

Spatio-temporal changes in density and distribution of burrow-nesting seabird colonies after rat eradication

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Abstract: The size and distribution of colonies of burrow-nesting petrels is thought to be limited partly by the availability of suitable breeding habitat and partly by predation. Historically, the availability of safe nesting habitat was restricted in New Zealand, due to the introduction of rats by humans. More recently, however, habitat has been restored by rat eradication. Petrel colony growth is mediated by both positive and negative density dependence, although it is unclear if, or how, density dependence will affect patterns in post-eradication colony recovery. Here, using burrow density as a proxy for relative abundance, we tested whether petrel colonies increase in density or area after rat eradication by sampling along a chronosequence of (1) five islands from which rats were eliminated 1 to 26 years ago, (2) two islands that never had rats, and (3) an island with rats still present, while controlling for habitat availability. We also measured a time series of burrow densities in plots on each island to compare temporal changes after rat eradication. Using Bayesian hierarchical modelling, after controlling for nesting habitat, we found that mean burrow density increased with time since rat eradication. Burrows remained clustered (i.e. spatially structured), but became more randomly distributed on islands with more time since eradication. Point density mapping indicated that colony extent increased with time since rat eradication, with colonies filling over 70% of surveyed areas on islands by 25 years after eradication. Increases in burrow density and colony area, but maintenance of clustered distribution, suggest both positive and negative density dependence may operate during colony expansion. Understanding patterns in petrel colony recovery is important, not only due to the indispensable role of petrels as island ecosystem engineers, reflecting the recovery of ecosystem functioning, but also to help guide post-eradication monitoring strategies.

Keywords: density dependence; eradication; ideal despotic Allee model; Procellariiformes; recovery; restoration; rodents

Introduction

Across the globe, the introduction of predators by humans has been implicated in the extinction, extirpation, or severe population reduction of numerous island species (Atkinson 1989; Towns et al. 2006). The most widespread of invading predators are rodents, which have invaded 90% of island groups (Jones et al. 2008). Colonial, burrow-nesting petrels (order: Procellariiformes) are particularly vulnerable to rodent introduction because of their easily accessed nests and lack of appropriate anti-predator behavioural adaptations (Moors & Atkinson 1984). Because petrels act as ecosystem engineers, providing islands with indispensable sources of nutrients and physical disturbance, the reduction of their populations has had dramatic cascading effects on island ecosystems (Croll et al. 2005; Fukami et al. 2006; Smith et al. 2011). Over the past three decades, efforts to eradicate introduced rodents and restore islands have accelerated, with over 800 islands cleared of rats and all other types of vertebrate pests (Keitt et al. 2011). Because petrels engineer island habitat, population response will likely play a disproportionately large role in the recovery of ecosystem functioning. Yet only now are factors

driving petrel colony recovery being studied (Jones 2010a; Buxton et al. 2014).

After predator eradication, the re-colonisation, re-distribution, and growth of an affected colony of seabirds is a complex process, with multiple ecological and anthropogenic drivers (Buxton et al. 2014). The structure of a remnant colony will depend on the type of predator, the vulnerability of different species to predation, and the spatio-temporal nature of interactions between predators and seabird prey (Jones et al. 2008; Lavers et al. 2010). As populations grow and recruitment increases, the selection of a nesting site will be both positively and negatively density-dependent (Crespin et al. 2006). Positive density dependence will initially be important, where colonial animals are more likely to settle among conspecifics owing to increased potential of finding mates, diluted predation risk, and indication of high-quality nesting habitat (Wittenberger & Hunt 1985; Danchin & Wagner 1997; Schippers et al. 2011). However, as more birds settle, inter- and intra-specific competition will eventually force new recruits into new, unoccupied habitat (Forbes & Kaiser 1994). This model of seabird colony growth is known as the 'ideal despotic Allee model': a hybridisation of the 'ideal

Allee' model, where the benefits of group living result in inverse density-dependence in small groups, and the 'ideal despotic' model, where dominant individuals secure good quality territories and force others into less favourable habitat (Fretwell & Lucas 1969; Fretwell 1972; Kildaw et al. 2005). The ideal despotic Allee model is thought to typify seabird colony formation and growth and could readily be used to examine colony recovery after predator removal.

The wide-reaching effects of predator introduction are well-exemplified in New Zealand, where rodents have invaded over 45% of islands ≥ 5 ha in the archipelago (Holdaway 1999; Towns et al. 2006) since the arrival of humans and rats in the 13th century AD (Wilmshurst et al. 2008). Fossil evidence suggests that the combined effects of disturbance, habitat alteration, and, notably, predation by introduced mammals such as rodents, have restricted once widespread burrow-nesting seabird populations to predator-free offshore islands (Jones 2000; Taylor 2000). The reduction in seabird numbers has resulted in reduced soil fertility and altered above- and below- ground ecosystem dynamics (Fukami et al. 2006). In response, New Zealand has performed more successful rodent eradications than any other country, resulting in over 30 000 ha of newly predator-free breeding space (Towns et al. 2013), and enormous opportunity for investigating how petrels respond to rodent eradication.

Although rodent eradication from islands has become extremely successful, evaluating the ecological response to such island restoration, especially for petrels, remains uncommon. Moreover, robust and consistent post-eradication monitoring programmes have yet to be designed for offshore islands in New Zealand. Developing a model of population growth in order to develop *a priori* predictions about recovery is one of the fundamental elements of effective monitoring (Lindenmayer & Likens 2010). Thus, here we examined the density and spatial distribution of petrel burrows on recently rat-free islands off the north-eastern coast of New Zealand's North Island to draw inference on patterns in colony growth and recovery. We used the ideal despotic Allee model as a framework to develop predictions and interpret spatial patterns of burrows following eradication.

