

Population growth estimates of a threatened seabird indicate necessity for additional management following invasive predator eradications

J. H. Fischer¹, G. A. Taylor², R. Cole³, I. Debski², D. P. Armstrong⁴ & H. U. Wittmer¹

¹ School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand

² Aquatic Unit, Department of Conservation, Wellington, New Zealand

³ Murikihu District Office, Department of Conservation, Invercargill, New Zealand

⁴ Wildlife Ecology Group, Massey University, Palmerston North, New Zealand

Keywords

Bayesian inference; Detection probability; *Pelecanoides whenuahouensis*; Population size; Population trend; Whenua Hou Diving Petrel; Predator eradications; Invasive species.

Correspondence

Johannes H. Fischer, School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand.
Tel: +64-221346676
Email: johannesfischer@live.nl

Editor: Res Altwegg

Associate Editor: Sarah Converse

Received 09 July 2018; accepted 26 April 2019

doi:10.1111/acv.12516

Abstract

The eradication of invasive predators from islands is a successful technique to safeguard seabird populations, but adequate post-eradication monitoring of native species is often lacking. The Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP) is a recently-described and 'Critically Endangered' seabird, restricted to Codfish Island (Whenua Hou), New Zealand. Invasive predators, considered the major threat to WHDP, were eradicated on Codfish Island in 2000. However, estimates of WHDP population size and trends remain unknown, hindering assessments of the success of the eradications. We collated intermittent burrow counts ($n = 20$ seasons) conducted between 1978 and 2018. To estimate the population growth rate (λ) before and after predator eradications, we used log-linear models in a Bayesian hierarchical framework while retrospectively accounting for differences in detection probabilities among burrow counts, due to differences in effort, marking and timing. The number of WHDP burrows was estimated at 40 (36–46) in 1978 and 100 (97–104) in 2018. The pre-eradication λ was estimated at 1.023 (0.959–1.088), while the post-eradication λ was estimated at 1.017 (1.006–1.029). The WHDP population appears to be increasing, yet the rate of increase is low compared to other Procellariiformes following predator eradications. The comparatively low post-eradication λ , combined with an apparent lack of change between pre- and post-eradication λ , indicates that additional threats might be limiting WHDP population growth and that further conservation management is required. The continuation of affordable and simple, albeit imperfect, monitoring methods with retrospective corrections facilitated the assessment of invasive predator eradications outcomes and should guide future management decisions. An abstract in *Te Reo Māori* (the Māori language) can be found in Appendix S1.

Introduction

Close to two-thirds of all recently reported extinctions have occurred on islands, the majority of which have been attributed to predation from invasive species (Tershy *et al.*, 2015; Jones *et al.*, 2016). To counter the detrimental effects of invasive predators, eradication attempts are conducted on many islands. Native species generally respond positively to eradication efforts. Over 200 animal species found on islands have benefited from invasive predator eradications through increases in abundance and/or distribution (Jones *et al.*, 2016; Brooke *et al.*, 2018a). Given these benefits, eradications of invasive predators have become a popular conservation practise with at least 850 island-wide eradications around the globe between 1950 and 2015 (DIISE, 2015).

Invasive predator eradications from islands often play a key role in seabird conservation, as many seabird species breed on islands, or are even endemic to them (Taylor, 2000a, 2000b; Spatz *et al.*, 2017; Brooke *et al.*, 2018a; Rodriguez *et al.*, 2019). Seabirds, and notably members of the order Procellariiformes, are one of the most threatened taxonomic groups on the planet (Croxall *et al.*, 2012; Rodriguez *et al.*, 2019). Many Procellariiformes are *K*-strategists (i.e., low fecundity and high longevity). Therefore, these species are highly susceptible to the reduced hatching/fledging success and heightened adult mortality that are typical consequences of invasive predators (Jones *et al.*, 2007; Spatz *et al.*, 2017; Brooke *et al.*, 2018a; Rodriguez *et al.*, 2019). Smaller species (<1 kg) are especially susceptible to invasive predators (Jones *et al.*, 2007). While Procellariiformes are *K*-

strategists, they can respond surprisingly quickly and positively to invasive predator eradications (Jones, 2010; Brooke *et al.*, 2018a). However, despite the clear conservation gains of invasive predator eradications, systematic post-eradication monitoring remains rare (Jones *et al.*, 2016), hindering the evaluation of success and assessments of complementary threats (Spatz *et al.*, 2017; Towns, 2018).

Codfish Island (Whenua Hou), New Zealand, hosts a diverse community of small Procellariiformes and invasive predators were eradicated from the island to restore this seabird community (Middleton, 2007). Specifically, Weka (*Galirallus australis*; a predatory bird species native to New Zealand but invasive to Codfish Island; Taylor, 2000a) were eradicated in 1984, followed by brush-tailed possums *Trichosurus vulpecula* in 1987, and Polynesian rats *Rattus exulans* in 2000 (dates here represent the year in which the eradications were completed; Brown & Sherley, 2002; McClelland, 2002; Middleton, 2007). One of the Procellariiform species that breeds on Codfish Island is the ‘‘Critically Endangered’’ Whenua Hou Diving Petrel *Pelecanoides whenuahouensis*; WHDP hereafter. This species faced major range restrictions and population declines due to the impacts of invasive predators and is now restricted to a single colony on Codfish Island, New Zealand (Taylor, 2000b; Holdaway, Jones & Athfield, 2003; Fischer *et al.*, 2018a). While invasive predators have been removed from Codfish Island, little is known about past and contemporary population estimates and trends of the WHDP, hindering any assessment of the population responses to the eradication efforts.

To better understand the effects of the eradications of invasive predators on the WHDP, we collated intermittent WHDP burrow counts ($n = 20$) between 1978 and 2018. We then modelled the annual WHDP population growth rates over two biologically relevant time periods: the pre-eradication period (1978–85) and the post-eradication period (2002–18). We accounted retrospectively for differences in detection probability among burrow counts due to differences in effort, marking, and timing, using expert elicitation and data on patterns of WHDP attendance at burrows. Finally, we used the existing literature to compare the annual WHDP population growth rate post-eradications with the post-eradication growth rates of other Procellariiformes species on Codfish Island.

