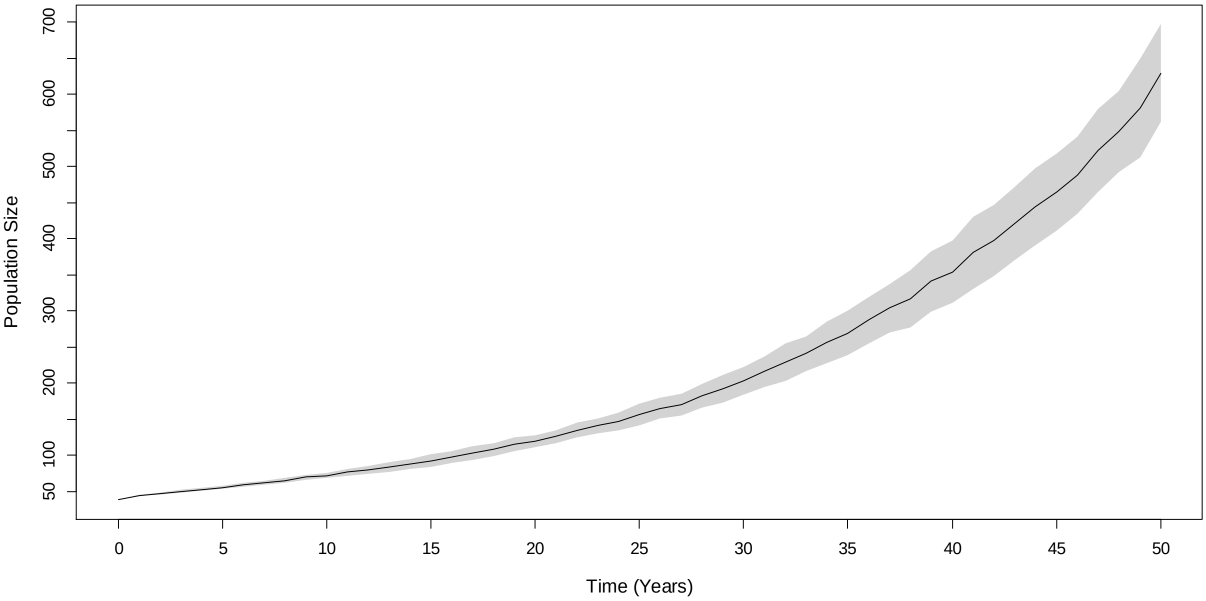


Figure 4.3 The population size as a function of time (years) averaged for ten stochastic simulations where populations were subjected to different values of breeding success, calculated for the 2011, 2012, 2013, hypothetical good and bad seasons, at each time step (—). The shaded area represents the 95% confidence interval for the population size.

4.4.5 Control Group

Reproductive parameters calculated for the 44 control and 22 study burrows on Te Hāwere-a-maki in the 2013 breeding season are presented in table 4.7. There is no evidence of differences between groups in the hatching success and overall breeding success (hatching success: $\chi^2_1 = 0.161$, p-value = 0.689; breeding success: $\chi^2_1 = 1.248$, p-value = 0.264). There is weak evidence that the fledging success calculated for the control group is greater than the study group ($\chi^2_1 = 3.274$, p-value = 0.070).

Table 4.7 The numbers of eggs, chicks and fledglings as well as the corresponding hatching, fledging and breeding success for Te Hāwere-a-maki grey-faced petrel control (n = 44) and study (n = 22) burrows in the 2013 breeding season.

Parameter	Control Group	Study Group
Eggs (n)	44	22
Chicks (n)	28	15
Fledglings (n)	25	10
Hatching Success (%)	63.6	68.2
Fledging Success (%)	89.3	66.7
Breeding Success (%)	56.8	45.5

4.5 Discussion

4.5.1 Control

There were no differences between Te Hāwere-a-maki control and study burrows in the hatching and overall breeding success and only weak evidence of a difference in the fledging success. Hence, there is no reason to believe that frequent handling of chicks has affected grey-faced petrel breeding success. Dunn (2013) similarly reported that frequent handling did not affect breeding success in his study on the grey-faced petrel. Chick growth and parental provisioning behaviours in the grey-faced petrel have also been found to be unaffected by frequent handling of chicks (Chapter Two; Chapter Three). Therefore, reasons other than frequent handling are expected to have contributed to the variations in breeding success, presented here.

4.5.2 Variation in Breeding Success

Breeding success on Te Hāwere-a-maki was highest in the 2013 breeding season, with 45.5% of study burrows producing fledglings, followed by the 2012 and 2011 breeding seasons (40.9% and 36.4%, respectively). These differences, however, were not statistically significant. Although overall breeding success was similar in all three seasons, the primary cause of nest failure varied between abandonment coupled with starvation in the 2011 and 2013 breeding seasons and predation in the 2012 breeding season. Values of breeding success calculated for both real (2011, 2012 and 2013) and hypothetical breeding seasons (good: 57.6%; bad: 28.7%) all fell within the range previously observed in the grey-faced petrel (0-65.4%; Imber et al., 2000; Chapter Two).