Since no pre-eradication data were available, we used a chronosequence approach (space-for-time substitution), where a series of islands representing a chronological sequence of

increasing time since eradication were used (Perrow & Davy 2002). We compared the density and spatial distribution of petrel burrows on eight islands that varied in the presence, absence, or times since eradication of Pacific rats (kiore, *Rattus exulans*). We hypothesised that when rats are present or were recently removed, birds will recruit into remnant colonies, making burrows clustered in distribution, burrow area limited, and burrow density low. As time passes after eradication, more birds recruit, and colonies grow; burrow density will increase and eventually colonies will expand in area and burrows will become less clustered in distribution. We counted burrow entrances along transects, measured burrow density and a suite of habitat variables in plots, and re-measured burrow density in a time series after rat eradication to address four questions. First, does burrow density or burrow clustering increase on islands with more time elapsed since rat eradication? Second, does the spatial extent of a colony increase on islands with more time since rat eradication? Third, does the relationship between burrow density, the spatial extent of burrows, and time since rat eradication change after controlling for nesting habitat availability? Fourth, are changes in burrow density along the chronosequence reflected in changes in burrow density over a time series within an island?

Methods

Study area and species

We assessed burrow density on eight islands off the north-eastern coast of New Zealand's North Island (Fig. 1). Five islands represented 1–26 years of recovery after eradication (Table 1): Pacific rats and European rabbits (*Oryctolagus cuniculus*) were eradicated from Korapuki, Kawhitu, and Ohinau in 1986, 1991, and 2005 respectively; and Pacific rats were eradicated from Whakau (Red Mercury) and Taranga in 1992 and 2011 respectively. Mauitaha (22 ha) is still inhabited by Pacific rats, whereas two islands, Ruamaahuanui (21 ha) and Atiu (13 ha), never had mammalian predators introduced.

All islands are within 7–13 km of New Zealand's mainland and have similar climate, geology, and vegetation structure. Climate is warm-temperate, soils are volcanic in origin and thus very friable, and dominant vegetation includes pōhutukawa (*Metrosideros excelsa*), kānuka/mānuka (*Kunzea ericoides*/

Table 1. Eight islands off the north-eastern coast of New Zealand's North Island surveyed for burrow-nesting seabirds using plots, transects, cluster analysis (Cluster), and plots assessed in a time series (Time series). Each island differs in the presence ('still present'), absence ('n/a'), or time since rat eradication.

Island	Area of island (ha)	Year rats eradicated	Month surveyed	Transects	Plots	Year surveyed	Cluster	Time series
Mauitaha	22	still present	December/October	31	68 ^a	2011/2012	Y	N
Taranga	470	2011	November/October	61	120 ^a	2011/2012	Y	N
Ohinau	32	2005	October	33	100 ^a	2012	Y	N
Kawhitu	100	1991	November	35	132 ^a	2012	Y	Y
Whakau	220	1992	October	n/a	10 ^b	1998	N	N
Korapuki	18	1986	December	41	101 ^a	2012	Y	Y
Ruamaahuanui†	21	n/a	November	n/a	76 ^a	2010	N	Y
Atiu	13	n/a	November	n/a	13 ^c	2003	N	N

^a 3-m radius circular plots

^b 4-m radius circular plots

^c 40 m² rectangular plots

† Data from Whitehead et al. (2014)

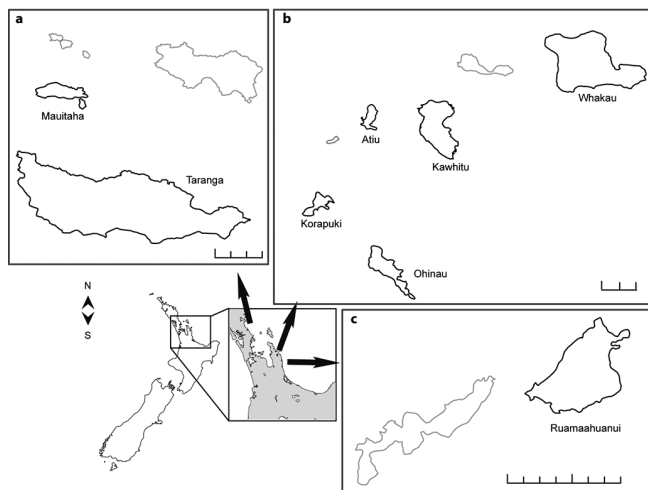


Figure 1. Location of study islands off the north-eastern coast of the North Island, New Zealand, including those in the Hen and Chicken group (a), the Mercury group (b), and the Aldermen group (c). Full scale bars indicate 1 km. Distance between islands has been reduced.

Leptospermum scoparium), and māhoe (*Melicactus ramiflorus*) (Sladden & Falla 1928; Edgar 1962; Wright 1978; McCallum et al. 1984; Taylor & Lovegrove 1997; Atkinson 2004; NIWA 2012). All islands were extensively burned and terraced by the first Polynesian settlers; thus, current vegetation reflects post-fire succession (Sladden & Falla 1928; Edgar 1962; McCallum et al. 1984). All islands have remained relatively undisturbed since the mid-19th century and are currently protected as nature reserves, primarily for the conservation of native terrestrial ecosystems (Towns et al. 2013), and with restricted public access.

