



Population status, breeding success and ecology of the Henderson Petrel after a failed rat eradication on Henderson Island

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ABSTRACT

One of the most important breeding colonies for gadfly petrels in the sub-tropics, Henderson Island in the South Pacific Ocean, was subjected to a rat eradication attempt in 2011, but the eradication failed. Here we examine whether the current population status of the endemic Henderson Petrel *Pterodroma atrata* is consistent with an ongoing population decline. We collected basic biological information on Henderson Petrels in 2015 to compare estimates of breeding population size and nest survival to data from 1991. We found that the extrapolated population size of 19 987 pairs was marginally higher than the comparable estimate of 18 668 in 1991. We also estimated the nest survival of 25 nests to be 28.5%, and most nest failures occurred within 7 days of hatching when chicks were killed by rats ($n = 3$) or a crab ($n = 1$). Breeding success was higher than in 1991, and possibly sufficient for a stable population. Although differences in survey effort render it difficult to directly compare estimates from 1991 and 2015, there is currently no evidence that the conservation status of the Henderson Petrel has deteriorated since it was listed as 'Endangered' by the IUCN.

KEYWORDS

Pterodroma; *Rattus exulans*; growth rate; breeding success; island restoration

Introduction

Gadfly petrels (*Pterodroma* spp.) are a particularly poorly known and threatened group of seabirds (Brooke 2004; Croxall *et al.* 2012; Sagar *et al.* 2015). One of the most important breeding colonies for gadfly petrels in the sub-tropics and tropics is Henderson Island in the South Pacific Ocean, which hosts large populations of Kermadec (*Pterodroma neglecta*), Murphy's (*P. ultima*), Herald (*P. heraldica*), and Henderson Petrel (*P. atrata*) (Brooke 1995a, 1995b). Although the island is currently uninhabited by humans, non-native Pacific rats (*Rattus exulans*) were introduced to Henderson by Polynesian settlers several centuries ago (Weisler 1995). Pacific rats can prey on seabirds and their offspring (Rayner *et al.* 2007; Jones *et al.* 2008; Towns 2009), and current evidence from Henderson Island suggests that they affect the seabird species breeding on the island, in particular the endemic Henderson Petrel (Brooke 1995a; Brooke *et al.* 2010).

The Henderson Petrel, formerly considered a dark morph of the Herald Petrel, was formally proposed as a separate species in 1996 on the basis of genetic,

behavioural and plumage differences (Brooke and Rowe 1996). Although very little is known about the species' breeding biology and population size, surveys in 1991–1992 (Brooke 1995a) combined with additional surveys in 2003 and a population model indicated that Henderson Petrels were in gradual decline owing to low breeding success due to rat predation (Brooke *et al.* 2010), and the species is currently classified as 'Endangered' by the International Union for the Conservation of Nature (IUCN). In 2011, a rat eradication was attempted on Henderson Island, but the operation failed to kill all rats on the island and rat densities had returned to pre-eradication levels by 2015 (Churchyard *et al.* 2013; Amos *et al.* 2016). Besides invasive rats, Henderson Island also harbours populations of native land crabs (*Coenobita* spp.), which have so far not been noted to interact with seabirds (Brooke 1995a; Cuthbert *et al.* 2012).

Here we examine whether the current population status of Henderson Petrels confirms previous extrapolations of an ongoing population decline. We also collected basic biological information on Henderson Petrels in 2015 to compare estimates of breeding

population size, nesting success, the nature and timing of nest predation, and chick growth rates to data from the only previous study on the species in 1991. In addition, we provide the first description of the length of incubation shifts, the chick feeding frequency, duration of chick feeding visits, and anecdotal information on the foraging range of Henderson Petrels. This study therefore contributes to an improved understanding of the natural history of an endangered species that will be valuable to prioritise conservation management decisions.