Despite similar overall breeding success being observed in the 2011 and 2013 breeding seasons, contrast exists in the stages at which breeding failure primarily occurred. While the 2011 breeding season was associated with the highest observed hatching success (86.4%), it also had the lowest fledging success (42.1%). Comparatively, the opposite was observed in the 2013 breeding season with relatively low hatching success coupled with high fledging success (68.2% and 66.7%, respectively). In both 2011 and 2013 breeding seasons the primary causes of embryo and chick mortality were abandonment coupled with starvation. These events are the consequence of parents experiencing difficulties in obtaining sufficient food (Smithers et al., 2003; Weimerskirch et al., 2001). This discrepancy between seasons may therefore reflect differences in the timing at which food supply became sufficiently scarce to lead to breeding failure.

The early stages of the 2011 breeding season were associated with a mild-medium La Niña event, characterised by a lowering of the sea surface temperatures throughout the central Pacific Ocean (Dunn, 2012). Decreases in sea surface temperatures have been shown to improve oceanic primary productivity (Wolff et al., 2012). Consequently, this leads to an improvement in foraging conditions experienced by breeding seabirds which flows on to increased breeding success (Weimerskirch et al., 2001). If breeding grey-faced petrels in 2011 experienced good foraging conditions during the period between the pre-laying exodus and hatching, parents returning to begin incubation shifts would have been in good condition. As a result, they would have been better prepared for long incubation spells and less likely to abandon their eggs during this period. This may provide an explanation for the high hatching success observed during the 2011 breeding season. As the season progressed, food was likely to have become scarcer as competition with other seabirds commencing their breeding seasons increased, and oceanic conditions worsened with the subsiding of the La Niña event (Gaskin and Rayner, 2013; Weimerskirch and Lys, 2000). Parents may have found it increasingly difficult to meet the demands of their chicks, resulting in longer intervals between meals. Parents with good foraging efficiency and experience were more likely to have continued provisioning chicks at a sufficient rate to enable growth (Weimerskirch, 1992). Additionally, chicks have been shown to adjust their metabolic rate with variable provisioning (Boersma et al., 1980; Warham, 1990). This ability is hypothesised to be related to the chick’s prior experience. If food appeared to be in abundance from hatching, chicks may have lacked the capabilities to promptly lower their metabolic rates in response to a food shortage (Chapter Three). Their body condition would have deteriorated more rapidly following a meal, reducing their chances of surviving until their next meal. A combination of these factors could reasonably explain the low fledging success observed in the 2011 breeding season.

Less than optimal foraging conditions were likely to have been experienced at the beginning of the 2013 breeding season as a consequence of neutral El Niño conditions. Comparatively worse foraging conditions in 2013 between the pre-laying exodus and hatching, may have meant that parents were less prepared for the long incubation shifts required of them (Hatch, 1990). If this was the case, they would have been more likely to abandon breeding attempts during incubation, explaining the relatively low hatching success observed during the 2013 breeding season. Given this, it is more likely that parents able to successfully hatch chicks would be more experienced and in better condition (Weimerskirch, 1992). Such parents would have had improved chances of finding sufficient amounts of food to provision both themselves and their chicks throughout the subsequent chick rearing period. If food was scarcer from the beginning of the 2013 breeding season, chicks may have been more capable of lowering their metabolic rate accordingly, as food became increasingly limited throughout the breeding season (Boersma et al., 1980; Warham, 1990). A combination of these factors could reasonably explain the relatively high fledging success observed during the 2013 breeding season. However, because the number of monitored birds was small, results must be considered with caution. Continued monitoring of breeding success in future seasons may provide more insight to the causal factors behind these patterns.

The close proximity of Te Hāwere-a-maki to the mainland makes it vulnerable to continuous ship rat (*Rattus rattus*) reinvasions (J. C. Russell pers. comm.). Rat predation of grey-faced petrel chicks at other colonies has been shown to severely impact breeding success and could result in persistent breeding failure on Te Hāwere-a-maki if unchecked (Imber et al., 2000; Russell, 2013). During the 2011, 2012 and 2013 breeding seasons, rat trapping was carried out on Te Hāwere-a-maki to minimise the likelihood of breeding failure as a result of egg and chick predation by rats (Dunn, 2012; Russell, 2013; Chapter Two). Despite this, predation by ship rats was observed to be the primary cause of grey-faced breeding failure in the 2012 breeding season (Russell, 2013). Grey-faced petrel eggs attended by parents are rarely targeted by rats but unattended eggs are at high risk of predation (Imber et al., 2000; J. C. Russell pers. comm.). Small chicks are particularly vulnerable in the first three weeks following hatching as they are sleepy, weak and undefended while parents forage (Imber et al., 2000). Rat trapping carried out at the beginning of the 2011 breeding season was sufficient to keep rat densities on the island low and prevent predation by rats on particularly vulnerable, young chicks (Russell, 2013). When rats reinvaded in the spring and summer of the 2011 breeding season, the older chicks would have been better able to defend themselves, reducing their chances of predation. However, this reinvasion is likely to have contributed to the peak in rat numbers observed in the 2012 breeding season and the subsequent inability of trapping to control them. The majority of deaths in the 2012 breeding season occurred early in the chick rearing period. It appears that continued trapping from the beginning of the 2013 breeding season was sufficient to prevent rat predation on chicks. However, the high incidence of predation in the 2012 breeding season highlights the importance of active predator control in improving breeding success. Subtle changes in breeding success caused by at sea conditions, which can be obscured by rat predation because it is unknown whether predation as a cause of failure early in the breeding season is additive or compensatory (Carlile et al., 2003; J. C. Russell pers. comm.). Therefore, successful predator control would be essential in determining the effect of at sea conditions on breeding success.