Seven species of burrow-nesting seabirds in the order Procellariiformes were present on the islands: grey-faced petrel (*Pterodroma macroptera gouldi*), fluttering shearwater (*Puffinus gavia*), flesh-footed shearwater (*Puffinus carneipes*), little shearwater (*Puffinus assimilis*), common diving petrel (*Pelecanoides urinatrix*), sooty shearwater (*Puffinus griseus*), and Pycroft's petrel (*Pterodroma pycrofti*). Limited available information suggests that burrows of all species tend to be sympatric, with more association between species than expected by chance (Hicks et al. 1975; Pierce 2002). Although some species have different physical nesting habitat preferences, general habitat use overlaps (Buxton 2014).

Field surveys

We used a systematic sampling approach to estimate burrow density and area, involving transects and plots on five islands: Mauitaha, Taranga, Ohinau, Kawhiti, and Korapuki (Table 1). A burrow was defined as a cavity >20 cm in length in the soil or below a rock or log, with an entrance >12 cm² (measured using a soil probe marked at 6 and 20 cm).

To distribute surveys evenly over the entire surface of each island, we ran search transects from coast to coast at even intervals perpendicular to an island's long axis. The resulting distance between transects was between 10 and 40 m, depending on island size. Transect direction was determined by compass bearing. Because of the steep terrain on Taranga, transects were shorter and constrained by proximity to existing tracks.

To estimate burrow density, we surveyed between one and six 3-m-radius circular plots along each transect at randomly-assigned distances. This resulted in a total of 68–132 plots on each island (Table 1). Within each plot we counted all seabird burrows where the midline of the entrance fell within plot limits. To assess the degree of burrow clustering on the five island transects, we measured and compared the distance between the plot centre (a random point) to the nearest burrow and the distance from that burrow to the nearest neighbouring burrow. Generally, on islands with low density (Mauitaha and Taranga), only one burrow could be found within plot limits. Thus, to maintain consistency, we used measurements to only one nearest neighbouring burrow per plot on all islands.

It was not possible to search transects on Ruamaahuanui because of high burrow density and thus high risk of burrow collapse. Instead, we used similar surveys of 3-m-radius circular plots whose locations were allocated randomly as part of a previous study (Whitehead et al. 2014). Burrow density estimates on Whakau and Atiu were based on opportunistic surveys from previous studies, involving 4-m-radius circular plots and 40-m² search transects respectively (GT unpubl. data; Table 1).

To estimate burrow area we searched 1 m either side of transect centre lines for seabird burrows. Each burrow was marked as a waypoint using a handheld satellite navigation system (GPSMAP 60CSx Garmin, Kansas, USA). We searched between 31 and 61 transects on Mauitaha, Taranga, Ohinau, Kawhiti and Korapuki (Table 1).

Finally, to account for nesting habitat availability on each island, we recorded key nesting-habitat variables in each 3-m-radius plot: aspect, slope, elevation, topography, soil depth, soil strength, soil texture, percentage cover of boulders, stem count for each species 2.5–10 cm in diameter at breast height (dbh), canopy species and percent cover. Habitat survey methods are detailed in Buxton et al. (2015).

Historical time-series data

To compare results from the chronosequence of islands with actual measures of change in burrow density over time, we examined permanent plots with time series of burrow counts where available. Plots with annual counts of burrow density after eradication were available on two islands, Kawhiti and Korapuki, and for one island (Ruamaahuanui) that never had rats (Table 1).

On Kawhiti, petrel burrow density was assessed in 1993, 1998, and 2003 using two methods: 5-m-radius circular plots every 10–20 m along a transect and three groups of small adjacent square plots, consisting of one 400-m² plot, assessed in 16 increments of 25 m². Circular plots were placed at every marker along the main north-western track from sea level, while square plots were placed randomly in the centre of the northern part of the island.

On Korapuki and Ruamaahuanui, 20 permanent occupancy plots of 100 m² were placed randomly over the surface of each island. The four corners of each plot were marked with aluminium poles and each burrow was marked with a cattle tag. In 2003 and 2012 on Korapuki, burrow abundance was also assessed within 21 transects of 40 m² (20 m long, searching 1 m either side of the centre line) deviating from the main ridgeline track.

Data analysis

To examine the relationships between burrow density and

clustering with time since eradication, we used a Bayesian hierarchical modelling approach. Because we were interested in burrow abundance among islands with varying availability of nesting habitat, we selected a hierarchical approach, which aligns complex data from various sources (Ellison 1996; Cressie et al. 2009). All models were fitted using OpenBUGS (Lunn et al. 2000), called from R version 2.14.2 using BRugs and R2WinBUGS (Sturtz et al. 2005; Thomas et al. 2006; R Development Core Team 2012). To ensure convergence and minimise autocorrelation between chains, we ran 40 000 iterations with a burn-in of 10 000 and a thinning rate of 20 on three chains (Gelman et al. 2004).