Methods

Study area

Henderson Island (24° 22' S, 128° 20' W) is an uninhabited raised limestone island in the Pitcairn group, South Pacific. The island is roughly 5 × 9 km in size, and the majority is a flat coral-limestone plateau (approximately 25 m a.s.l.) with stunted but very dense forest vegetation. A prominent forest species is the possibly non-native *Pandanus tectorius*, an emergent tree with an abundant fruit crop and robust leaves that form a dense, multi-layered leaf litter under trees (Waldren *et al.* 1995). Some beach, cliff, and coastal vegetation exists, but Henderson Petrels nest exclusively on the raised plateau in the interior of the island (Brooke 1995a).

Nest monitoring

From May to November 2015 we established a trail network from the northern coast and penetrating up to 2 km into the interior plateau of the island (Figure 1). This trail network consisted of 8981 m of narrow trails

usually <1 m wide where vegetation was cleared sufficiently for easy human passage. We walked along this trail network almost daily to conduct rodent and land-bird studies, and recorded and marked every Henderson Petrel nest that was encountered. Encounters of Henderson Petrels were opportunistic due to the dense nature of the vegetation, thus nests were found at various stages of incubation or chick rearing. Once found, nests were marked with flagging tape and a handheld GPS device, and known nests were monitored at least every 4 days to assess nest success.

To assess whether nest failure was associated with certain characteristics of nest placement, we recorded nine environmental variables at nest sites (Table 1): whether the nest was in *Pandanus* leaf litter (yes/no) because this dense leaf litter can form a structure similar to subterranean burrows; the distance to the nearest *Pandanus* tree, whether there was a fruiting *Pandanus* tree, and whether there was fresh fruit available within 5 m of the nest cup because *Pandanus* fruits could conceivably attract rats to the vicinity of nests or distract rats and therefore either increase or decrease nest predation. We also recorded the structural cover of the nest cup by estimating the overhead cover (in

Table 1. Structural variables measured at 25 Henderson Petrel nests in July 2015 on Henderson Island to examine whether breeding success was related to certain nest characteristics

| Nest variable | Mean | Min | Max |
|------------------------------------------------------------|------|------|-------|
| Distance to nearest path (m) | 3.7 | 0.5 | 14.2 |
| Overhead nest cover (%) | 68.1 | 0.0 | 100.0 |
| Height of overhead nest cover (cm) | 38.9 | 22.0 | 80.0 |
| Nest in <i>Pandanus</i> leaf litter (1/0) | 0.4 | 0.0 | 1.0 |
| Presence of fresh <i>Pandanus</i> fruit within 5 m (1/0) | 0.4 | 0.0 | 1.0 |
| Presence of fruiting <i>Pandanus</i> tree within 5 m (1/0) | 0.7 | 0.0 | 1.0 |
| Distance to nearest <i>Pandanus</i> tree (m) | 3.5 | 0.0 | 15.0 |
| Lateral cover of the nest cup (0–8) | 4.0 | 0.0 | 7.0 |
| Canopy cover of forest above the nest (%) | 50.7 | 0.0 | 90.0 |

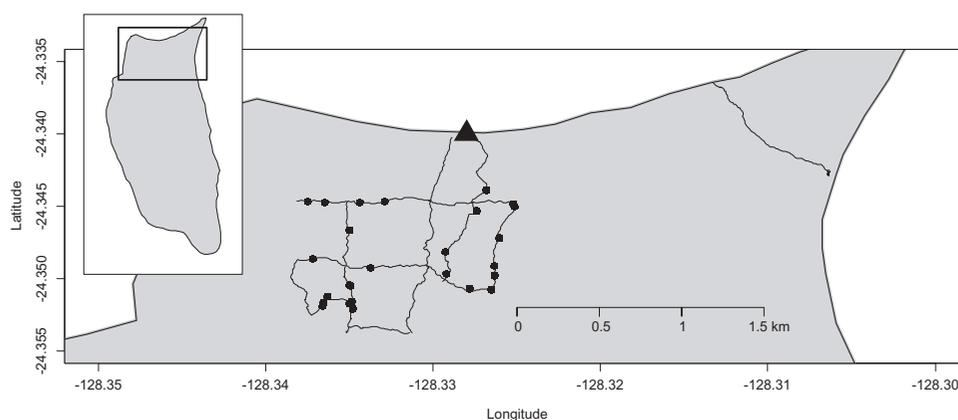


Figure 1. Map outline of the northern part of Henderson Island, showing the paths searched for Henderson Petrel nests in 2015 (thin black lines), and the location of all nests encountered (black dots). The large black triangle indicates the location of the research camp.

