



Chick Provisioning in Grey-Faced Petrel (*Pterodroma gouldi*) under Environmental Stress

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Simple Summary: Grey-faced Petrels breed on islands around the upper North Island of New Zealand and raise one chick per year from September to December. Parents forage at sea and return to the colony intermittently to feed chicks. We monitored the feeding rate of chicks every 12 h for 10 consecutive days in 2011 and 2013 at the colony on Te Hāwera-a-Maki (Goat Island). In both years tropical Pacific Ocean winds bringing warmer surface air temperatures made raising chicks more difficult for parents. We found chicks processed their meals during the day and conserved energy from five days after their last meal, not knowing when their next meal might arrive. Body mass loss after meals did not depend on chick age nor body mass, but heavier chicks were more likely to survive. Measurements of feeding rates of chicks that were not included in our study showed no negative effect of our intensive monitoring on feeding rates of chicks in our study. Chicks being fed on average 100-gram meals every 10 days from each parent is unlikely to sustain them.

Abstract: Grey-faced Petrels (*Pterodroma gouldi*) are colonial burrowing seabirds predominantly nesting on offshore islands of the upper North Island of New Zealand. We studied their chick provisioning on Te Hāwera-a-Maki during two years of unfavourable warmer La Niña conditions in 2011 and 2013. We intensively monitored chicks in each year, weighing chicks every 12 h for 10 consecutive days to estimate meal sizes following chick provisioning and to estimate 12-hourly body mass loss as a function of time since last feeding. We found a quadratic relationship of body mass loss with time since last feeding, with rapid digestion of meals following provisioning followed by a period of fasting from five days post feeding as chicks waited an unknown and variable amount of time until their next meal. The rate of body mass loss did not depend on chick age nor body mass, and did not differ between years, but heavier chicks included in our study were more likely to successfully fledge, suggesting a legacy of adult provisioning prior to our study commencing. Our regular handling of chicks for monitoring has no discernible impact on parent provisioning compared to a set of control chicks. The mean estimates of 100-gram meal sizes and 10-day foraging trip durations are likely to be below the break-even point for this species.

Keywords: climate; foraging; petrel; provisioning; reproduction; seabird; southern oscillation



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1. Introduction

Life history theory emphasises the trade-off between survival and reproduction [1], with longer-lived species favouring survival over reproduction [2]. Longer-lived species tend to raise fewer offspring simultaneously, investing more resources over a longer rearing period into those fewer offspring [3]. These offspring are thus more sensitive to variation in provisioning rates over time, such as in relation to environmental conditions [4]. Although adults can buffer the impact of environmental variation to some extent, annual changes in resource availability impact parental coordination [5] and provisioning rates [6]. In extreme cases, adults may abandon offspring to prioritise their own survival [7].

Procellariids lay only one egg and raise one offspring each breeding season, and so resource allocation to this chick depends only on the ability of both parents to successfully provision the chick traded-off against their own fitness, and not against other competing offspring [8]. Adults typically alternate short and long foraging trips prioritising the chick and their own fitness, respectively [9], but just after egg hatching breeders seem to employ a unimodal breeding strategy and avoid a dual trip duration [10]. Seabird chick provisioning rates are highly dependent on adult foraging success at sea, which depends on adult health and endurance, but is also constrained by prevailing environmental conditions [11] and prey quality [12]. However, although more experienced seabirds may be better foragers, feeding rate may not depend on experience [13]. Adults in pairs may coordinate their trips to minimise the interval between feeds for chicks; however, variation in the interval may not impact chick growth itself [14].

The Grey-faced Petrel (*Pterodroma gouldi*) is a medium-sized winter breeding Procellariid classified as 'least concern' [15], with an estimated 250,000 pairs breeding in the upper North Island of New Zealand [16,17]. Most colonies are found on predator-free offshore islands protected from the threat of introduced mammalian predators, especially mustelids (*Mustela* spp.) and rats (*Rattus* spp.). However, La Niña events of the El Niño Southern Oscillation reduce chick growth rates and fledgling success on these islands [18]. La Niña conditions bring more north-easterly winds, and warmer seas occur towards northern New Zealand [19]. How Grey-faced Petrel chicks physiologically cope with feeding stress during these La Niña conditions remains unknown. We therefore intensively investigated chick provisioning rates of Grey-faced Petrels for 10 days each during two different years of La Niña conditions. As found in other Procellariids [20], we hypothesised that as the time since the last feed increased, the rate of body mass loss would decline, and that this would constitute an adaptive strategy for chicks to cope with unknown variable intervals between feedings.