Burrow density and clustering

To examine the relationship between time since eradication and burrow density (i.e. burrow entrances per m²), we used a varying intercept Bayesian hierarchical regression model. We modelled burrow density (X_{jk}) as:

$$X_{jk} \sim \text{Normal}(\psi_{jk}, \sigma_{jk}^2) \quad (1)$$

where ψ_{jk} was the mean predicted density of burrows in plot j on island k , with precision σ_{jk}^2 , and was estimated in a linear regression of the form:

$$\psi_{jk} \sim \alpha_{jk} + \beta_{tse} TSE + \sum_{l=1}^L \beta_{lk} x_{lk} \quad (2)$$

where β_{tse} was the rate at which burrow density increased with the number of years after eradication, and β_{lk} was the effect of nesting habitat variation among islands k and environmental covariates l . Environmental covariates included soil depth, southern and western aspect, slope, rock cover, karamū (*Coprosma macrocarpa*) stem count, māhoe (*Melicytus ramiflorus*) stem count, and total stem count, and were selected based on habitat selection models (Buxton et al. 2015). The intercept (α_{jk}) came from a prior distribution of hyper-parameters M_α and σ_α^2 :

$$\alpha_{jk} \sim \text{Normal}(M_\alpha, \sigma_\alpha^2), \quad (3)$$

$$M_\alpha \sim \text{Normal}(0, 1000), \quad (4)$$

$$\sigma_\alpha^2 \sim \text{InverseGamma}(0.1, 0.1) \quad (5)$$

The prior distribution of β_{lk} was based on hyperparameters M_{β_n} and $\sigma_{\beta_n}^2$, with the same structure as Eqns 3–5, while β_{tse} had a non-informative prior distribution (i.e. $\beta_{tse} \sim \text{Normal}(0, 1000)$) (Gelman & Hill 2007).

We ran two separate models: one excluding environmental covariates ($\sum_{l=1}^L \beta_{lk} x_{lk}$, Eqn. 2), including density data from all eight islands; and another including environmental covariates and only six islands with habitat data, to determine the effect of nesting habitat availability on change in burrow density after eradication. Posterior distributions were summarised by generating mean β_{tse} values (and mean β_{lk} for the model including environmental covariates) with 95% credible intervals (CI). To quantify model fit, we regressed observed burrow density versus model-predicted burrow density and compared the slope (r^2) with a 1:1 relationship (Piñeiro et al. 2008).

To examine the degree of burrow clustering, we compared the distances between random points and burrows and between neighbouring burrows with time since eradication on five islands (Mauiitaha, Taranga, Ohinau, Kawhitu, and Korapuki). We used two models with similar structure to Eqns 1 and 2; one where ψ_{jk} was the mean predicted distance between random points and burrows and one where ψ_{jk} was the mean

predicted distance between neighbouring burrows. If neither distance changed with relation to time since eradication, we assumed no difference in clustering. If distances between random points and burrows decreased (relative to distances between neighbouring burrows) with time since eradication, we interpreted this as a decrease in the amount of clustering.

Burrowed area

To determine the spatial extent of burrowed areas (hereafter ‘colonies’), all calculations were performed in ArcGIS for Desktop (10.1, ESRI Inc., USA). We first calculated point densities of burrows marked during transect (or, in the case of Ruamaahuanui, plot) searches. In ArcMap, ‘point density’ calculates the density of point features, in this case burrows, in a neighbourhood defined around each output raster cell (Silverman 1986). We used a neighbourhood radius size of 10 m, because most burrows still considered to be within a cluster were found at this distance (RTB unpubl. data), and a raster size of 15 × 15 m, which matched the reference frame of digital elevation models (DEM) used below. We then reclassified point densities into three classes – low (1–15 burrows), medium (16–30 burrows), and high (31+ burrows) – and converted them to polygons. The total area of each polygon, representing a colony of particular density class, was then calculated using the ‘calculate areas’ tool in ArcMap spatial statistics. The total area of colonies of each density class was corrected for survey effort and island size by dividing by survey area and island surface area. Finally, we created a raster layer of surveyed areas (along transects) with and without burrows present.

To estimate the effects of varying nesting habitat availability on colony area, we compared observed presence of a burrow in a raster (above) with burrow presence predicted from models of habitat use. If burrows were present in a large proportion of rasters where predicted probability of use was high (>50%), this suggested that birds were nesting in, and potentially filling, suitable habitat. Whereas, if burrows were absent from a large proportion of habitat where predicted probability of use was high, this suggested that birds were not occupying potentially suitable habitat (i.e. habitat availability was not necessarily a limiting factor).

To build predictive habitat models, the presence of a burrow in a raster was modelled as a binomial process:

$$Y_{jk} \sim \text{Bernoulli}(\varphi_{jk}) \quad (6)$$

where the probability of a burrow being present (φ_{jk}) in plot j on island k was estimated in a logistic regression based on the form:

$$\text{logit}(\varphi_{jk}) = \alpha_{jk} + \sum_{l=1}^L \beta_{lk} x_{lk} \quad (7)$$

where x_{lk} were the environmental covariates l and β_{lk} were the associated parameters. We included only environmental covariates that were available as GIS layers from DEMs: slope, elevation, and categorical aspect. Aspect was transformed into a dummy variable by setting one class as a reference class with a coefficient of zero (Hardy 1993). The intercept α_{jk} and parameters β_{lk} were given similar prior distribution as shown in Eqns 3–5. To determine which combination of environmental covariates resulted in the best predictive power, we examined the deviance information criterion (DIC; Spiegelhalter et al. 2002) and area under the receiver-operator characteristic curves (AUC, PresenceAbsence package; Freeman & Moison 2008). DIC values represent model fit and are penalised by the number of effective parameters; however, the number of

parameters is not clearly defined for multilevel models and is unstable, even from simulations that have converged (Zhu & Carlin 2000; Gelman & Hill 2007). AUC values vary between 0 and 1, with values ≤ 0.6 indicating a model performance no better than random, and values ≥ 0.7 considered useful; however, AUC values are also known to be unreliable in certain situations (Fielding & Bell 1997; Lobo et al. 2008). Thus we assessed model fit using a combination of the lowest DIC and highest AUC value.