Materials and methods

Study species and study area

The Whenua Hou Diving Petrel is a small (~130 g) Procellariiform seabird, which was previously considered conspecific with the South Georgian Diving Petrel (*P. georgicus*; Fischer *et al.*, 2018a). Following the designation as a new species, the WHDP warrants listing as ‘‘Critically Endangered’’ on the IUCN Red List (Fischer *et al.*, 2018a). WHDPs were historically widespread through southern New Zealand, but predation by invasive species caused local extinctions throughout their range, including the Chatham Islands, Auckland Islands, Stewart Island and the Otago

peninsula (Worthy, 1998; Taylor, 2000b; Holdaway *et al.*, 2003; Wood & Briden, 2008; Fischer *et al.*, 2017b). Today, the WHDP is restricted to Codfish Island (Whenua Hou, 14 km², Fig. 1) located circa 3 km west of Stewart Island (Rakiura), New Zealand. We conducted our study within the only WHDP colony, which is located in the Sealers Bay dunes (−46.766° S, 167.645° E; Fischer *et al.*, 2017a, 2018b). WHDPs breed in burrows in these dunes from early September to late January, but colony attendance varies with breeding stages (i.e., the species’ phenology), which complicates burrow counts.

Burrow counts

We collated intermittent counts of WHDP burrows based on (1) our own WHDP burrow counts (1991–93, 2002–04, 2008, 2015–18), (2) the scientific literature, and (3) unpublished management reports from the New Zealand Department of Conservation (DOC) (Table 1). All burrow counts were conducted by walking the entirety of the extremely small (approx. 0.018 km²) colony back and forth (Taylor & Cole, 2002; Fischer *et al.*, 2018b). After the first count in 1978 (the year in which the colony was discovered; Imber & Nilsson, 1980), all detected burrows were marked with stakes during each count (Cox, 1991, R Nilsson pers. comm. 2018). When we found more than one count per season in the literature, we used the earlier count. We only considered counts of occupied WHDP burrows, because not all open burrows in the study area are occupied. We assessed burrow occupancy through stick palisades, sometimes in combination with playback/human mimics (Imber & Nilsson, 1980; Taylor, 1991; Taylor & Cole, 2002; Fischer *et al.*, 2018b). As occupancy assessments require > 1 day, we excluded counts conducted within a single day. Here, we report the calendar year in which the season started.

Modelling population WHDP growth rates

To estimate the yearly rate of WHDP population growth before and after the invasive predator eradications on

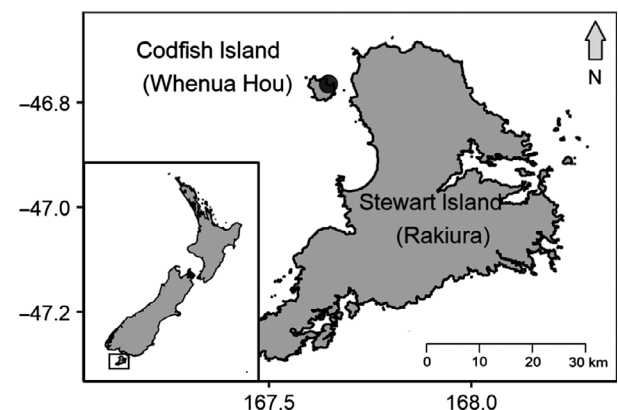


Figure 1 Location of the study site, Sealers Bay dunes, Codfish Island (Whenua Hou), New Zealand, as indicated by the dark-grey circle.

Table 1. Raw Whenua Hou Diving Petrel burrow counts, number of survey days per count (d), marking of burrows, the timing of the count, proportion of attendance ($p_{a,t}$) and corresponding retrospectively corrected estimates (\hat{N}_t with 95% credible intervals). \hat{N}_t listed here are based on $p_{d,t}$ distributions informed by all 11 experts

Season	Count	d	Marked	Timing with respect to phenology	$p_{a,t}$	\hat{N}_t	Source
1978	35	2	No	Prospecting-incubation	0.962	40 (36–46)	Imber & Nilsson, 1980, R Nilsson pers. comm. 2018
1980	32	2	Yes	Incubation	0.962	35 (32–39)	West & Imber, 1989, R Nilsson pers. comm. 2018
1981	33	2	Yes	Chick-rearing	0.734	45 (38–52)	West & Imber, 1989, R Nilsson pers. comm. 2018
1983	38	1	Yes	Chick-rearing	0.734	–	West & Imber, 1989, A Cox <i>in lit.</i> 2018
1985	41	10	Yes	Prospecting	0.902	45 (42–50)	West & Imber (1989)
1990	42	2	Yes	Prospecting	0.902	48 (44–54)	Johnson & Rance (1990)
1991	43	3	Yes	Incubation	0.962	45 (43–49)	Taylor (1991)
1992	41	2	Yes	Incubation	0.962	45 (41–49)	Buckingham <i>et al.</i> (1995)
1993	35	6	Yes	Chick-rearing	0.734	49 (42–57)	Cole & Roberts (1994)
1998	64	1	Yes	Chick-rearing	0.734	–	Imber (1999)
2002	75	5	Yes	Incubation	0.962	78 (75–81)	Cole (2004)
2003	54	5	Yes	Incubation-chick-rearing	0.962	57 (54–60)	Cole (2004)
2004	60	10	Yes	Incubation	0.962	63 (60–66)	Present study
2005	72	5	Yes	Incubation	0.962	75 (72–78)	Trainor (2008)
2006	79	7	Yes	Chick-rearing	0.734	99 (90–108)	Trainor (2008)
2008	76	4	Yes	Chick-rearing	0.734	97 (88–106)	Trainor (2009)
2015	74	37	Yes	Incubation-chick-rearing-fledging	0.962	78 (74–82)	Fischer <i>et al.</i> (2018b)
2016	78	30	Yes	Prospecting-incubation-chick-rearing-fledging	0.962	82 (78–86)	Present study
2017	99	114	Yes	Prospecting-incubation-chick-rearing-fledging	0.962	103 (99–107)	Present study
2018	96	102	Yes	Prospecting-incubation-chick-rearing-fledging	0.962	100 (97–104)	Present study

Codfish Island while retrospectively correcting estimates of burrow counts, we fitted log-linear models with a Poisson error term in a Bayesian hierarchical framework. Specifically, we fitted the data to:

$$\log N_t = \alpha + rt + \varepsilon_t \quad (1)$$

in which N_t is the number of WHDP burrows at year t , α is $\log N_0$ (the number of WHDP burrows at year 0), r is the log λ (the finite rate of increase), t is the number of years between 0 and t , and ε_t is random annual variation (Caughley, 1977; Caughley & Sinclair, 1994). We used log-linear models because we assumed the WHDP population to exhibit exponential growth rates. We considered the number of burrows counted each year to be a sampled from a binomial distribution:

$$N_t \sim B(N_t, p_t) \quad (2)$$

in which p_t is the probability that a burrow was detected in year t . We modelled the expected variation in p_t as:

$$p_t = 1 - (1 - p_{d,t})^d p_{a,t}, \quad (3)$$

in which $p_{d,t}$ is the daily probability that a burrow was detected and identified as occupied by WHDPs, d is the number of survey days in year t , and $p_{a,t}$ is the proportion of the WHDP burrows that were attended to at the time of the breeding season that the count was conducted. We thus retrospectively accounted for imperfect detection in WHDP

burrow counts by modelling (1) the search effort each year, (2) the marking of the burrows, and (3) the timing of the count in relation to the species' phenology.