4.5.3 Population Dynamics

Grey-faced petrel populations experienced growth despite being subjected to the varying levels of breeding success calculated for the 2011, 2012, 2013, hypothetical good and bad breeding seasons. It is worth noting that, as highlighted by the sensitivity analyses, grey-faced petrels, like other Procellariiform species, are more susceptible to the loss of adults than chicks (Chastel et al., 1993; Jenouvrier et al., 2005). Additionally, when the value for breeding success was averaged, population decline was evident following a decrease in adult survival of just 7.5%. However, varying breeding success by 30% between hypothetical good and bad breeding seasons consistently resulted in population growth.

Fortunately, adult survival in long-lived species is unlikely to show significant annual variations, with the exception of the occasional catastrophic event (Chastel et al., 1993). Jones et al. (2011) showed this for the grey-faced petrel, finding no support for temporal variation in adult survival at both study sites in mark-recapture models. Comparatively, natural year-to-year variation in breeding success is well documented in the Procellariiformes, including the grey-faced petrel. (Chastel et al., 1993; Imber et al., 2000; Simons, 1984; Weimerskirch and Jouventin, 1987). The breeding success of the snow petrel (*Pagodroma nivea*) varied greatly over a 27 year period, with as little as 21% of eggs producing fledglings to as high as 80% (Chastel et al., 1993). Similarly, the breeding success of the wandering albatross (*Diomedea exulans*) in the Crozet Islands ranged from 22% of eggs producing fledglings to 77% over 15 breeding seasons (Weimerskirch and Jouventin, 1987). Imber et al. (2000) found the breeding success of grey-faced petrels from Moutohora varied from 0% to 52% over a 26 year period. Theoretically, long-lived species, such as the Procellariiformes, should prioritise their own survival over that of their chick's to maximise their lifetime reproductive potential (Chastel et al., 1993). They are therefore likely to refrain from breeding if conditions are unfavourable, explaining the often high variability in breeding success seen among members of the Procellariiform order.

While this means populations have evolved to be less susceptible to the loss of chicks, if poor breeding success is sustained, they can face a serious risk of extinction (Carlile et al., 2003; Imber et al., 2000). Natural random fluctuations in breeding success experienced by a small population, when coupled with extrinsic factors, such as predation by introduced species, could result in accelerated population declines (Simons, 1984). Grey-faced petrel populations have been shown by Imber et al. (2000) to be vulnerable to decline if low levels of breeding success are sustained. Rat predation on eggs and chicks reduced the breeding success on Moutohora to below 7% over a ten year period. If this had been allowed to continue it would have endangered this important population of grey-faced petrels. In simulations, the degree to which population growth was positive varied significantly among the different values calculated for breeding success. After 50 years of being subjected to breeding success corresponding with the hypothetical bad year, the starting population of 38 individuals had barely doubled in size. With such low values the population was shown to be more vulnerable to small decreases in breeding success as well as other demographic parameters, in particular adult survival. If breeding success this low was sustained for several years, a season with high predation could drastically affect the population (Simons, 1984). Given the low breeding success observed on Te Hāwere-a-maki in the 2012 season, despite predator control, this is a likely event if the colony was left to its own devices.

Due to delays in reaching maturity, decreases in breeding success can take years before their effect on population dynamics become apparent (Jenouvrier et al., 2005; Thompson and Ollason, 2001a). Fortunately, improving breeding success is often an accessible conservation technique (Carlile et al., 2003; Imber et al., 2000; Rayner et al., 2012). Low breeding success was a major cause in the decline of four sub-tropical *Pterodroma* species; Zino’s petrel (*Pterodroma madeira*), the Bermuda petrel (*Pterodroma cahow*), Gould’s petrel (*Pterodroma leucoptera leucoptera*) and the Hawaiian petrel (*Pterodroma sandwichensis*; Carlile et al., 2003). With a focus on improving breeding success by minimising the threats imposed during the breeding season at known colonies, the recovery programmes implemented for all four *Pterodroma* species have resulted in population expansion. Efforts to improve the breeding success of the endangered Chatham petrel (*Pterodroma axillaris*), including provision of artificial nest boxes, daily observations and swapping of eggs, have enabled the active establishment of new colonies (Rayner et al., 2012). The eradication of rats from Moutohora has since led to an increase in breeding success of grey-faced petrels on the island and the recolonisation of abandoned habitats, suggesting an expanding population.