To estimate where burrows would be present, we predicted the probability of presence within rasters in DEMs from Land Information New Zealand (LINZ; Columbus et al. 2011). We calculated slope, elevation, and aspect within rasters using the spatial analysis extension in ArcMap. Aspect rasters were separated into north, south, east, and west. We limited predictions to rasters with point density data (i.e. along transects).

Time-series

To examine the relationship between years and burrow density in permanent plots measured as a time series (Table 1), we used a separate Bayesian linear regression model for each island, where burrow density was modelled as:

$$X_j \sim \text{Normal}(\varphi_j, \sigma_j) \quad (8)$$

where (φ_j) was the mean predicted density of burrows in plot j with precision σ_j , and was estimated in a linear regression of the form:

$$\varphi_j \sim \alpha_j + \sum_{l=1}^L \beta_l x_l \quad (9)$$

On Kawhitsu and Korapuki, where different plot types were used, covariates x_l included the effects of year and plot type; while x_l for Ruamaahuanui included year only. Both α_j and β_l had non-informative prior distributions.

Results

Burrow density and clustering among islands

We estimated the relationship between burrow density and time since eradication by counting burrow entrances in 707 plots among eight islands (Table 1). We found that burrow density was positively related to time since eradication (mean effect size 0.003, 95% CI 0.001–0.015; Fig. 2a). However, this model had low predictive power ($r^2 = 0.11$). To remove the effects of variation in habitat availability between islands, we used burrow entrance data and environmental covariates from 597 plots on six islands. In this model, burrow density was still positively related to time since eradication, although the relationship was weaker (mean effect size 0.002, 95% CI 0.001–0.011, $r^2 = 0.42$; Fig. 2b). On at least one island, burrow density was also positively related to soil depth, slope, rock cover, southerly aspect, and the presence of māhoe and karamū (*Coprosma macrocarpa*) stems (Appendix S1 in Supplementary Material).

We found no evidence of change in distance between neighbouring burrows with time since eradication (95% CI overlapped zero: -1.0 to 0.1). Distance between random points and burrows decreased on islands with more time since eradication (mean effect size -2.6 , 95% CI -5.7 to -0.1). On Korapuki, an island with more than 25 years since eradication, the ratio between distances of random points to burrows and between neighbouring burrows was close to one (Fig. 3). This

indicated that burrows were less clustered (more randomly distributed) on islands with more time since eradication.

Burrow area among islands

We searched a total of 214 transects on five islands (supplemented with 76 plots on Ruamaahuanui). Using point density functions we found a total of 5 colonies on Mauitaha (Pacific rats present), 91 on Taranga (rats removed 2011), 117 on Ohinau (rats removed 2005), 451 on Kawhitsu (rats removed 1991), 179 on Korapuki (rats removed 1986), and 84 on Ruamaahuanui (rats never introduced). The maximum density of colonies increased with time since eradication from 1.78 (burrows/225 m² raster) on Mauitaha to 247.22 (burrows/225 m² raster) on Ruamaahuanui. Total burrowed