2. Materials and Methods

2.1. Study Site

We monitored the chick provisioning of Grey-faced Petrels in 2011 and 2013 on Te Hāwera-a-Maki, a 9.3 ha island lying 50 m offshore from the University of Auckland Leigh marine laboratory in the Cape Rodney-Okakari Point (Goat Island) Marine Reserve (Figure 1). The island is covered in native broadleaf and podocarp forest. Occurring along the coastal margins is a single, widespread Grey-faced Petrel colony that supports a breeding population of approximately 100 pairs. Most burrows can be found along the southern landward coast. The average Southern Oscillation Index over the chick-rearing period from August to January was +1.15 in 2011 and +0.29 in 2013 indicating strong and weak La Niña years, respectively (compared to favourable El Niño years of −0.15 in 2012, −0.91 in 2014 and −1.58 in 2015) [18].

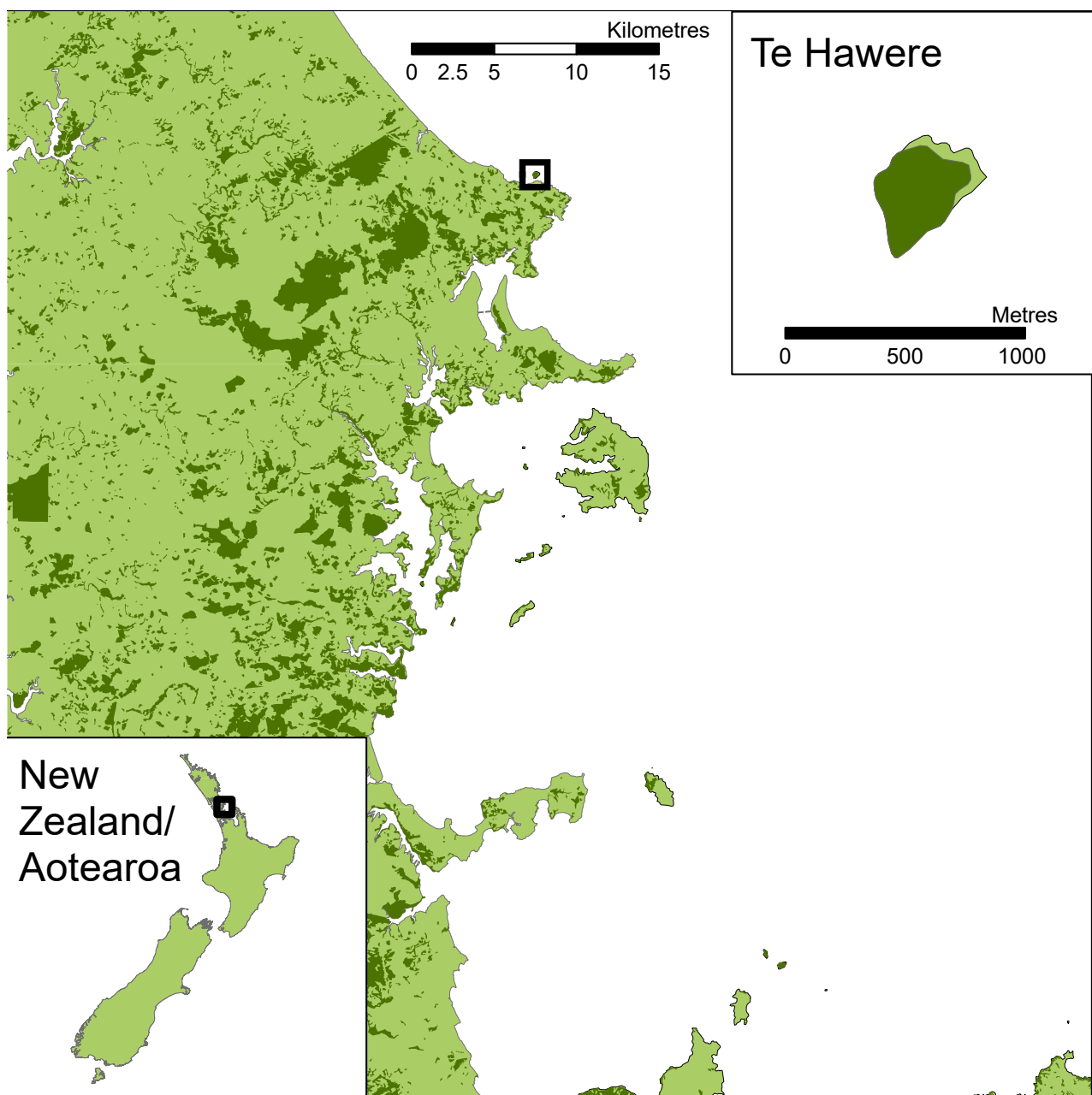


Figure 1. North Auckland, New Zealand, with study island inset. Dark green indicates forest, light green indicates other land uses.