To obtain probability distributions for $p_{d,t}$, we (JHF, DPA and HUW) designed an expert elicitation based on the Delphi method (Linstone & Turoff, 1975; Kuhnert, Martin & Griffiths, 2010; Martin *et al.*, 2012). We consulted every living person who had conducted a WHDP burrow count and considered them an expert (excluding JHF, but including GAT, RC, and ID; $n = 18$). Our approach (Delphi method) consisted of two rounds. In round one, we asked experts independently to provide us with a three-point estimate (their best guess, the minimum and the maximum) of p_d , provided the colony is (1) marked or (2) unmarked. We thus requested separate values for a marked (i.e., after 1978) and an unmarked colony (i.e., 1978) from the experts, allowing us to adjust $p_{d,t}$ according to whether burrows were marked that year. We assumed that p_d was otherwise constant (e.g., no variation due to learning curves of observers, changes in dune vegetation, or other factors that may have varied among years other than marking). In addition, we assumed that all burrows were equally likely to be detected and that misidentification of WHDP burrows was impossible. The experts were aided in their decision in round one by a graph depicting hypothetical detection probabilities ($p_d = 0.1$ – 0.9) as a function over time (Fig. S1). We then compiled responses ($n = 11$; 61%) and sent anonymous summary statistics to each respondent, allowing them to adjust their initial response (round two; Linstone & Turoff, 1975;

Kuhnert *et al.*, 2010; Martin *et al.*, 2012). Only one response (6%) was adjusted in round two (Fig. 2). We obtained beta-PERT distributions (Clark, 1962) for $p_{d,t}$ based on the three-point estimates from the expert responses in round two.

To obtain a meaningful numerical value for $p_{a,t}$, we monitored WHDP burrows during the entire 2017 and 2018 season ($n = 86$ and 81 , respectively). Specifically, we monitored the daily activity of these burrows using stick palisades (Imber & Nilsson, 1980; Taylor & Cole, 2002; Fischer *et al.*, 2018b) to create an attendance curve throughout the season. At the same time, we monitored a subset of burrows in 2017 and 2018 ($n = 29$ and 25 , respectively) with a burrowscope (Taupe model, Sextant Technologies, Wellington, New Zealand; Lavers, Hutton & Bond, 2019) to assess mean dates of key phenology events (i.e., lay, hatch, and fledge dates). We summed the daily burrow attendance per week and allocated these into phenologically relevant stages based on the timing of the count (i.e., prospecting, incubation, chick-rearing or fledging). We then obtained $p_{a,t}$ by averaging the weekly values per phenological category. When counts fell into several phenological stages, we allocated the count into the category with the highest $p_{a,t}$. We assumed that the timing of key phenology events during the 2017 and 2018 season were representative of previous seasons.

We used Equation 1–3 to estimate λ for two biologically relevant time periods: before and after the predator eradications. To estimate the λ before the predator eradications, we fitted a model to data between 1978 and 1985. We used the 1978–1985 timeframe because we anticipated a 2-year lag (i.e., the average age at first breeding; Miskelly & Taylor, 2004, 2007) of the WHDP population to respond to eradication efforts, in the absence of immigration (Codfish Island hosts the only WHDP colony). To estimate λ after the predator eradications, we fitted a model to data between 2002 and 2018. In addition, to explore the influence of the expert assessment of $p_{d,t}$ on \hat{N}_t and $\hat{\lambda}$, we repeated our analysis

three times using distributions for $p_{d,t}$ that were informed by: (1) the average best guess, minimum and maximum from all experts, (2) the values provided by the most pessimistic expert, and (3) the values provided by the most optimistic expert.

We fitted the models using OpenBugs 3.2.3, which uses Markov chain Monte Carlo (MCMC) algorithms to obtain posterior distributions for parameters, allowing all sources of error to be propagated into those distributions (Lunn *et al.*, 2000; Spiegelhalter *et al.*, 2014). We used uninformative priors ($N[0, 10]$) for α and r . In most cases we pooled three independent MCMC chains with 100 000 iterations each after a “burn-in” of 50 000 iterations, resulting in posterior distributions based on 150 000 iterations. Inspection of the Gelman-Rubin statistic (\hat{R}) showed slow convergence of chains for the pre-eradication data based on pessimistic values for $p_{d,t}$, so we increased the number of iterations to 2 100 000 with a burn in of 50 000, giving satisfactory convergence for all estimates ($\hat{R} < 1.05$) (Paxton *et al.*, 2016). We report posterior distributions of N_t and λ as means \pm 95% credible intervals (CI).

Comparison with other Procellariiformes

We compared the λ of the WHDP population after the eradications of invasive predators with the post-eradication λ of other small Procellariiform populations breeding on Codfish Island. Specifically, we used existing literature to source N_t of both Cook’s Petrels (*Pterodroma cookii*; ~190 g) and Mottled Petrels (*P. inexpectata*; ~315 g) on Codfish Island and calculated the λ post eradications using Equation 1 (Marchant & Higgins, 1990). When population estimates were reported as a range only, we used the midpoint as N_t . As published estimates of both Cook’s and Mottled Petrels lacked detail (e.g., details of historic counts were lost and/or counts were only conducted in small parts of the colonies),

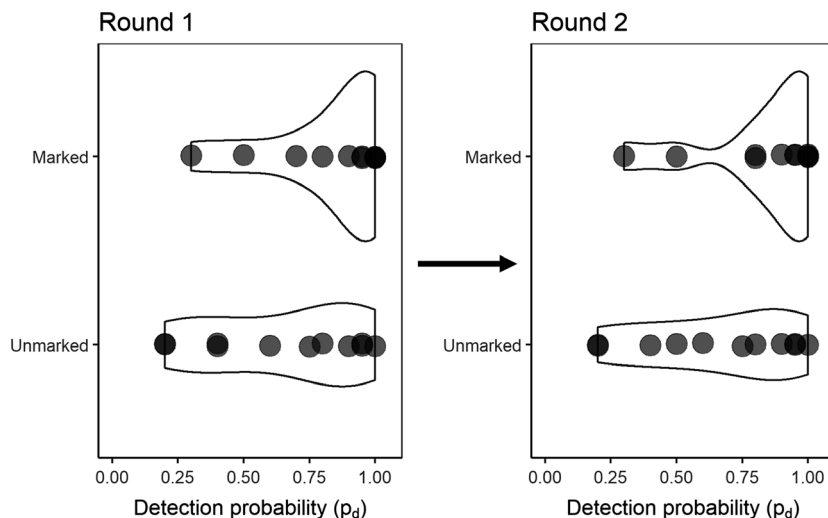


Figure 2 Violin plots illustrating the distribution of best guesses of detection probabilities (p_d) of WHDP burrows in marked/unmarked systems, as provided by experts ($n = 11$) during the two rounds of an expert elicitation following the Delphi method.

we did not apply Equation 2 and 3 to retrospectively correct these estimates.