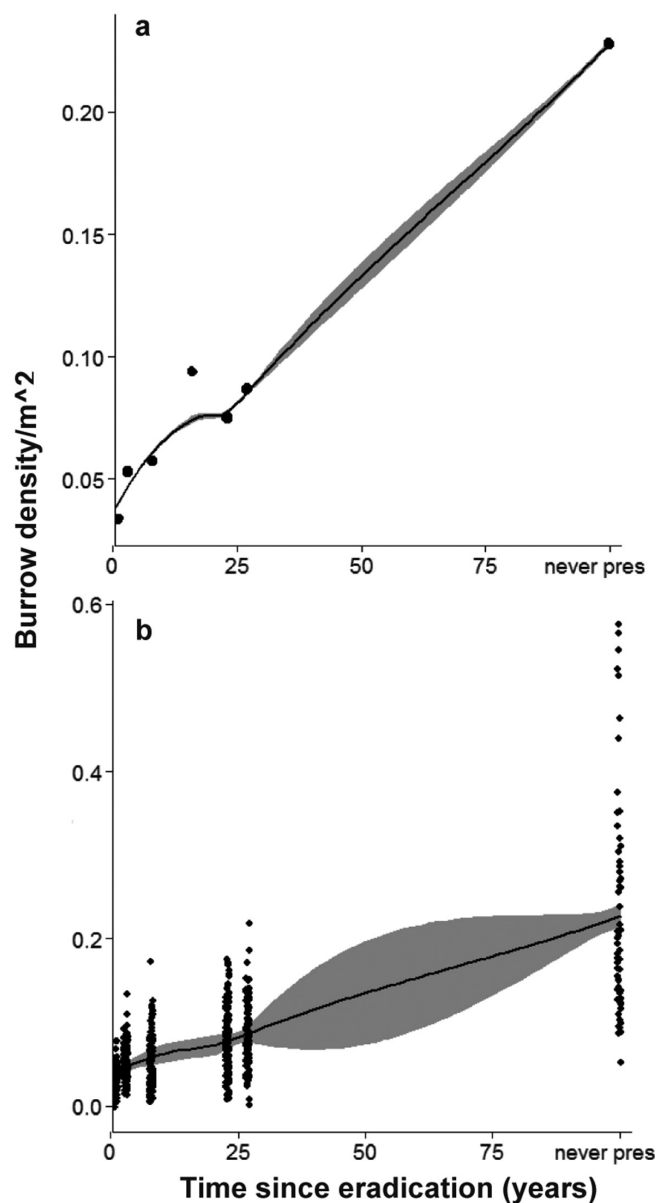


Figure 2. Predicted burrow density (per m²) at different time periods after rat eradication. Lines represent the mean posterior effect size from Bayesian hierarchical models of burrow density versus time since rat eradication (a), with the effects of nesting habitat included (b). Grey shading represents loess slope smoothing based on the variation in predicted densities.

area, in proportion to survey and island area, was larger on islands with more time since eradication, from 0.007 on Mauitaha, 0.001 on Taranga, 0.06 on Ohinau, and 0.04 on Kawhiti, to 0.15 on Korapuki, and 0.37 on Ruamaahuanui (Figs 4 and 5). Finally, the proportion of area searched with at least one burrow increased with time since eradication from

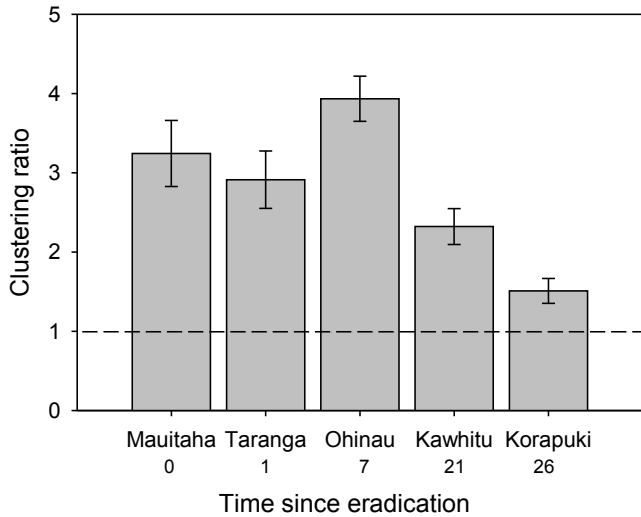


Figure 3. Ratio (‘clustering ratio’) between the distances of random points and burrows and between neighbouring burrows (\pm standard error) on islands off the north-eastern coast of New Zealand’s North Island with different times since Pacific rat (*Rattus exulans*) eradication (number of years since eradication on the x-axis). A clustering ratio of one (dashed line) indicates no spatial structuring among burrows.

0.31 on Mauitaha, 0.37 on Taranga, 0.39 on Ohinau, 0.50 on Kawhiti, and 0.71 on Korapuki, to 0.93 on Ruamaahuanui.

Predictive habitat models of burrow presence with the highest predictive power ($AUC = 0.77 \pm 0.02$) included slope, elevation, aspect, and the interaction between slope and aspect (Appendix S2). Burrows were more likely to be found in areas with steeper slopes (Appendix S3). Islands with less time since eradication (and smaller colony area; Fig. 5) had a higher proportion of rasters with high predicted probability of use but no burrows present (Table 2). This suggested that although the habitat was suitable, burrows were absent; that is, habitat was not limiting burrow distribution. Conversely, on islands with more time since eradication (with larger colony area), there was a low proportion of rasters with burrows absent where predicted probability of burrow presence was high. This suggested that birds were filling suitable habitat. Furthermore, on islands with more time since eradication, burrows were present in a higher proportion of rasters with low predicted probability of presence, suggesting that birds were also occupying less suitable habitat (Table 2).

Burrow density time series

Although we had a low sample size, results from our (intra-island) burrow density time series model confirmed chronosequence results. On Kawhiti and Korapuki, islands with rats removed 21 and 26 years ago respectively, we found a small rate of burrow density increase within permanent plots over time (mean effect sizes 0.005 and 0.001 respectively; Table 3). On Ruamaahuanui, a predator-free island, we found no evidence of burrow density increase with year, as 95% CIs overlapped zero (mean effect size 0.003; 95% CI -0.002 to 0.008).