2.2. Field Methods

Chick provisioning was monitored for 10 days from 10 to 20 November in 2011 ($n = 13$ burrows) and 3 to 13 October in 2013 ($n = 14$ burrows). We indirectly measured meal size by weighing chicks before and after every night when adults would return to feed them. This meant we did not interfere directly with adults feeding chicks. All chicks were assumed to be being fed by two parents, and from our data no instance of a chick being fed by both parents on the same night took place. Chicks were weighed approximately every 12 h (1800 and 0600, range 10–15 h) in the same order each day to estimate body mass change. This was done in a dark cotton, breathable bag using a 1000 g Pesola spring scale to the nearest 5 g (2011) or a 600 g Pesola spring scale to the nearest 1 g (2013), although repeatability had a margin-of-error of 10 g. The mass of the bag was subtracted from this measurement to give the body mass of the chick. No chicks regurgitated any food while being handled during this study. The ages of the chicks were ascertained from observations

of hatching and fledging dates. Adult colony attendance was recorded using stick gates positioned across the burrow entrance that are dislodged when adult birds enter burrows. To assess any effects of repeated handling of the chick on the provisioning behaviour of adults, in 2013 ‘control’ burrows ($n = 11$ burrows) were also monitored for time between adult visits.

2.3. Statistical Methods

Assuming an equal and independent feeding behaviour between adults in pairs, the frequency of feeding by each adult, P , can be estimated using the methodology described by Ricklefs [20]. Body mass gains (defined as greater than 10 g) indicating a chick having been fed the previous night were used to estimate the probability that the chick was not fed by either parent on any given night ($Z = (1 - P)^2$), where P = the probability that an adult feeds the chick. P is then found by rearranging and solving $P = 1 - \sqrt{Z}$. Probability of an adult feeding a chick was compared between years using a two-tailed t -test assuming unequal variances. The mean waiting time (for a chick to be fed by one parent) is then found from the geometric distribution as the inverse of P and can be interpreted as a mean foraging duration. This method relies on identifying nights where chicks were fed by both parents, but no instances of this were recorded in our study. Body mass gain following feeding was compared between years using a two-tailed t -test assuming unequal variances.

The twelve-hourly body mass loss (i.e., excluding nights where chicks were fed) was regressed against chick age, days since last feeding, day or night, chick outcome (fledged or died) and year using a linear mixed effect model. Chick identity was included as a random factor to control for repeated observations of the same individual. Because days since last feeding can only be estimated following a known feeding event during the study period (i.e., is conditional upon knowing the last feeding, otherwise left censored), we can only analyse data with known values (two-thirds of our data set). Body mass of chicks in our study was compared against fledging outcome, controlling for year, using an analysis of variance. Time between visits was compared between years (2011 and 2013) and study and control burrows (2013 only) using a two-tailed t -test assuming unequal variances. All analyses were conducted in R 4.1.0 [21] with $\alpha = 0.05$ for significance and we used package nlme for mixed models [22].

3. Results

The Grey-faced Petrel chicks at the start of our study ranged in age from 67 to 84 days in 2011 ($n = 13$) and 26 to 48 days in 2013 ($n = 14$), both ranges falling within the middle of chick rearing (which is up to 125 days). The smallest chick in 2011 died of starvation during our study, presumably due to a legacy of malnourishment, and the fledging rate from our study chicks at the end of the breeding season was 64% in both years. Chicks received between one to four feeds over the course of our study (Figure 1). The mean nightly probability of an adult returning to feed each chick was estimated at 0.10 (range: 0.05 to 0.23, $n = 27$), with no significant difference between years ($p = 0.56$). The mean waiting time (inverse of the probability) to be fed by one parent is thus 10 days (range: 4.4 to 19.5), giving an indication of the mean length of a Grey-faced Petrel foraging trip during years of La Niña conditions.