Results

WHDP population growth rates

A total of 20 raw WHDP burrow counts were collated from 1978 to 2018 (one per breeding season), but two single-day counts were excluded from our analyses (Table 1). The estimates of daily detection probability ($p_{d,t}$) obtained by averaging the data from the 11 experts were 0.832 (minimum = 0.761, maximum = 0.898) in a marked colony and 0.662 (0.578–0.749) in an unmarked colony (Fig. 2). The data from the most pessimistic expert produced an of $p_{d,t}$ of 0.30 (0.01–0.60) for a marked system and 0.20 (0.01–0.40) for an unmarked system. The data from the most optimistic expert produced an estimate of $p_{d,t}$ of 0.99 (0.97–1.00) for a marked system and 0.99 (0.95–1.00) for an unmarked system. The proportion of attended WHDP burrows ($p_{a,t}$) per phenological stage was as following: prospecting: September - mid October $p_{a,t} = 0.902$; incubation: mid-October – late November $p_{a,t} = 0.962$; and chick rearing: late November – mid-January $p_{a,t} = 0.734$ (Fig. 3). No counts were conducted solely during fledging.

When using $p_{d,t}$ data informed by the 11 experts, the estimated number of WHDP burrows (\hat{N}_t) varied from 40 (36–46) in 1978 to 100 (97–104) in 2018 (Table 1, Fig. 4), the pre-eradication λ (1978–85) was estimated at 1.023 (0.959–1.088), and the post-eradication λ (2002–18) was estimated at 1.017 (1.006–1.029) (Fig. 5). However, when using the $p_{d,t}$ data informed by the most pessimistic expert, \hat{N}_t varied from 59 (48–72) in 1978 to 100 (96–104) in 2018 (Fig. S2), the pre-eradication λ was estimated at 0.915 (0.833–0.991), and the post-eradication λ was estimated at 1.014 (1.002–1.026). When using the $p_{d,t}$ data informed by the most optimistic expert, \hat{N}_t varied from 36 (35–39) WHDP burrows in

1978 to 100 (97–104) WHDP burrows in 2018 (Fig. S3), the pre-eradication λ was estimated at 1.038 (0.975–1.103), and post-eradication λ was estimated at 1.017 (1.006–1.029).

Comparison with other Procellariiformes

The Cook’s Petrel population on Codfish Island grew from 100 burrows in 1980 to approximately 5000 (3500–7000) burrows in 2007. The λ for this period for Cook’s Petrel was 1.156 (Fig. 5). The Mottled Petrel population on Codfish Island grew from 10 000–50 000 burrows in 1980 to 300 000–400 000 burrows in 1996. The λ for this time period for Mottled Petrel was 1.155.

Discussion

We presented WHDP burrow estimates for the last four decades, which ranged from $\hat{N}_t = 40$ (36–46) burrows in 1978 to $\hat{N}_t = 100$ (97–104) burrows in 2018 (using $p_{d,t}$ data averaged from the 11 experts). Under the assumption that every burrow was occupied by two adults, these estimates would equate to 80 (72–92) adults in 1978 and 200 (194–208) adults in 2018. These estimates highlighted that the WHDP population slowly increased over the last 40 years but remains very low. In addition, we also presented the first estimates of the annual population growth rate of the WHDP. The pre-eradication λ (1978–85) was 1.023, while the post-eradication λ (2002–18) was 1.017 using $p_{d,t}$ data informed all 11 experts. Both estimates of N_t and λ (based on $p_{d,t}$ data informed all 11 experts) indicated that the WHDP population was slowly increasing before invasive predator eradications and still is slowly increasing afterwards.

Comparing raw burrow counts with our estimates derived from retrospective corrections highlighted the importance of accounting for differences in detection probability among burrow counts due to differences in effort and timing.

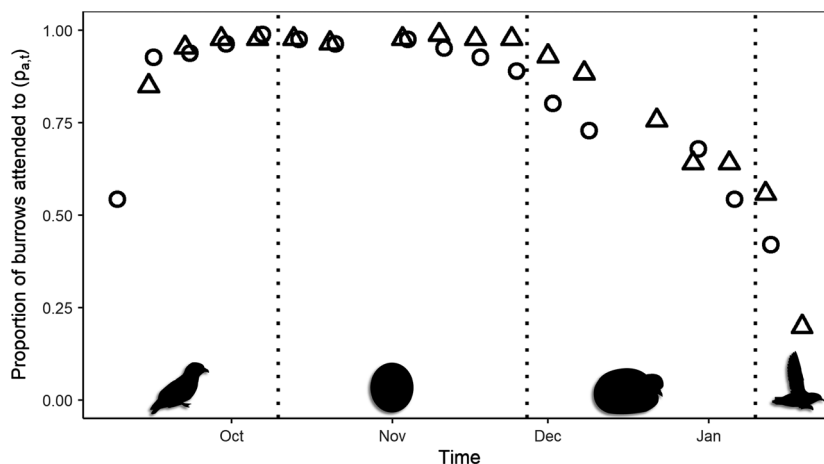


Figure 3 The proportion of Whenua Hou Diving Petrel burrows that were attended to ($p_{a,t}$) in relation to key phenology events (prospecting, incubation, chick-rearing or fledging) during the 2017 (triangles; $n = 86$) and the 2018 (circles, $n = 81$) breeding seasons. Dotted lines represent mean lay (09 October), hatch (26 November) and fledge dates (11 January).

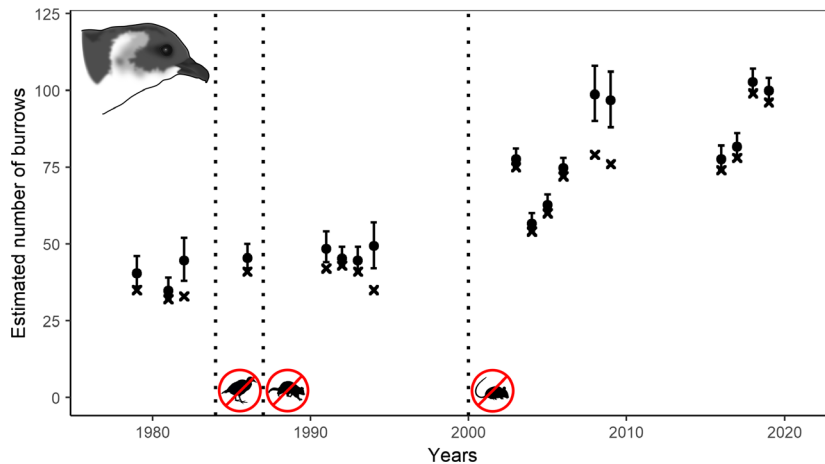


Figure 4 Raw Whenua Hou Diving Petrel burrow counts (crosses) and retrospectively corrected estimates (\hat{N}_t ; filled circles with 95% credible intervals), based on $p_{d,t}$ distributions informed by all 11 experts, in relation to invasive predator eradications (dotted lines).