%), the lateral cover (in 1/8ths, by judging whether the nest was laterally visible from all cardinal and sub-cardinal directions), and we measured the distance between the nest cup and overhead cover (in cm) using a tape measure.

Analysis of population size and nest survival

Population size was extrapolated in the same way as in 1991 (Brooke 1995a) to provide comparable estimates. We first calculated the length of the trail network from GPS tracks, and calculated the area effectively searched for petrel nests assuming that we would have found all nests ≤ 3 m on either side of the path (Brooke 1995a). We then divided the total number of nests found by the effective search area (53.88 ha), and multiplied this estimate of nest density by the total area of Henderson Island (4308 ha). Because Brooke (1995a) used an incorrect island area (3700 ha), we also corrected the previous estimate to adjust it to the actual size of the island.

To estimate nest survival we had to account for the fact that nests had been encountered at different stages of development, and that nests that had failed during incubation were less likely to be detected. We therefore estimated daily nest failure probabilities using a Mayfield logistic regression (Hazler 2004), which accounts for varying time intervals during which a nest was monitored and makes no assumptions about the day of nest failure between two subsequent visits.

To test whether any of the measured structural nest variables could explain variation in breeding success, we constructed six competing Mayfield logistic regression models and evaluated support for each model using Akaike's information criterion corrected for small sample size AIC_c (Burnham and Anderson 2002; Galipaud *et al.* 2014). The six models considered that breeding success might vary with (1) the distance to the nearest path (observer disturbance; Carey 2009); (2) the presence of *Pandanus* leaf litter forming an enclosed cavity; (3) the distance to the nearest *Pandanus* tree and the presence of fresh fruit as rat attractant or distraction; (4) the lateral cover of the nest limiting access by rats; (5) the height of the overhead cover effectively determining the openness of the nest cup; (6) none of the measured variables (constant breeding success). We fitted all models in R 3.1.2 (R Development Core Team 2014) and present the parameter estimates (± 1 standard error) and estimates of daily and total nest survival from the most parsimonious model. To estimate total nest survival, which reflects annual productivity of the population, we extrapolated daily nest survival probabilities over 136 days of combined incubation (45 days; Hutton and

Priddel 2002) and chick rearing (91 days; Brooke 1995a).

Assessment of incubation shift length and frequency of chick feeding

At nests that were found during the incubation stage we marked one of the adult birds with a non-toxic golden nail polish on the back of the head to allow temporary identification of the two members of a pair. We then checked the identity of the incubating bird every day until the nest hatched to determine the length of incubation shifts. Incubating adult birds were not handled to reduce disturbance and we recorded no nest abandonment as a result of monitoring.

At five nests that hatched we installed infrared motion sensor video cameras (Ltl Acorn™ 5310A) 50 cm from the nest to record frequency of feeding and to document predation events. The camera was set to record 1 min videos for every movement detected in the nest, and batteries and memory cards were changed daily. We maintained video surveillance until the chick had been depredated or was 25 days old, and reviewed video material to quantify the frequency and duration of adult feeding events. We did not monitor older chicks, as feeding frequency was low, and chick movements too numerous, resulting in rapid depletion of camera batteries and unreliable information about chick feeding frequency.