Understanding the effects of long term variations in breeding success can enable prediction of changes in population dynamics under varying environmental conditions and levels of predation. Continuing such studies with small, remnant grey-faced petrel populations could provide an understanding of factors enabling their persistence. This could in turn improve management not only for the grey-faced petrel but other, more endangered, *Pterodroma* species. Though the grey-faced petrel is considered ‘least concern’ by the IUCN and ‘not threatened’ by New Zealand’s own threat ranking system, it is more feasible to conserve populations now as opposed to re-establishing them in the future (IUCN, 2013; Miskelly et al., 2008; Taylor, 2000b).

4.6 Conclusion and Recommendations

This chapter presents data on natural variations in grey-faced petrel breeding success observed in monitored burrows on Te Hāwere-a-maki in the 2011, 2012 and 2013 seasons, as well as feasible hypothetical seasons. It then goes on to simulate the effects of these different values on population growth over 50 year periods. These data were obtained with the intention of better understanding variation in breeding success and the effects they could have on the dynamics of small grey-faced petrel populations like the one on Te Hāwere-a-maki. Values of breeding success were found to be within the ranges previously observed for this species (Imber et al., 2000; Chapter Two). Despite similarities in the values calculated for the 2011, 2012 and 2013 breeding seasons, the primary cause of nest failure varied between abandonment coupled with starvation (2011, 2013) and predation (2012). Population growth was evident under all values of breeding success, however, the extent to which populations increased was variable. Populations could be in jeopardy from catastrophic events, such as high levels of predation, if subjected to several years with breeding success as low as that calculated for the hypothetical bad year (28.7%).

The results from this study highlight the importance of pest control, particularly early in the season, in improving breeding success in the grey-faced petrel. This is likely to be crucial in the persistence of the Te Hāwere-a-maki and other small populations. Additionally they highlight the importance of long-term monitoring of populations to improve understanding of their dynamics. For populations that are small or undergoing rapid expansion, subtle decreases in breeding success associated with variations in climate can be difficult to recognise (Carlile et al., 2003). Therefore, determining the effects of climate change on the dynamics of a small population may prove challenging. This is particularly important for the grey-faced petrel as, understanding factors behind its increasing population, are important in protecting these and other, more endangered, *Pterodroma* species.

Though the simulations here did not thoroughly investigate the effects of variation in other demographic parameters on population dynamics, which was outside its scope, breeding success is not the only fluctuating parameter which could impact population dynamics. Over the 2011, 2012 and 2013 breeding seasons, Te Hāwere-a-maki chicks have experienced stunted growth and fledged in reduced condition (Chapter Two). Chicks fledging in poor condition are less likely to survive the initial post-fledging period. This is because they are required to overcome less than optimal starts to life, while being faced with the challenges of foraging for patchy and scarce food resources (Asmussen, 2006). Chicks raised on Te Hāwere-a-maki fledging in reduced condition could have important implications for juvenile survival. Reductions in juvenile survival have been found to be the primary causes of population decline for a number of Procellariiform species (Prince et al., 1994; Thompson and Ollason, 2001b). The potential for this to be a problem for the grey-faced petrel should be further investigated.

Chapter Five

Conclusion

Plate 5.1 Along with acoustic attraction, the installation of nesting boxes has been used at Tawharanui Regional Park in the hope of encouraging grey-faced petrels to breed on the peninsula. Though it is early days, it appears to be working; this pair showed particular interest in the nesting boxes at the beginning of the 2013 breeding season (M. Friesen pers. comm.). It is hoped they will be back in the 2014 season to breed! Photograph by Megan Friesen.

5 Conclusion

Key Words: Procellariiformes, *Pterodroma*, conservation, grey-faced petrel, *Pterodroma macroptera gouldi*, chick growth, provisioning behaviour, breeding success

5.1 The Importance of Seabirds

New Zealand supports a diverse seabird community; 96 of the world's 633 seabird species and subspecies breed throughout it (Taylor, 2000a). Remarkably, in global terms 49 of these, close to 10% of all seabird species and subspecies, breed only in New Zealand. Home to 53 Procellariiform species and subspecies, New Zealand also supports the greatest diversity of this significant seabird order. However, the Procellariiformes include some of the world's most threatened groups of seabirds (Croxall et al., 2012). Unfortunately, throughout New Zealand Procellariiformes are becoming increasingly limited to islands free of introduced mammalian predators (Bellingham et al., 2010; Towns and Ballantine, 1993).

In locations free of introduced mammalian predators where Procellariiformes form colonies, often large and dense, during their breeding seasons, they dominate the terrestrial ecosystem. As providers of marine nutrients and the main contributors to natural disturbance regimes, they assume a crucial role in terrestrial ecosystem functioning throughout their breeding distributions (Bancroft et al., 2005; Bellingham et al., 2010; Fukami et al., 2006; Roberts et al., 2007). Procellariiformes transport nutrients from the sea to their breeding grounds in substantial quantities by means of their guano, feathers, carcasses, eggs and food for their young (Fukami et al., 2006). Throughout their breeding season wedge-tailed shearwaters contributed nitrogen to their colony in Western Australia at a rate of 51 kg of nitrogen $ha^{-1}yr^{-1}$ (Bancroft et al., 2005). Comparatively agricultural lands in the same area were fertilised at a rate of 8-20 kg of nitrogen $ha^{-1}yr^{-1}$. The risk of losing Procellariiform populations at many coastal locations is a cause for concern in maintaining their historic ecosystem functioning into the future.