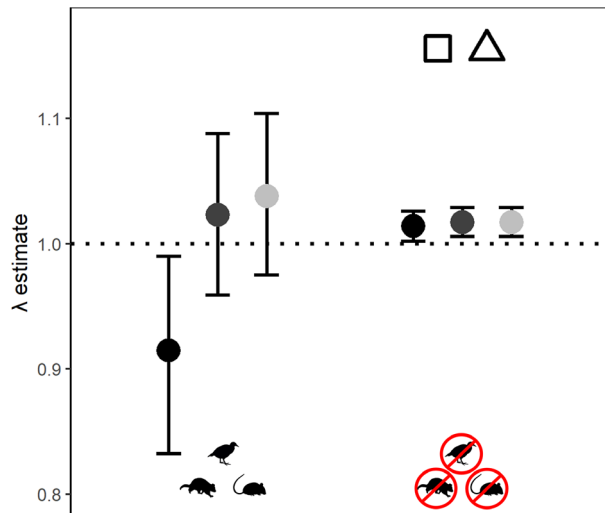


Figure 5 Estimates of yearly rates of WHDP population growth (λ), before and after eradications of invasive predators (filled circles with 95% credible intervals; orange = based on $p_{d,t}$ distributions informed by most pessimistic expert, black = based on $p_{d,t}$ distributions informed by all 11 experts, and green = based on $p_{d,t}$ distributions informed by most optimistic expert), in comparison with estimates of Cook's Petrel (hollow triangle) and Mottled Petrel (hollow square) λ post eradications. Cook's and Mottled Petrel population λ are based on (Robertson & Bell, 1984; Taylor, 2000a; Imber, West & Cooper, 2003; Rayner, Parker & Imber, 2008).

Seasons in which counts were conducted during chick-rearing (i.e., counts with the lowest $p_{a,t}$) had the greatest difference between the raw burrow counts and \hat{N}_t . Furthermore, burrow counts with a low number of survey days (d) resulted in \hat{N}_t with larger credible intervals, highlighting the importance of spending adequate time in the field

(MacKenzie *et al.*, 2002, 2003). The increased confidence in estimates caused by increased survey effort is also apparent in the λ estimates. The time spent in the WHDP colony after the eradications is considerably higher than before the eradications. Consequently, the λ estimates post-eradications do not vary, even with different distributions for $p_{d,t}$. In contrast, the pre-eradication λ vary substantially under different distributions for $p_{d,t}$. Most noticeably, when using the $p_{d,t}$ data informed the most pessimistic expert, the pre-eradication λ indicated a decreasing WHDP population ($\lambda = 0.915$). However, when compared to detection probabilities of burrows of other Procellariiform species that breed in more vegetated habitats than the WHDP (Barbraud *et al.*, 2009; Defos du Rau *et al.*, 2015), the $p_{d,t}$ distributions informed by the most pessimistic expert appeared to be underestimates. As such, the $p_{d,t}$ distributions based on values provided by all eleven experts seemed a more realistic estimate.

The post-eradication λ of the WHDP population contrasted with the λ of other small Procellariiformes post eradications. For example, the population doubling time (t_d) for the Cook's ($t_d = 4.49$ years) and Mottled Petrels ($t_d = 4.52$ years) on Codfish Island was 9.2 and 9.1 times shorter, respectively, than the population doubling time of the WHDP ($t_d = 41.18$ years) (Caughley & Sinclair, 1994). The average population growth rate of 24 Procellariiform populations (17 small [< 1 kg] species) after invasive predator eradications was $\lambda = 1.079$ (populations established after the eradications were excluded; Brooke *et al.*, 2018a). Therefore, the average population doubling time of small Procellariiformes population was $t_d = 8.86$ years, which is 4.65 times shorter than the t_d of the WHDP. Brooke *et al.* (2018a) highlighted that many seabird species respond rapidly to eradications, potentially due to a pool of immature birds. Our intermittent time series did not cover the two years after the eradications (2000-2002; the timeframe in which WHDP immatures would have responded; Miskelly & Taylor, 2004, 2007), preventing assessments of WHDP

responses immediately after the eradications. Regardless of this shortcoming in our study, the population responses of most other Procellariiformes post-eradication efforts were considerably higher than the population response of the WHDP.

The lack of change between the pre- and post-eradication λ and the low post-eradication λ indicated that after the invasive predator eradications other factors remained that limit the WHDP population growth and that additional management is required. Various factors could be limiting WHDP population recovery. The distinct preference of the WHDP to only breed in fragile foredunes suggests that the species is extremely vulnerable to storms and storm surges (Fischer *et al.*, 2018b). For example, a storm in October 2003 eroded the foredune in which the WHDP breeds, caused nest failures, and increased adult mortality (Cole, 2004). A translocation could reduce the vulnerability of the WHDP to these stochastic events (Miskelly & Taylor, 2004; Miskelly *et al.*, 2009). Density dependence could be another explanation to the limited population growth of the WHDP. However, diving petrel colonies have been shown to reach much higher densities (e.g., 6 burrows/m²; Taylor, 2000b) than the current density of the WHDP colony (0.006 burrows/m²). Negative interspecific interactions between the WHDP and the Common Diving Petrels (Fischer *et al.*, 2017a) could also be limiting population growth. While the (meta)population of the Common Diving Petrel within the WHDP colony appeared small (Taylor & Cole, 2002; Fischer *et al.*, 2018b), measures reducing interspecific interactions (e.g., burrow flaps; Gummer *et al.*, 2015) could be considered. Furthermore, no pelagic threats to the WHDP have been assessed to date. Therefore, its pelagic distribution and associated threats, including deck strikes, accidental bycatch in commercial fisheries or environmental variability, should be investigated (Taylor, 2000a, 2000b; Black, 2005; Pardo *et al.*, 2017).