Measurement of chick growth

To examine whether chick growth rates of Henderson Petrels had changed since 1991 (Brooke 1995a), possibly reflecting changes in marine food availability, we measured chick body mass on a daily basis if no adult bird was attending the chick. Chicks were suspended in a sock from a spring balance (Pesola™) accurate to the nearest 1 g. Once a week we measured culmen length and the length of head and bill using digital callipers accurate to 0.1 mm. We also measured straightened wing length using a metal ruler accurate to the nearest 1 mm. Such measurements have not adversely affected the growth rates of other *Pterodroma* chicks (O'Dwyer *et al.* 2006). We estimated chick growth rates using logistic growth curves with the formula

$$y = \frac{A}{(1 + m \times e^{-k \times (\text{age} - i)})^{1/m}},$$

where A , k , i and m are the asymptote, rate parameter, inflection point and shape parameter, respectively, of a

Richards growth curve, and y is the response variable (wing length, body mass, culmen length, or head and bill length). We estimated parameters for the growth curves in the R package 'FlexParamCurve' (Oswald *et al.* 2012) in R 3.1.2 (R Development Core Team 2014). The field measurement methods of chick sizes were identical to Brooke (1995a), but more frequent. Our estimates of growth rates were based on quantitative regression methods and thus differed from Brooke (1995a), who fitted growth curves visually to a scatterplot.

GPS tracking of adult foraging trip

To describe foraging movements of Henderson Petrels, we captured three adult birds during early incubation (determined by egg flotation). We caught birds by hand on the nest and attached a GPS logger (nanoFix-GEO, PathTrack, UK) to the base of four central tail feathers using Tesa tape. GPS loggers were programmed to provide a location fix every 40 min. The weight of the logger with the tape attachment was ~3 g (~1.5% of body mass), and therefore below the threshold associated with adverse impacts (Phillips *et al.* 2003; Barron *et al.* 2010). All birds were handled for <10 min and returned to their nest upon release.

Results

Population size

We found a total of 25 Henderson Petrel nests along the 8.9 km trail network over a 6 month period from late May to late November 2015. No petrel nests were found along five trail sections with a total length of 3.3 km, but petrel nests were broadly dispersed (Figure 1). In addition, we found five large chicks that were several weeks old and proceeded to fledge, but we did not include those in our estimates of nest survival and density because they were found after they had likely dispersed from their original nest location. Assuming that our detection rate was similar to Brooke (1995a) within the effectively searched area of 53.88 ha, the density of Henderson Petrel nests in 2015 was 4.64 nests/ha, and therefore slightly higher than the 4.33 nests/ha estimated in 1991 (Brooke 1995a). Extrapolated across the 4308 ha of the island, the estimated population size in 2015 was 19 987 pairs; the corrected estimate for 1991 was 18 668 pairs.

Breeding biology

During incubation, we marked one adult partner on 12 nests and recorded the time interval of eight complete incubation shifts. The mean incubation shift length was

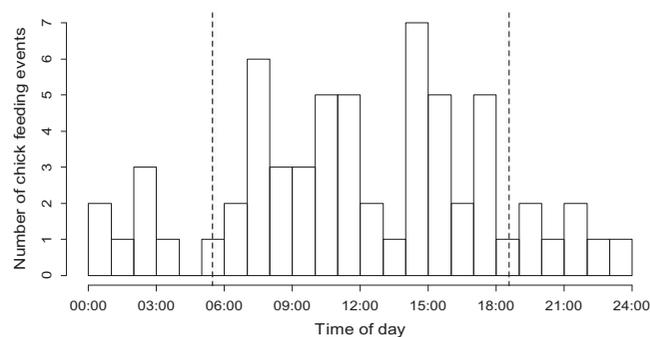


Figure 2. Daily distribution of Henderson Petrel chick feeding events observed with motion sensor video cameras installed at three nests in July 2015. Dashed lines indicate beginning and end of daylight.

11.3 days (SD: 5.3; range 4–22 days, $n = 8$), and these incubation shifts ended on average 7.3 days (SD: 4.2; range 2–14 days, $n = 7$) before the respective nests hatched.