Because of their important role in terrestrial ecosystem functioning, in locations where Procellariiform species have retained populations it is more feasible to conserve those populations now as opposed to re-establishing them in the future. A better understanding of these species' breeding biologies and population processes can allow determination of the stages intervention may be required and consequently more efficient species management

(Pinet et al., 2009; Rayner et al., 2012). However, managing existing populations may not always be an option. Where restoration projects often desire to re-establish a functioning ecosystem, at coastal sites from which Procellariiformes have been extirpated the inclusion of Procellariiform species management is central to this desire (Bellingham et al., 2010; Buxton et al., 2014a). Restoring lost populations through attraction or chick translocations may be necessary (Mitchell and Mitchell, 2009; Tennyson and Taylor, 1990). However, given the time and resources that are invested in such projects, their success may be jeopardised if small populations are then left to their own devices. Until they reach a size where they are sustainable, good management of populations is necessary to improve the outcome of such restoration projects.

Due to rapid decline or small populations and ranges the *Pterodroma* are the most threatened group of seabirds after the albatrosses (Croxall et al., 2012). Eleven *Pterodroma* species and subspecies breed throughout New Zealand, five of which are considered threatened by either the New Zealand or the IUCN threat ranking systems (IUCN, 2013; Miskelly et al., 2008; Taylor, 2000a; Taylor, 2000b). Their effective conservation is often hindered by a lack of basic biological knowledge (Pinet et al., 2009; Rayner et al., 2012). Similarities in the *Pterodroma*'s physiologies, breeding biologies and diets, mean management techniques developed for one species are often transferrable to others.

The grey-faced petrel (*Pterodroma macroptera gouldi*) persists as a large meta-population, making it one of New Zealand's few remaining Procellariiformes to assume the crucial role in the functioning and health of the terrestrial ecosystems in which it breeds (Bellingham et al., 2010). Though large and increasing colonies are supported on some offshore islands, many are small and at risk of extinction. Understanding aspects of the grey-faced petrel's breeding biology that make it so successful in comparison to many other species in the *Pterodroma* genus, may allow better planning for the management of this species (Hutton and Priddel, 2002). This may also allow for an improvement in the conservation strategies employed for other *Pterodroma* species at more immediate risk of extinction.

The overall aim of this research was to characterise natural annual (2011, 2012 and 2013 breeding seasons) and geographical (east coast and west coast) variations in grey-faced petrel chick growth, parental provisioning behaviours and annual variations in breeding success. This has been done in the hope that a better understanding of the grey-faced petrel's breeding biology on land, will give insight into aspects that favour population growth, inform the conservation of small grey-faced petrel populations, and improve success rates when translocating chicks to sites from which they have been extirpated.

5.2 Summary of Main Findings

Chapter Two: Chick Growth in the Grey-Faced Petrel

In the 2013 breeding season, hatching of grey-faced petrel chicks on Ihumoana and Te Hāwere-a-maki was highly synchronised. Chicks from both islands hatched within a four week window from the 15th of August to the 8th of September with an average hatching date for both islands of the 26th of August. Hatching dates were similar to those observed in the 2011 and 2012 breeding seasons on Te Hāwere-a-maki of the 26th and 25th of August, respectively (Dunn, 2012; Russell, 2013). Chicks raised on Ihumoana during the 2013 breeding season fledged approximately three weeks earlier than chicks raised on Te Hāwere-a-maki during the same breeding season. Therefore, the average rearing period for chicks raised on Ihumoana (116 days ± 7 days; range: 105 to 131 days) was significantly shorter than for chicks raised on Te Hāwere-a-maki (139 days ± 9 days; range: 128 to 157 days). Chicks raised on Te Hāwere-a-maki in the 2011, 2012 and 2013 breeding seasons fledged at similar times with no observed differences in the lengths of the chick rearing periods.

There was no detectable effect of frequent handling on the growth of chicks. The morphological development of chicks raised in the 2011, 2012 and 2013 breeding seasons has conformed to the general pattern of growth reported for other *Pterodroma* and Procellariiform species. However, chicks raised on Ihumoana during the 2013 breeding season, and generally for most previous years, grew much faster and were in better condition at fledging, in comparison to chicks raised on Te Hāwere-a-maki during the same breeding season (G. A. Taylor pers. comm.). Chicks raised on Te Hāwere-a-maki have had similar growth rates and fledged in similar conditions among all three breeding seasons (2011, 2012 and 2013).