While we were unable to identify the factor(s) limiting WHDP population growth, our study illustrated the value of inexpensive and simple, albeit imperfect, field data in combination with retrospective corrections to evaluate the success of invasive predator eradications. Eradications of invasive predators from islands have been extremely successful in restoring seabird populations (Jones *et al.*, 2016; Spatz *et al.*, 2017; Brooke *et al.*, 2018a) and the eradications on Codfish Island clearly were beneficial for the Cook's and Mottled Petrel populations (Fig. 5). Yet, eradications of invasive predators do not exclude the need for follow-up conservation measures (e.g., a translocation for WHDPs). Brooke *et al.* (2018a) found that seven seabird populations did not respond to eradication efforts (e.g., Gould's Petrel *Pterodroma gouldii*) and at least 23 seabird populations responded negatively ($\lambda < 1$), suggesting that the limited population response of the WHDP was not an isolated case. Due to the prevalent assumption that native species will be secured following island eradications, monitoring of native fauna post-eradication is rare and thus cases requiring additional management are unlikely to be recognized (Jones *et al.*, 2016; Brooke *et al.*, 2018a, 2018b; Towns, 2018). The "unavailability of economical ways to measure change" was listed as another

impediment to post-eradication monitoring (Towns, 2018). In addition, the allocation of sparse funds towards (1) monitoring the responses of native species following eradications or (2) future eradications continues to be debated (Brooke *et al.*, 2018b). This conundrum is aggravated by the longevity of seabirds (among other long-lived species), as the post-eradication monitoring of these species would ideally span decades, further elevating monitoring costs (Brooke *et al.*, 2018a, 2018b; Towns, 2018). Both Towns (2018) and Brooke *et al.* (2018b) highlight the need for simple, inexpensive monitoring methods that have the potential to assess eradication outcomes over extended time periods. Although detailed (and thus often expensive) monitoring schemes following invasive predator eradications (or even in general) are largely missing (Paleczny *et al.*, 2015; Towns, 2018), basic, but imperfect data (such as burrow counts) do often exist (e.g., Taylor, 2000a, 2000b). Our results demonstrate that relatively inexpensive monitoring approaches (e.g., burrow-counts), combined with retrospective corrections, can be informative and allow for evaluations of management success across extended time periods, even when monitoring has been intermittent. We thus advocate the use of imperfectly collected historic data and recommend the continuation of similar simple and inexpensive monitoring methods post-eradications to inform outcomes of invasive predator eradications and consequently, future conservation management.

Acknowledgements

We are very grateful to the Ngāi Tahu for granting visits to Codfish Island. We are greatly indebted to dozens of volunteers over the past four decades for their assistance in the field. We thank William Brockelsby for his assistance in retrieving unpublished reports. We are also grateful to all experts who participated in the expert elicitation. Additionally, we thank Janne de Hoop, David Young and Victor Anton for providing the electronic artwork. Finally, we thank Victor Anton, Sarah Converse, Michelle McLellan, Alice Rogers, and two anonymous reviewers for commenting on previous versions of this manuscript.

Conflict of interest

The authors have no conflict of interest to declare.

Funding information

This work was supported by the New Zealand Department of Conservation, the National Geographic Society [WW-249C-17], the Ornithological Society of New Zealand [Bird NZ Research Fund 2015, 2017], the Encounter Foundation, Forest and Bird [JS Watson Trust 2017], a public Experiment.com crowdfunder [<https://doi.org/10.18258/7331>], the Centre for Biodiversity and Restoration Ecology [Student Award 2015, 2017], the Coastal Restoration Trust of New Zealand [Postgraduate Student Study Award 2016], The Royal Society of New Zealand [Hutton Fund 2017], and the Australasian Seabird Group [Student Grant 2016].

Ethics statement

All field protocols were approved by the internal Animal Ethics Committee of DOC and/or the Animal Ethics Committee of Victoria University of Wellington (VUW AEC 22252 and 23283).

References

- Barbraud, C., Delord, K., Marteau, C. & Weimerskirch, H. (2009). Estimates of population size of white-chinned petrels and grey petrels at Kerguelen Islands and sensitivity to fisheries. *Anim. Conserv.* **12**, 258–265.
- Black, A. (2005). Light induced seabird mortality on vessels operating in the Southern Ocean: incidents and mitigation measures. *Antarct. Sci.* **17**, 67–68.
- Brooke, M.L., Bonnaud, E., Dilley, B.J., Flint, E.J., Holmes, N.D., Jones, H.P., Provost, P., Rocamora, G., Ryan, P.G., Surman, C. & Buxton, R.T. (2018a). Seabird population changes following mammal eradications on islands. *Anim. Conserv.* **21**, 3–12.
- Brooke, M.L., Bonnaud, E., Dilley, B.J., Flint, E.J., Holmes, N.D., Jones, H.P., Provost, P., Rocamora, G., Ryan, P.G., Surman, C. & Buxton, R.T. (2018b). Enhancing the value of future island eradications needs improved understanding of past outcomes. *Anim. Conserv.* **21**, 19–20.
- Brown, K.P. & Sherley, G.H. (2002). The eradication of possums from Kapiti Island, New Zealand. *Turning the Tide* **27**, 46–52.
- Buckingham, R., Torr, S., Hamish, L. & Cole, R. (1995). *Management of Codfish Island: October 1992 - June 1993*. Invercargill: Department of Conservation.
- Caughley, G. (1977). *Analysis of vertebrate populations*. Toronto: John Wiley and Sons.
- Caughley, G. & Sinclair, A.R.E. (1994). *Wildlife ecology and management*. Oxford: Blackwell Science.
- Clark, C.E. (1962). Letter to the editor – the PERT model for the distribution of an activity time. *Oper. Res.* **10**, 405–406.
- Cole, R. (2004). *Summary of South Georgian Diving Petrel field observations for 2003/04, Codfish Island/Whenua Hou*. Invercargill: Department of Conservation.
- Cole, R. & Roberts, A. (1994). *Management of Codfish Island: July 1993 – June 1994*. Invercargill: Department of Conservation.
- Cox, A. (1991). *Scientific and management marking Codfish Island*. Invercargill: Department of Conservation.
- Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A. & Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* **22**, 1–34.
- Defos du Rau, P., Bourgeois, K., Thévenet, M., Ruffino, L., Dromzée, S., Ouni, R., Abiadh, A., Estève, R., Durand, J.-P., Anselme, L., Faggio, G., Yahya, J.M., Rguibi, H., Renda, M., Miladi, B., Hamrouni, H., Alilech, S., Nefta, A., Jaouadi, W., Agrebi, S. & Renou, S. (2015). Reassessment of the size of the Scopoli's Shearwater population at its main breeding site resulted in a tenfold increase: implications for the species conservation. *J. Ornithol.* **156**, 877–892.
- DIISE. (2015). The Database of Island Invasive Species Eradications, developed by Island Conservation, Coastal Conservation Action Laboratory UCSC, IUCN SSC Invasive Species Specialist Group, University of Auckland and Landcare Research New Zealand. Available at <http://diise.islandconservation.org>. (accessed 14 March 2018).
- Fischer, J.H., Debski, I., Taylor, G.A. & Wittmer, H.U. (2017a). Assessing the suitability of non-invasive methods to monitor interspecific interactions and breeding biology of the South Georgian diving petrel (*Pelecanoides georgicus*). *Notornis* **64**, 13–20.
- Fischer, J.H., Hjorsvarsdottir, F.O., Hiscock, J.A., Debski, I., Taylor, G.A. & Wittmer, H.U. (2017b). Confirmation of the extinction of South Georgian diving petrels (*Pelecanoides georgicus*) on Enderby Island. *Notornis* **64**, 48–51.
- Fischer, J.H., Debski, I., Miskelly, C.M., Tennyson, A.J.D., Fromant, A., Tessler, J., Hiscock, J.A., Cole, R., Bost, C.-A., Taylor, G.A. & Wittmer, H.U. (2018a). Analyses of phenotypic differentiations between South Georgian Diving Petrel (*Pelecanoides georgicus*) populations reveal an undescribed and highly-endangered species from New Zealand. *PLoS ONE* **13**, e0197766.
- Fischer, J.H., Debski, I., Taylor, G.A. & Wittmer, H.U. (2018b). Nest-site selection of South Georgia Diving-petrels on Codfish Island (Whenua Hou), New Zealand: implications for conservation management. *Bird Conserv. Int.* **28**, 216–227.
- Gummer, H., Taylor, G., Wilson, K.J. & Rayner, M.J. (2015). Recovery of the endangered Chatham Petrel (*Pterodroma axillaris*): A review of conservation management techniques from 1990 to 2010. *Glob. Ecol. Conserv.* **3**, 31–330.
- Holdaway, R.N., Jones, M.D. & Athfield, N.R.B. (2003). Establishment and extinction of a population of South Georgian diving petrel (*Pelecanoides georgicus*) at Mason Bay, Stewart Island, New Zealand, during the late Holocene. *J. Roy. Soc. New Zeal.* **33**, 601–622.
- Imber, M.J. (1999). *Report on Codfish Island trip to set up Cook's petrel long-term monitoring grids for Southland Conservancy*. Invercargill: Department of Conservation.
- Imber, M.J. & Nilsson, R.J. (1980). South Georgian diving petrels (*Pelecanoides georgicus*) breeding on Codfish Island. *Notornis* **27**, 325–330.
- Imber, M.J., West, J.A. & Cooper, W.J. (2003). Cook's petrel (*Pterodroma cookii*): historic distribution, breeding biology, and effects of predators. *Notornis* **50**, 221–230.
- Johnson, P. & Rance, B. (1990). *Codfish Island Trip Report*. Invercargill: Department of Conservation.
- Jones, H.P. (2010). Seabirds take mere decades to recover following rat eradications. *Ecol. App.* **20**, 2075–2080.
- Jones, H.P., Tershy, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E. & Howald, G.R. (2007). Severity of