Around the time of hatching or shortly thereafter both partners united at the nest and fed the freshly hatched chick. Within 24–48 h both parents departed from the nest and left the young chick alone and exposed in the nest cup. During the first 3 weeks of age, one parent returned on average every 15.8 h (SD: 15.0; range 0.1–67.9 h, $n = 59$) to feed the chick. Chick feeding bouts lasted on average 9.4 min (SD: 6.0; range 1–25 min, $n = 40$). Only 24% of chick feeding events occurred during darkness (between 1830h and 0530h, UTC-8), while the remaining feeding events were evenly spread throughout the day (Figure 2).

Breeding success and causes of nest failure

Of the 25 nests found, 21 hatched chicks (84%), and 10 (40%) of these chicks either fledged or were still alive in an advanced stage of development (large and mostly feathered) by the time the monitoring ended. The 10 chicks in an advanced stage of development were considered as fledged in our analysis, and the remaining 11 were depredated. The mean time between hatch and predation was 6 days (SD: ± 5.2); nine chicks (82%) were depredated within 7 days of hatching, and two survived to 12 and 19 days of age, respectively. Video cameras near the nest provided evidence that rats killed small chicks ($n = 3$), in one case without consuming the chick. We also found one chick being killed and consumed by a large crab (*Coenobita spinosus*).

Henderson Petrel nests varied from hidden under dense *Pandanus* leaf litter that formed a cavity to fairly open nest cups under overhanging branches or trunks with little lateral or overhead cover, but most nests were sheltered by some overhead and lateral vegetation

Table 2. Model selection table evaluating the effect of different biological hypotheses on nest failure probability of Henderson Petrels on Henderson Island in 2015. See text for description of models. k = number of estimable parameters, AIC_c = Akaike's information criterion, ΔAIC_c = difference in AIC_c units to the most parsimonious model, ωAIC_c = relative weight of evidence for each model

| Model | k | AIC_c | ΔAIC_c | ωAIC_c | Deviance |
|------------------------------------------------|-----|---------|----------------|----------------|----------|
| Height of overhead nest cover | 2 | 68.50 | 0.00 | 0.63 | -31.98 |
| Null | 1 | 71.14 | 2.65 | 0.17 | -34.48 |
| Distance to path | 2 | 72.80 | 4.30 | 0.07 | -34.13 |
| Leaf litter | 2 | 73.02 | 4.52 | 0.07 | -34.24 |
| Lateral cover | 2 | 73.46 | 4.96 | 0.05 | -34.46 |
| Distance to <i>Pandanus</i> and fruit presence | 3 | 75.95 | 7.45 | 0.02 | -34.40 |

(Table 1). Accounting for discovery error and the different exposure time of nests, the model that best explained variation in nest failure probability included the height of the nest cover (Table 2), and indicated that nests were less likely to fail if cover was higher above the nest ($\beta = -0.07 \pm 0.03$ SE, $p = 0.038$). Based on this model we estimated daily nest survival probability as 0.988 (95% CI: 0.979–0.997) and overall nest survival probability as 0.285 (0.142–0.673).

Chick growth rates and adult body size

We measured 23 Henderson Petrel chicks for up to 90 days after hatching. Structural variables relating to skeletal growth such as culmen length, head and bill length, and body mass appeared to reach an asymptote

after about 50 days, while wing length started to increase strongly after about 35 days when primary feathers started to grow (Figure 3; Table 3). Maximum body mass of 510 g was reached after 40–50 days, and for some chicks body mass declined gradually with increasing age and the estimated asymptote of body mass was 373 g (Table 3); however, body mass showed very large daily fluctuation depending on when a chick had last been fed. The maximum daily increase in body mass was recorded when chicks were between 10 and 20 days old, during which period some chicks increased mass by up to 131% per day (increase of up to 155 g in 1 day). Mean daily growth rates across