Differences in chick growth between Ihumoana and Te Hāwere-a-maki are likely to be indicative of differences in provisioning rates and/or meal sizes between the two colonies. Proximity to the continental shelf, as well as weather conditions around colonies and en route to foraging grounds, have the potential to directly influence the time taken and energy requirements of adults to reach foraging grounds (Davoren and Montevecchi, 2003; Hulsman and Smith, 1988; Weimerskirch et al., 2012). The closer proximity of Ihumoana to the continental shelf could result in parents travelling shorter distances to reach foraging grounds in comparison to Te Hāwere-a-maki parents (CANZ, 1997; Imber, 1973). The more consistent wind speeds and directions surrounding Ihumoana could improve the flying efficiency of parents raising chicks on Ihumoana (Rayner et al., 2008). Competition and oceanic conditions at foraging grounds have the potential to directly influence the quantity of food at foraging grounds, and therefore the time parents are required to search for sufficient food to sustain both themselves and their chicks (Ballance et al., 2009; Weimerskirch et al., 2001). The greater number of breeding Procellariiformes nesting on the east coast of New Zealand’s North Island could deplete prey availability close to Te Hāwere-a-maki (Gaskin and Rayner, 2013). Lower sea surface temperatures in the oceans surrounding Ihumoana could lead to increases in primary productivity and consequently the quantity of food at foraging grounds (Chiswell, 1994). The possibility also exists that the differences in growth rates between Ihumoana and Te Hāwere-a-maki reflect genetic differences between the colonies (Barbraud et al., 1999).

Chapter Three: Parental Provisioning behaviour in the Grey-Faced Petrel

Patterns of weight loss observed in 26 to 48 day old grey-faced petrel chicks raised on Te Hāwere-a-maki in the 2013 breeding season were similar to those previously recorded for this species and to those of other *Pterodroma* chicks (Bester et al., 2002; Chaurand and Weimerskirch, 1994; Dunn, 2012; Imber, 1976a). Hourly chick weight loss decreased with the time elapsed since the last meal. However, hourly weight loss increased with the weight of the chick immediately preceding its last meal along with the weight of the meal. Chicks that died before fledging generally experienced increased hourly weight losses. As observed in other Procellariiform species, grey-faced petrel chicks appeared to be able to adjust their metabolic rate as a consequence of variable provisioning and meal sizes (Boersma et al., 1980; Schultz and Klomp, 2000). Surviving chicks may have been better able to adjust their metabolic rate as food became limited, enabling their food to sustain them till their next meal.

During October of the 2013 breeding season, grey-faced petrel adults breeding on Te Hāwere-a-maki returned infrequently to provision their chicks. The average duration chicks were required to wait between successive meals was close to double what has been reported elsewhere for this species (Dunn, 2012; Imber, 1976a). These differences could be indicative of geographical or annual variations in foraging conditions but must be interpreted with caution due to the different methods employed by these studies (Schultz and Klomp, 2000).

Additionally the similarity in chick growth rates observed in the 2011 and 2013 breeding seasons suggest that the feeding frequencies experienced by chicks should be more similar.

The duration of a foraging trip was found to decrease with the duration of the previous foraging trip. This suggests that parents were able to take their chick into consideration when making decisions as to the duration of a trip. Though the chick’s age and post-provisioning weight were not found to be important predictors of foraging trip duration, chicks may be conveying information as to their condition and food requirements to their parents in some other way (e.g. begging calls). The weight of a meal delivered to a chick increased with its parent’s pre-provisioning weight and surprisingly decreased with the time elapsed since the parent’s last visit. The size of a meal was found to be almost entirely dependent on the parent and very little on the chick.

During this study, parents undertook trips that fell into two distinct categories: short trips, lasting between two and five days, and long trips, lasting more than eight days. Though this dual foraging strategy has been observed in other Procellariiform species, grey-faced petrel parents did not have a tendency to gain weight during long trips as might be expected (Baduini and Hyrenbach, 2003; Chaurand and Weimerskirch, 1994; Congdon et al., 2005; Weimerskirch, 1998; Weimerskirch et al., 2003). Weight losses corresponding with complete foraging trips longer than 15 days were observed, suggesting that very long trips are energetically inefficient. If grey-faced petrel parents returning to the colony spend their time in flight as opposed to foraging, as do other Procellariiform parents, those returning from very long trips could be expected to use up the reserves gained on their trip (Catard et al., 2000; Magalhães et al., 2008). Such long foraging trips could be a consequence of a multitude of factors that impact parent’s abilities to find sufficient food for themselves and their chicks. These could include distances to the continental shelf and weather conditions en route to foraging grounds as well as competition and oceanic conditions at foraging grounds (CANZ, 1997; Chiswell, 1994; Gaskin and Rayner, 2013; Imber, 1973; Rayner et al., 2012).