- the effects of invasive rats on seabirds: A global review. *Conserv. Biol.* **22**, 16–26.
- Jones, H.P., Holmes, N.D., Butchart, S.H.M., Tershy, B.R., Kappes, P.J., Corkery, I., Aguirre-Munoz, A., Armstrong, D.P., Bonnaud, E., Burbidge, A.A., Campbell, K., Courchamp, F., Cowan, P.E., Cuthbert, R.J., Ebbert, S., Genovesi, P., Howald, G.R., Keitt, B.S., Kress, S.W., Miskelly, C.M., Opper, S., Poncet, S., Rauzon, M.J., Rocamora, G., Russel, J.C., Samaniego-Herrera, A., Seddon, P.J., Spatz, D.R., Towns, D.R. & Croll, D.A. (2016). Invasive mammal eradication on island results in substantial conservation gains. *Proc. Natl Acad. Sci. USA* **113**, 4033–4038.
- Kuhnert, P.M., Martin, T.G. & Griffiths, S.P. (2010). A guide to eliciting and using expert knowledge in Bayesian ecological models. *Ecol. Lett.* **13**, 900–914.
- Lavers, J.L., Hutton, I. & Bond, A.L. (2019). Changes in technology and imperfect detection of nest contents impedes reliable estimates of population trends in burrowing seabirds. *Glob. Ecol. Conserv.* **17**, e00579.
- Linstone, H. A. and Turoff, M. (1975). *The Delphi Method*. Reading: Addison-Wesley.
- Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000). WinBUGS — a Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* **10**, 325–337.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003). Estimating site occupancy, colonization, and local extinction probabilities when a species is detected imperfectly. *Ecology* **84**, 2200–2207.
- Marchant, S. and Higgins, P.J. (1990). *Handbook of Australian, New Zealand & Antarctic birds. Volume 1, ratites to ducks, part A, ratites to petrels*. Melbourne: Oxford University Press.
- Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S., McBride, M. & Mengersen, K. (2012). Eliciting expert knowledge in conservation science. *Conserv. Biol.* **26**, 29–38.
- McClelland, P.J. (2002). Eradication of Pacific rats (*Rattus exulans*) from Whenua Hou Nature Reserve (Codfish Island), Putauhinu and Rarotoka Islands, New Zealand. *Turning the Tide* **27**, 173–181.
- Middleton, A. (2007). *Two hundred years on Codfish Island (Whenuahou)*. Invercargill: Department of Conservation.
- Miskelly, C.M. & Taylor, G.A. (2004). Establishment of a colony of Common Diving Petrels (*Pelecanoides urinatrix*) by chick transfers and acoustic attraction. *Emu* **104**, 205–211.
- Miskelly, C.M. & Taylor, G.A. (2007). Common Diving Petrel (*Pelecanoides urinatrix*) breeding at 1 year old. *Notornis* **54**, 239–240.
- Miskelly, C.M., Taylor, G.A., Gummer, H. & Williams, R. (2009). Translocations of eight species of burrow-nesting seabirds (genera *Pterodroma*, *Pelecanoides*, *Pachyptila* and *Puffinus*: Family Procellariidae). *Biol. Conserv.* **142**, 1965–1980.
- Paleczny, M., Hammill, E., Karpouzi, V. & Pauly, D. (2015). Population Trend of the World's Monitored Seabirds, 1950–2010. *PLoS ONE* **10**, e0129342.
- Pardo, D., Forcada, J., Wood, A.G., Tuck, G.N., Ireland, L., Pradel, R., Croxall, J.P. & Phillips, R.A. (2017). Additive effects of climate and fisheries drive ongoing declines in multiple albatross species. *Proc. Natl Acad. Sci. USA* **114**, E10829–E10837.
- Paxton, E.H., Camp, R.J., Gorresen, P.M., Crampton, L.H., Leonard, D.L. & VanderWerf, E.A. (2016). Collapsing avian community on a Hawaiian Island. *Sci. Adv.* **2**, e1600029.
- Rayner, M.J., Parker, K.A. & Imber, M.J. (2008). Population census of Cook's petrel *Pterodroma cookii* breeding on Codfish Island (New Zealand) and the global conservation status of the species. *Bird Conserv. Int.* **18**, 211–218.
- Robertson, C.J.R. and Bell, B.D. (1984). Seabird status and conservation in the New Zealand region. In *Status and conservation of the world's seabirds*: 573–586. Croxall, J.P., Evans, P.G.H. and Schreiber, R.W. (Eds.). Cambridge: ICBP Technical publication 2.
- Rodriguez, A., Arcos, J.M., Bretagnolle, V., Dias, M.P., Holmes, N.D., Louzao, M., Provencher, J., Raine, A.F., Ramirez, F., Rodriguez, B., Ronconi, R.A., Taylor, R.S., Bonnaud, E., Borrelle, S.B., Cortes, V., Descamps, S., Friesen, V.L., Genovart, M., Hedd, A., Hodum, P., Humphries, G.R.W., Le Corre, M., Lebarbenchon, C., Martin, R., Melvin, E.F., Montevecchi, W.A., Pinet, P., Pollet, I.L., Ramos, R., Russell, J.C., Ryan, P.G., Sanz-Aguilar, A., Spatz, D.R., Travers, M., Votier, S.C., Wanless, R.M., Woehler, E. & Chiaradia, A. (2019). Future directions in conservation research on petrels and shearwaters. *Front. Mar. Sci.* **6**, 94.
- Spatz, D.R., Holmes, N.D., Reguero, B.G., Butchart, S.H.M., Tershy, B.R. & Croll, D.A. (2017). Managing invasive mammals to conserve globally threatened seabirds in a changing climate. *Conserv. Lett.* **10**, 736–747.
- Spiegelhalter, D., Thomas, A., Best, N. & Lunn, D. (2014). *OpenBUGS User Manual, Version 3.2.3*. Cambridge: MRC Biostatistics Unit.
- Taylor, G. (1991). *Report on a visit to Codfish Island 1–7 November 1991*. Wellington: Department of Conservation.
- Taylor, G.A. (2000a). *Action Plan for Seabird Conservation in New Zealand. Part A: Threatened seabirds*. Wellington: Department of Conservation.
- Taylor, G.A. (2000b). *Action Plan for Seabird Conservation in New Zealand. Part B: Non-threatened seabirds*. Wellington: Department of Conservation.
- Taylor, G. & Cole, R. (2002). *South Georgian Diving Petrel (Pelecanoides georgicus) survey, Codfish Island/Whenua Hou*. Wellington: Department of Conservation.
- Tershy, B.R., Shen, K.-W., Newton, K.M., Holmes, N.D. & Croll, D.A. (2015). The importance of islands for the