The mean body mass gain of Grey-faced Petrel chicks on mornings following feeding was estimated at 84.5 g (range: 15 to 150, $n = 47$), with no significant difference between years ($p = 0.92$). However, this does not account for body mass loss on the same night of the feeding immediately following it, which we estimated from body mass loss on the subsequent night following feeding as 14.5 g. Together, this suggests an average meal size of just under 100 g. Twelve-hourly body mass loss (excluding body mass gains after feeding events) ranged from 54 to -8 g ($n = 406$, two outliers removed), and days since last feed ranged as high as 8.5 days (Figure 2).

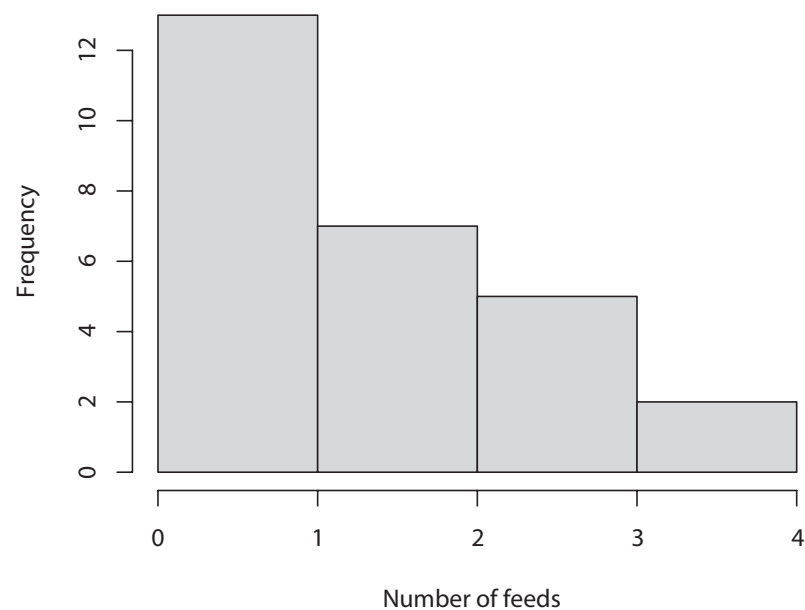


Figure 2. Number of feeds received over 10 days by Grey-faced Petrel chicks on Te Hāwera-a-Maki during La Niña conditions in 2011 and 2013.

The twelve-hourly body mass loss following feeding was significantly affected by time since last feeding (a quadratic relationship; Figure 3) and the time of the body mass loss (night or day), but not age nor body mass of chicks, nor did it differ significantly between years. The rate of body mass loss during our study did not relate to whether chicks successfully fledged or not, but chicks which successfully fledged entered our study with significantly higher body masses ($p < 0.001$), suggesting a historical impact of chick provisioning. There was no significant difference in the time between visits by a breeder between years nor between chicks in our study ($n = 14$) and control ($n = 11$) burrows in 2013.

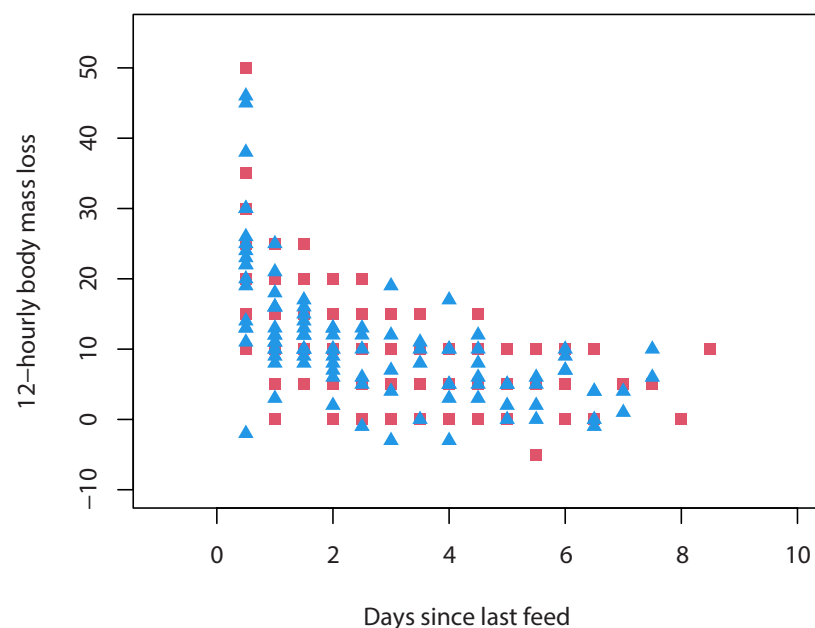


Figure 3. Twelve-hourly body mass loss (excluding measurements after feeding events) versus days since last feed for Grey-faced Petrel chicks on Te Hāwera-a-Maki during La Niña conditions in 2011 (red squares) and 2013 (blue triangles).