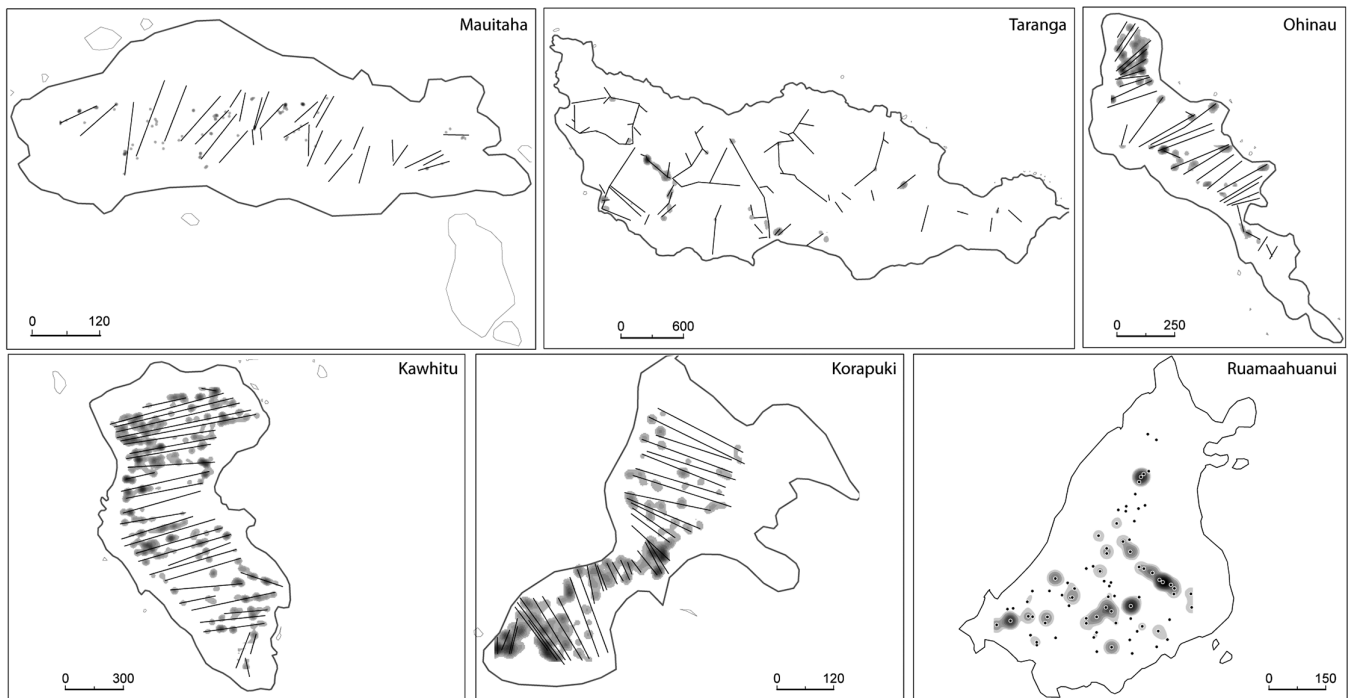


Figure 4. Point density functions calculated from burrows marked along search transects (black lines) or within plots (dots) from islands off the north-eastern coast of New Zealand’s North Island. Islands are arranged with increasing time since Pacific rat (*Rattus exulans*) eradication from left to right, top to bottom, where rats are still present on Mauitaha and were never introduced to Ruamaahuanui. Darker shades of greyscale indicate higher density burrow clusters. Scale bars indicate distances in metres.

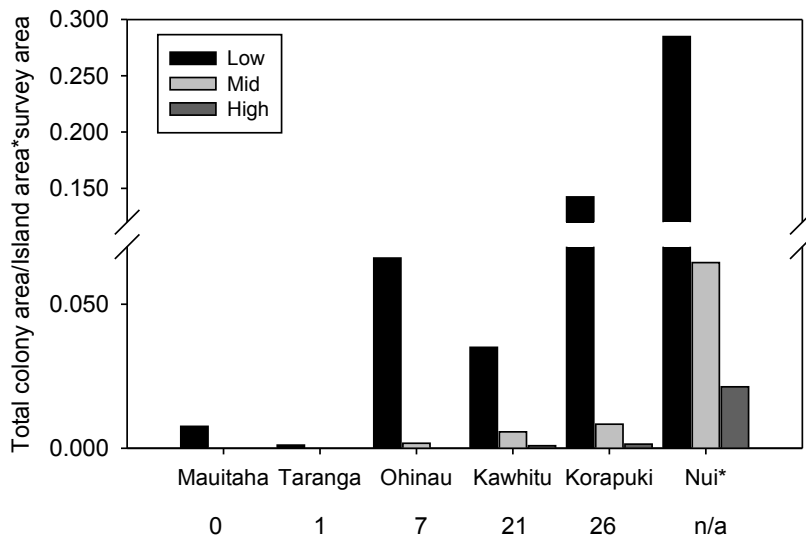


Figure 5. Proportion of island area with ≥ 0.001 burrows/m² measured using point density calculations and corrected for surveyed area ('Proportional colony area') on six islands off the north-eastern coast of New Zealand's North Island, each with a different amount of time since rat eradication (years since eradication indicated on the x-axis). Burrow densities per 225-m² raster were low (1–15 burrows), mid (16–30), and high (≥ 31 burrows).

*Ruamaahuanui

Table 2. Total proportion of rasters with burrows present (Burr pres) or absent (Burr abs) on six islands off the north-eastern coast of New Zealand's North Island, where the predicted presence (P(pres)) from predictive habitat models of a burrow was greater or less than a threshold† (T). Islands are in ascending order from least to most time since Pacific rat (*Rattus exulans*) removal, where Mauihaha still has rats present and Ruamaahuanui never had rats introduced.

Island	Burr abs, P(pres)>T	Burr pres, P(pres)<T	Burr pres, P(pres)>T	Burr abs, P(pres)<T
Mauihaha	0.37	0.13	0.18	0.32
Taranga	0.32	0.11	0.26	0.30
Ohinau	0.25	0.17	0.21	0.37
Stanley	0.22	0.20	0.29	0.29
Korapuki	0.16	0.39	0.32	0.13
Ruamaahuanui	0.07	0.34	0.55	0.04

†The threshold was calculated as the mean predicted probability on each island (Liu et al. 2005)

Table 3. Median effect sizes and 95% credibility intervals from Bayesian logistic regression models predicting the relationship between years since Pacific rat (*Rattus exulans*) eradication (on Kawhitsu and Korapuki) and petrel burrow density in permanent plots on three islands in north-eastern New Zealand.