- protection of biological and linguistic diversity. *Bioscience* **65**, 592–597.
- Towns, D.R. (2018). Understanding seabird responses to invasive mammal eradications from islands needs systematic monitoring. *Anim. Conserv.* **21**, 15–16.
- Trainor, S. (2008). *Codfish Island South Georgian Diving Petrel: a summary of field observations 2004–2007 and recommendations for future management*. Invercargill: Department of Conservation.
- Trainor, S. (2009). *South Georgian Diving Petrel: a summary of field observations 2007–2009 on Codfish Island*. Invercargill: Department of Conservation.
- West, J. & Imber, M.J. (1989). Surveys of South Georgian diving petrels (*Pelecanoides georgicus*) on Codfish Island. *Notornis* **36**, 157–158.
- Wood, J.R. & Briden, S. (2008). South Georgian diving petrel (*Pelecanoides georgicus*) bones from a Maori midden in Otago Peninsula, New Zealand. *Notornis* **55**, 46–47.
- Worthy, T.H. (1998). Fossils indicate *Pelecanoides georgicus* had large colonies at Mason Bay, Stewart Island, New Zealand. *Notornis* **45**, 229–246.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Hypothetical detection probabilities ($p_{d,t}$) with values varying between 0.1 and 0.9 as a function of time to aid experts in their decision-making during an expert elicitation.

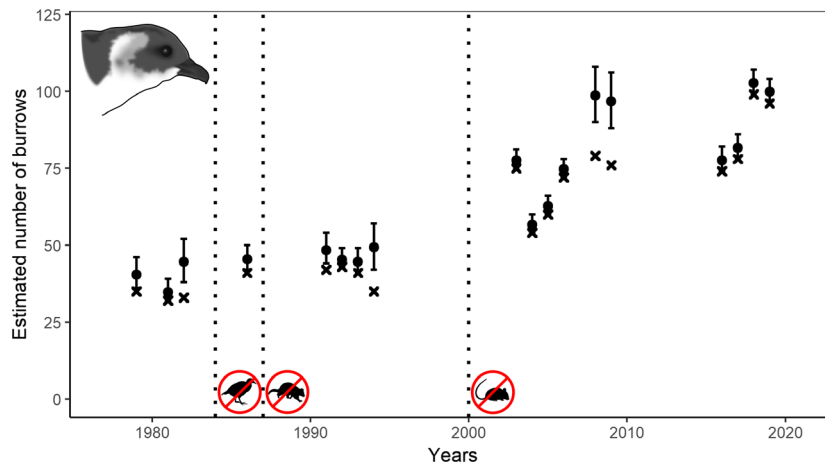
Figure S2. Raw Whenua Hou Diving Petrel burrow counts (crosses) and retrospectively corrected estimates (; filled circles with 95% credible intervals), based on $p_{d,t}$ distributions informed by the most pessimistic expert, in relation to invasive predator eradications (dotted lines).

Figure S3. Raw Whenua Hou Diving Petrel burrow counts (crosses) and retrospectively corrected estimates (; filled circles with 95% credible intervals), based on $p_{d,t}$ distributions informed by the most optimistic expert, in relation to invasive predator eradications (dotted lines).

Appendix S1. Abstract in *Te Reo Māori*/the Māori language.

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main article.



The eradication of invasive predators from islands is a successful technique to safeguard seabird populations, but adequate post-eradication monitoring of native species is often lacking. To estimate the population growth rate (λ) of Whenua Hou diving petrels (WHDP) before and after predator eradications, we used log-linear models in a Bayesian hierarchical framework while retrospectively accounting for differences in detection probabilities among burrow counts, due to differences in effort, marking and timing. Results showed a comparatively low post-eradication λ and an apparent lack of change between pre- and post-eradication λ , indicating that additional threats might be limiting WHDP population growth and that further conservation management is required.