4. Discussion

We found Grey-faced Petrel chicks moderated their digestion of food in response to time since the last feeding. Most food is processed in the first few days following a feed before chicks apparently enter a period of fasting around day five where body mass loss stops (within the repeatability margin-of-error of our measurement methods). This is typical for procellariiform chicks that experience periods of extended fasting and often enter a state of torpor after several days without food during which their body temperature drops [23]. This physiological adaptation is likely a response to unknown and variable intervals between feeds by parents. The ability of chicks to be able to adjust metabolic rates has also been observed in tropicbirds [24–26]. We also found chicks digested food, hence losing body mass, more often during daylight hours, rather than nocturnal hours when they were waiting for feeds from returning adults. This has also been found in studies of other Procellariids [20].

We found no significant difference in rates of body mass loss between years, noting that both years were periods of known environmental stress for Grey-faced Petrel chick rearing due to La Niña conditions [18]. Although we do not have comparative chick provisioning data during El Niño conditions, chicks are known to grow and survive better in such years [18], presumably due to better provisioning in some way (i.e., any of provisioning rate, meal size or meal quality). Although the rate of body mass loss did not differ between chicks that subsequently went on to successfully fledge or not, the body mass of chicks entering our study differed significantly between chicks that subsequently went on to successfully fledge or not. Chicks that went on to successfully fledge entered our study larger already, suggesting a legacy of adult provisioning. This body mass difference between chicks which successfully fledged or not was more marked in 2011, when our study occurred later in the breeding season, and the different periods of the breeding season monitored is a limitation of our study. Our short study period of 10 days in both years was unable to determine long-term trends in chick provisioning across the entire chick-rearing period where accumulated differences in chick provisioning by adults would lead to substantial body mass gain differences among chicks. However, fortnightly measurements of chick growth across the entire chick-rearing period in the same years have shown such substantial differences [18].

We estimated that adult foraging trips were on average 10 days, though ranging from 5 to 20 days (rounding up), over the course of the study. Adult seabirds provisioning offspring respond to variations in prey availability by changing foraging trip duration and/or range [27–30], switching to more predictable but less energetic prey [31–33] or increasing chick provisioning frequency in order to compensate for smaller, less available prey [34,35]. The high variability in foraging trip duration likely reflects the bimodal distribution of short and long foraging trips by parents [36], where we only observed one of either trip for each parent over the short course of our study. We estimated average meal size to be about 100 g, though also ranging widely from 15 to 150 g, over the course of the study. This suggests substantial variability in the success of individual foraging trips, although from our study we cannot determine if foraging trip duration or type and success are correlated. However, adult seabirds can potentially coordinate short and long foraging trips [37] and utilise them as a response to poor food quality [38]. Meal size and feeding frequency can also change over the course of chick rearing [39], but this was not observed in meal sizes in our study, which in both years took place in the middle of chick rearing.

In both years, 64% of our study chicks fledged (fledging young per chick hatched successfully), which is low for Procellariids and reflects the environmental stress from La Niña. Furthermore, this fledging estimate is positively biased because our study commenced well into chick rearing in both years. The actual fledging rate was far lower in both years [18]. However, it was reassuring in our study from the use of control burrows that the repeated regular handling of chicks did not affect the rate of adults provisioning the chicks. We have also previously shown that this level of intensive monitoring also does not affect chick growth [18]. Establishing this was critical in our study and we urge other seabird

scientists to routinely assess the impacts of their studies on their target species [40]. Our study demonstrates that Grey-faced Petrel chicks are sensitive to time since their last feed, including both an adaptive component evolved to respond to unknown variable intervals between feedings, but also a vulnerability to foraging trip duration by adults. Given our study took place during environmentally stressful years for Grey-faced Petrel, an average meal size of 100 g coupled with an average foraging trip duration of 10 days is likely to be below the break-even point for this species

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Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are openly available in FigShare at <http://doi.org/10.17608/k6.auckland.20306406>.

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Conflicts of Interest: The authors declare no conflict of interest.

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