Chapter Four: Breeding Success and Population Dynamics in the Grey-Faced Petrel

Estimates of breeding success calculated for the 2011, 2012, 2013, hypothetical good and bad breeding seasons on Te Hāwere-a-maki were within the range previously observed for the grey-faced petrel (Imber et al., 2000; Chapter Two). Though breeding success in the 2011, 2012 and 2013 seasons was similar, the cause of nest failure varied between abandonment coupled with starvation (2011, 2013) and predation (2012). Hatching success was highest for the 2011 breeding season and lowest for the 2013. Comparatively, fledging success was highest for the 2013 breeding season and lowest for the 2011. This contrast is suggested to reflect a disparity in the timing of food becoming sufficiently scarce to lead to breeding failure: after hatching in the 2011 season and before hatching in the 2013 season (Weimerskirch and Lys, 2000). While the La Niña event is expected to have better prepared parents for incubation early in the 2011 season, they are likely to have found it increasingly difficult to find sufficient food for both themselves and their chicks as the season progressed (Weimerskirch, 1992; Weimerskirch and Lys, 2000; Wolff et al., 2012). In contrast, with neutral El Niño conditions early in the 2013 season, parents are likely to have been in comparatively worse condition during incubation and consequently more likely to abandon breeding attempts at this stage (Hatch, 1990). Parents with more experience and greater foraging efficiency are more likely to have successfully hatched chicks and therefore better able to adequately provision them throughout the chick-rearing period (Weimerskirch, 1992). A reinvasion of ship rats late in the 2011 breeding season is suspected to have contributed to peak rat numbers and the high levels of rat predation on young chicks in the 2012 breeding season (Russell, 2013). Despite the implementation of predator control, the high incidence of predation highlights the importance of predator control in preventing declines in breeding success.

Fifty year simulations were carried out using the different estimates calculated for the 2011, 2012, 2013, hypothetical good and bad breeding seasons and random combinations of these. Values for adult survival, fecundity, juvenile survival and maturation were obtained from previous studies of the grey-faced petrel or, in their absence, the great winged petrel (Chastel, 1995; Jones et al., 2011). While populations were shown to be more susceptible to the loss of adults as opposed to chicks, breeding success shows natural annual fluctuations (Chastel et al., 1993; Simons, 1984; Weimerskirch and Jouventin, 1987). Additionally, populations of *Pterodroma* species, including the grey-faced petrel, have been put at serious risk of extinction following decreases in breeding success, which can take years to become apparent at the population level (Carlile et al., 2003; Imber et al., 2000; Rayner et al., 2012). In all simulations the initial population increased in size, however, the rate of growth varied significantly. In the simulation using the value of breeding success corresponding to the hypothetical bad year, the population had barely doubled in size after 50 years. If such low values in breeding success were sustained for several years, the population would be more vulnerable to experiencing negative growth with decreases in breeding success and other demographic parameters (Simons, 1984).

5.3 Conclusions

This research provides new information and proposed causes regarding annual and geographical variations in chick growth, parental provisioning behaviour and annual variations in breeding success for the otherwise well studied species, the grey-faced petrel. There was a disparity in the growth rates of chicks raised on the west coast (Ihumoana) and the east coast (Te Hāwere-a-maki). Chicks on Ihumoana grew significantly faster, fledging approximately a month earlier and in better condition. The extended chick rearing periods and stunted growth observed on Te Hāwere-a-maki during the 2011, 2012 and 2013 breeding seasons alludes to conditions experienced by chicks being relatively typical for this island, contrary to previous suggestions (Dunn, 2012). The low frequency at which Te Hāwere-a-maki chicks, raised during the 2013 breeding season, were fed suggests parents struggled to find sufficient food to provision both themselves and their chicks, who suffered as a result. Growth was observed in all populations in 50 year simulations using different values for breeding success obtained from the 2011, 2012 and 2013 breeding seasons. However, if low values of breeding success were sustained for several years, small populations may be made more susceptible to decline following catastrophic events impacting breeding success or other demographic parameters (e.g. predation at the colony).

The faster chick growth rates observed on Ihumoana in the 2013 breeding season suggests the stunted growth observed on Te Hāwere-a-maki over the 2011, 2012 and 2013 seasons is a likely consequence of its geographical location. This is in opposition to changes in the El Niño-Southern Oscillation (ENSO) suggested by Dunn (2012). This is likely to be the case given the insignificant changes in growth among the three breeding seasons on Te Hāwere-a-maki, despite changes in the ENSO: mild-medium La Niña event in 2011 to neutral conditions in 2012 and 2013. Geographical differences in foraging conditions experienced by parents from both islands should be investigated further. However, the potential for changes in the ENSO to affect breeding success exists. El Niño events are well documented to result in breeding failure among seabirds (Abraham and Sydeman, 2004; Smithers et al., 2003). The opposing extremes of values for hatching and fledging success in the 2011 and 2013 breeding seasons could reflect changes in the ENSO. By employing identical methodologies in future studies concerning chick growth and parental provisioning behaviours, the extent of geographical and annual variations could be determined. This could enable a better understanding of the factors, be they geographical or climate, leading to them. No aspect of the grey-faced petrel's population biology is particularly apparent in promoting its population to increase in size when the majority of other New Zealand *Pterodroma* and Procellariiform populations are doing the opposite. Despite this, it is encouraging that under all scenarios where populations were subjected to different levels of breeding success, populations experienced growth. However, continued monitoring of breeding success in future seasons may provide more insight into factors behind these patterns. Maintaining low levels of predation would be essential in determining subtle changes in breeding success caused by oceanic conditions which could become obscured by a high incidence of predation.

The high incidence of predation in the 2012 breeding season highlights the potential of predator control to prevent breeding failure. Populations grew slowly when subjected to the lowest breeding success, calculated for a hypothetical bad year. If such low levels of breeding success were sustained for several seasons, populations may be more susceptible to decline in the event that predation dramatically increased. An improvement in breeding success by removing predators has been observed for other grey-faced petrel populations which would have otherwise been at risk from extinction (Imber et al., 2000). Predator control early in the breeding season would be a successful management technique for local conservation groups looking to conserve populations of grey-faced petrels or other, similar species.