Table 3. Parameter estimates for logistic growth curves of four body measurements of Henderson Petrel chicks measured between age 0 and 90 days on Henderson Island in 2015

| Variable | Parameter | Estimate | SE | t | p |
|---------------|------------|----------|------|-------|-------|
| Wing | Asymptote | 276.4 | 21.5 | 12.8 | 0.000 |
| | m | 1.8 | 0.9 | 2.0 | 0.052 |
| | k | 0.1 | 0.0 | 2.8 | 0.005 |
| Culmen | Inflection | 56.0 | 2.5 | 22.5 | 0.000 |
| | Asymptote | 27.1 | 0.2 | 165.6 | 0.000 |
| | m | 11.7 | 5.5 | 2.1 | 0.034 |
| Head and bill | k | 0.1 | 0.0 | 2.9 | 0.004 |
| | Inflection | 20.8 | 6.2 | 3.4 | 0.001 |
| | Asymptote | 69.8 | 0.5 | 143.4 | 0.000 |
| Body mass | m | 5.2 | 2.2 | 2.3 | 0.023 |
| | k | 0.1 | 0.0 | 4.6 | 0.000 |
| | Inflection | 10.1 | 6.3 | 1.6 | 0.107 |
| | Asymptote | 373.4 | 6.8 | 54.6 | 0.000 |
| | m | 3.9 | 2.1 | 1.8 | 0.069 |
| | k | 0.1 | 0.1 | 2.6 | 0.009 |
| | Inflection | 27.1 | 4.4 | 6.2 | 0.000 |

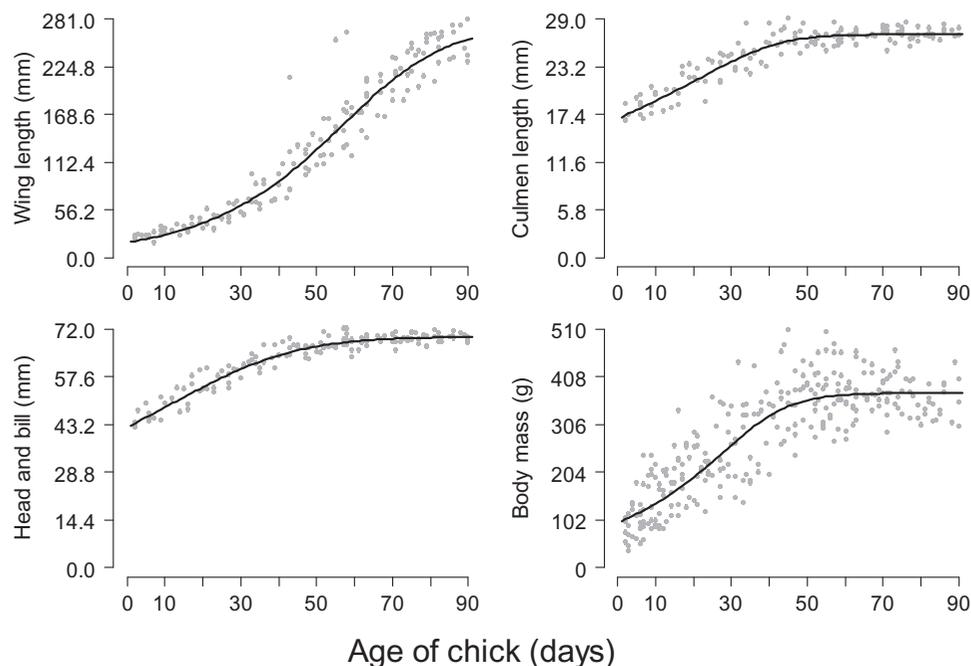


Figure 3. Growth rates of Henderson Petrel chicks from hatch to age of 90 days, after which fledging may occur (Brooke 1995a). Lines are based on logistic growth curves (see Table 3 for parameter estimates).

the chick rearing period were 3.4% of body mass (increase of 3.3 g/day assuming linear growth; for logistic growth curve parameters see Table 3).

Three adult birds were measured while being captured for logger deployment. Their wing lengths were 273, 266, and 274 mm, and the body masses of the first two birds were 326 and 350 g, respectively. Culmen length was 29.3 and 29.8 mm for two birds, and head and bill length was 72.0 mm for one bird.

Foraging range

We deployed three GPS loggers onto birds incubating an egg; however, in two of these birds logger batteries were depleted before the bird departed, and no data were retrieved. The only bird for which a foraging track could be retrieved travelled for 23.3 days, but the return portion of the trip was truncated due to battery depletion. During the 14 days the bird was tracked at sea it covered at least 3202 km in a northerly direction from Henderson Island, and travelled with an overall average speed of 9.4 km/h. The bird reached a maximum distance from its nest of 1637 km, and at the time of battery failure was still 1497 km from its nest, suggesting that the total trip distance was at least 4700 km.

Extrapolating the measured travel speed of 9.4 km/h to the incubation shift durations of adult birds marked on their nests suggests that Henderson Petrels travel on average 2565 km (range 905–4978 km, $n = 8$) during their incubation breaks.

Discussion

Prior to Polynesian settlement, Henderson Petrel populations were estimated to be much larger than today before predation by humans and introduced rats led to large population declines (Weisler 1995). Tens of thousands of birds were harvested for food every year before Polynesian habitation ceased, and Henderson Petrel populations in the pre-human past may have been as large as hundreds of thousands or even millions (Brooke 1995a). We extrapolated the population size on Henderson Island, the only known breeding site for this species, as 19 987 pairs in 2015, which is marginally higher than the corrected population estimate of 18 668 pairs in 1991, but both extrapolations are based on the crude assumption that nesting density is uniform across 4308 ha of the island and therefore surrounded by large uncertainty. Nonetheless, if the predicted population decline of 0.82% per year (Brooke *et al.* 2010) had persisted for the 24 years between 1991 and 2015, the Henderson Petrel

population in 2015 would have been around 13 158 pairs, corresponding to a density of 3.55 nests/ha. Although this ~18% decline of the population may have been very difficult to detect given the small sample sizes and opportunistic sampling strategy, our data appear to be inconsistent with an ongoing population decline of Henderson Petrels (Brooke *et al.* 2010).

Substantial differences in spatial and temporal search effort render direct comparisons between the population estimates in 1991 and 2015 complicated. In 2015, the network of regularly visited trails was longer, but was confined to an area within 2 km of the coast, whereas the 1991 trail network led across the interior of the island where the density of nesting petrels was lower (Brooke and Rowe 1996). On the other hand, search effort in 1991 encompassed 12 months, and was therefore twice as long as the effort in 2015, although the peak breeding period from May to July was covered during both expeditions (Brooke 1995a). Although we cannot assert conclusively that the Henderson Petrel population is currently stable, it is unlikely that the conservation status of Henderson Petrels has deteriorated in the past decades.

The projected population decline of Henderson Petrels was based on low breeding success of 17.5% in 1991. We estimated mean nest survival as 28.5%, with a lower confidence limit overlapping with the figure from 1991 (Brooke 1995a; Brooke *et al.* 2010). This estimate may be very conservative, because the Mayfield method assumes constant daily nest failure rates throughout the nesting period, but petrels likely have very low nest failure probability early and late in the nesting period (Hervías *et al.* 2013), and Henderson Petrel adults appeared aggressive enough to deter approaching rats from attended eggs. The population model from which an ongoing decline was inferred indicated that the population would be stable at annual breeding success of around 25% (Brooke *et al.* 2010). Because our breeding success estimates fall within the range where the population could be stable, our population size estimate suggesting that the population has not declined since 1991 is fully consistent with the estimated breeding success found in 2015.