5.4 Management Recommendations

The results from the studies presented in Chapters Two, Three and Four highlight a number of potential management strategies for conserving the grey-faced petrel and other more vulnerable species into the future:

- Depending on the extent of developmental differences in grey-faced petrel chicks, projects focusing on active restoration of colonies may need to shift focus to the west coast rather than the east. This may improve the chances of a population successfully establishing, without the need for extensive management, particularly if developmental differences are primarily caused by differences in foraging conditions experienced by parents and their abilities to provision their chicks.

- Increasing management at colonies may be required to improve breeding success and give chicks and fledglings a better chance of survival. This may be in the form of increased predator control during incubation and the initial post-hatching period, when vulnerable eggs and young chicks may experience periods alone at sites where grey-faced petrels and introduced predators co-exist.

- Alternatively, increased management may also be in the form of supplementary feeding of chicks. Chicks were able to go long periods without receiving food, in some cases up to 16 days. However, a chick was found dead after only 10 days without a meal. Therefore, it is probably best to provide supplementary feeding when a chick has gone without a meal for between 10 and 16 days. Exactly when in this time frame can be determined by the state of the chick; if the it is lethargic, abnormally light and has an hourly weight loss close to zero, supplementary feeding should be considered sooner. Supplementary feeding may be required in years when ocean productivity is expected to be low and chicks may consequently be more susceptible to dying of starvation. This would not only give chicks a better chance of surviving to fledge but also of surviving to maturity after they fledge. It should be noted that handling of chicks does not appear to effect growth, parental provisioning behaviour or breeding success (Chapter Two; Chapter Three; Chapter Four). Therefore, intervening in this way should not be considered as having negative consequences.

5.5 Future Research Requirements

The results from the studies presented in Chapters Two, Three and Four highlight a number of areas for continued research investigating aspects of the grey-faced petrel’s breeding biology and their population dynamics:

- Additional years of data on grey-faced petrel growth rates and breeding success on both Ihumoana and Te Hāwere-a-maki would allow a better understanding of annual and geographical variations. Such studies could be expanded to include other west and east coast islands to determine the extent of the geographical developmental differences observed in Chapter Two. Incorporating a tracking aspect may provide valuable insight into which factors may be more causal to the differences in growth rates observed between Ihumoana and Te Hāwere-a-maki chicks (K. Bourgeois unpub.).

- Experimental swapping of eggs between Ihumoana and Te Hāwere-a-maki could provide insight into the potential for a genetic basis underpinning the differences in chick growth rates between the islands. Experimental swapping of eggs among Te Hāwere-a-maki parents could allow determination of a genetic or an environmental basis underpinning differences in chick metabolism.

- Longer studies employing consistent methodologies and incorporating a number of colonies that vary in size may allow determination of the geographical and annual flexibility in the foraging strategies employed by grey-faced petrel parents. Such studies should incorporate a tracking aspect which will, at least, enable quantification of distances travelled and times spent in commute versus foraging. This may enable an understanding of foraging decisions made at sea.
- Supplementary feeding experiments may make it possible to determine if adults are able to adjust their foraging decisions based on their chick's condition or if the lengths of foraging trips are constrained by marine conditions. Additionally, recording chick begging calls during provisioning may shed light on the potential of chicks to convey information on their condition to adults, and the ability of adults to adjust their provisioning behaviours accordingly.
- The probability of survival for Te Hāwere-a-maki juveniles in their first year at sea should be determined. The potential of variations in juvenile survival to affect population dynamics should be further investigated. Decreases in juvenile survival, along with low levels of breeding success, are likely to make small grey-faced petrel populations vulnerable to decline. Given the reduced growth rates and sizes at fledging sustained on Te Hāwere-a-maki over the 2011, 2012 and 2013 breeding seasons, juveniles are less likely to survive the post-fledging period and could have reduced probabilities of survival within the first year.

5.4 Closing Remarks

Procellariiformes carry out an important ecological and cultural role throughout New Zealand. Unfortunately due to the decline in many Procellariiform populations, this role is in jeopardy. Though the grey-faced petrel meta-population is generally considered to be increasing, many of its populations are small and at risk of local extinction. It is hoped that by providing a better understanding of unknown aspects of this species' breeding biology, such populations will be able to be more efficiently conserved. It is more feasible to conserve these populations now as opposed to attempting to re-establish them in the future. Additionally, this understanding may help in the development of improved management techniques for more at-risk *Pterodroma* species throughout New Zealand.

New Zealand conservationist and ornithologist, the late Don Merton, is insightful when considering the importance of conservation in New Zealand:

> *They are our national monuments. They are our Tower of London, our Arc de Triomphe, our pyramids. We don't have this ancient architecture that we can be proud of and swoon over in wonder, but we do have something that is far, far older than that. No one else has kiwi, no one else has kakapo. They have been around for millions of years, if not thousands of millions of years. And once they are gone, they are gone forever. It's up to us to make sure they never die out.*
>
> — Don Merton in Griggs (2005)

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