Annual variation in breeding success is common among seabirds, and based on the 2 years in which Henderson Petrels were studied we cannot conclude which productivity estimate may be more typical. The higher nest survival in 2015, which is similar to nest survival estimates of other gadfly petrel populations persisting with Pacific rats (Rayner *et al.* 2007; Jones *et al.* 2015), could potentially be a consequence of different rat densities in 1991 and 2015. Although the eradication operation in 2011 was unsuccessful, the rat

population on Henderson Island was temporarily reduced by >99% to ~60–80 individuals (Amos *et al.* 2016). While we have no information about rat abundance in 1991, we consider it unlikely that the temporary reduction of the rat population in 2011 persisted until 2015 based on rat trapping in 2013 and 2015 which indicated that rat abundance had recovered to pre-eradication levels (Churchyard *et al.* 2013). Petrel breeding success immediately following the eradication may have been substantially higher than in the preceding years, but given that petrels usually do not start breeding until 4–5 years old, it is unlikely that any recruits would have returned to Henderson Island and boosted population sizes in 2015 (Brooke 2004). Given the potential for significant annual variability in rat population sizes and petrel breeding success, we cannot conclude that the breeding success found in 2015 is representative of a long-term average, which would be necessary for the population to be stable (Brooke *et al.* 2010).

In contrast to breeding success, growth rates of Henderson Petrel chicks appeared to be very similar in 2015 and in 1991. Seabird chick growth rates can be negatively affected by food availability (Quillfeldt *et al.* 2003; Williams *et al.* 2007; McKinnon *et al.* 2012), and the apparent similarity in chick growth rates between 1991 and 2015 provides some reassurance that changes in food availability that may have occurred due to fisheries (Myers and Worm 2003; Pauly *et al.* 2005) have not affected the foraging success of Henderson Petrels. The foraging range of Henderson Petrels remains essentially unknown, but based on the length of incubation shifts and the anecdotal information of one tracked bird it is likely that Henderson Petrels forage at distances >1000 km away from their breeding location, which is similar to foraging ranges of other gadfly petrels in the South Pacific (Rayner *et al.* 2012, 2016). The travel speed of the one bird we tracked was consistent with travel speeds for other gadfly petrels measured by ship radar tracking (Spear and Ainley 1997), but has to be considered a minimum due to the coarse temporal resolution of our tracking data. A better understanding of the at-sea distribution of this species will require further tracking efforts.

Prior to this study, predation of Murphy's Petrel chicks by rats had been observed and, by extension, predation by rats and possibly even crabs of Henderson Petrel chicks was predicted but had never been observed or confirmed. We found higher nest survival of Henderson Petrels than of Murphy's Petrels nesting on the same island (Brooke 1995a; Churchyard *et al.* 2013), possibly because Henderson Petrels exhibited more aggressive defence behaviour. Nonetheless, we provided the first confirmation

that Henderson Petrel chicks are depredated by introduced rats and by native crabs. We found most predation events occurred during the early chick rearing period, when the small and relatively defenceless chick was left alone by its parents – a typical pattern in many seabirds facing introduced predators (Imber *et al.* 2000; Hervías *et al.* 2013; Jones *et al.* 2015). We did not observe predation of eggs, and speculate that the aggressive behaviour of adults may be sufficient to guard the egg against predators.

Besides direct predation, rats may also have sublethal effects and reduce growth rates of seabird chicks due to an increase in energy consumption from disturbance (Major *et al.* 2006). The growth rates of Henderson Petrels of ~3 g/day described here were similar to growth rates of Mottled Petrels (*Pterodroma inexpectata*) (Sagar *et al.* 2015), Providence Petrels (*P. solandri*) (Binder *et al.* 2013), Gould's Petrels (*P. leucoptera*) (O'Dwyer *et al.* 2006, 2007), and Pycroft's Petrels (*P. pycrofti*) (Gangloff and Wilson 2004). Given the large daily fluctuations in chick mass caused by episodic feeding events from parents, any reduction in growth rate due to rat disturbance may be difficult to measure with our small sample size.

In summary, our study indicates that Henderson Petrel breeding success in 2015 was higher than in 1991, and that this level of productivity might be sufficient for the population to be currently stable. Introduced rats are, however, still responsible for the loss of petrel chicks, and the eradication of rats from Henderson Island would benefit Henderson Petrels and other seabirds on this island.

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