	Year rats eradicated	Years measured	Median effect size	Credible intervals	
				5%	95%
Kawhitsu	1991	1993, 1998, 2003	0.001 [†]	0.0002	0.003
Korapuki	1986	2003, 2010, 2012	0.005 [†]	0.002	0.009
Ruamaahuanui	Never present	2006-2008, 2010, 2012	0.003	-0.002	0.008

† Credible intervals do not overlap 0, indicating strong evidence for a relationship between years and burrow density within an island

Discussion

Our results indicate that on islands where more time has elapsed since rat eradication, mean burrow density was higher and colony area greater. Although burrows were clustered in distribution on all islands, clustering decreased on islands with more time since eradication. These results suggest that both burrow density and burrowed area may increase on islands after rat eradication. Furthermore, both positive and negative density dependence may be mediating recruitment and colony growth; birds initially recruit into attractive remnant colonies until crowding forces birds to settle in new empty habitat.

Changes in burrow density and distribution

A common assumption in petrel ecology is that predator removal may be insufficient to achieve population recovery, owing to high levels of philopatry, low incidence of new colony formation, long generation times, low reproductive output, and at-sea conditions impeding passive recovery (Warham 1996; Jones & Kress 2012). However, increasing evidence suggests that seabird island ecosystem restoration through burrow-nesting seabird population recovery, may occur within a few decades after eradication (Jones 2010a, b), although patterns and rates of recovery of the birds themselves were unknown (Buxton et al. 2014). Our data demonstrate that petrel

burrow density increased among islands with more time since rat eradication at an annual rate as great as 0.01 burrows/m² (Table 3). This rate of increase is similar to those found in other burrow-nesting seabird populations after predator eradication: for example, a colony of ancient murrelets (*Synthliboramphus antiquus*) doubled in size 5 years after the removal of black (*Rattus rattus*) and Norway rats (*R. norvegicus*), while two species of tropicbirds (red-billed *Phaethon aethereus* and white-tailed *P. lepturus*) recolonised and grew in population size by 2% per year after the removal of feral cats (*Felis catus*; Regher et al. 2007; Ratcliffe et al. 2010).

We found the highest level of burrow clustering was on islands with rats still present or recently removed, while clustering decreased on islands with more time since eradication (Fig. 3). We infer that the presence of Pacific rats may have restricted petrels to nest in clusters where they could minimise predation. For example, nest sites may persist where petrel density was high before rat invasion and predation was swamped or in areas infrequently used by predators (Lyver et al. 2000; Regher et al. 2007). Because rodents generally use all areas of an island (Moller & Craig 1987), the former explanation is the most likely. Furthermore, when predators are present, many colonial seabirds are known to have higher breeding success and lower mortality in larger, denser colonies (Gilchrist 1999; Cuthbert 2002). Clustering was highest on Ohinau, an island with 7 years since eradication. This may reflect philopatry and conspecific attraction, where individuals initially recruiting after eradication establish near previously occupied remnant breeding habitats, thus increasing clustering (Warham 1990; Forbes & Kaiser 1994; Whitworth et al. 2013).

Finally, we found that the extent of burrowed areas increased with time since eradication: burrows were found in 50% of areas searched on islands with 20 years since rat eradication and in over 70% of areas searched on islands with over 25 years since eradication. Expansion of colony area has been reported in several seabird species in response to increased nesting habitat, either due to climate change (LaRue et al. 2013), the creation of habitat by humans (Sherfy et al. 2012), or the removal of a source of mortality (i.e. predation or hunting; Kress 1997; Keitt & Tershy 2003; Whitworth et al. 2013).

We postulate that the pattern of burrow density and distribution found in our study suggests the ideal despotic Allee model may apply to petrel recruitment and colony growth after rat eradication (Kildaw et al. 2005). An increase in burrow density and maintenance of burrow clustering on islands with more time since eradication suggest that persisting colonies may be initially attractive. The attractiveness of established colonies to new recruits is thought to be pervasive among gregarious animals, such as burrow-nesting seabirds (Danchin & Wagner 1997). However, as time passes after eradication, and the number of recruits into remnant areas increases, established colonies may become crowded, making it more advantageous for recruitment into new habitat (Fretwell 1972; Forbes & Kaiser 1994). This was also observed in our data, where burrows were found in almost all suitable habitat (Table 3), colony area was greater (Figs 4 and 5), and clustering decreased on islands with more time since rat eradication.

Effect of nesting habitat abundance

Environmental covariates are known to affect the density and distribution of burrow-nesting seabirds (Buxton et al. 2015). Abiotic and biotic factors determining nesting habitat quality often include soil type, which must be soft enough to excavate, but strong enough to avoid collapse; canopy and

understorey vegetation, which adults must penetrate safely to reach their burrow; ground cover, which must be avoided or burrowed under; slope, which affects soil drainage; and aspect, elevation, and topography, which affect the ease of take-off and landing (Burger & Gochfeld 1991; Thompson & Furness 1991; Rodway et al. 1998; Bancroft et al. 2005a).

Our data suggest that environmental factors affected both burrow density and colony area. For example, among islands, higher burrow density was associated with deeper soil, the presence of large boulders, southern aspect, and the presence of māhoe and karamū stems (Appendix S1). Furthermore, burrows were more likely to be found in areas with steeper slopes (Appendix S3). However, there were large amounts of variation in burrow density and colony area that could not be explained by environmental factors alone (Table 2). For example, there was a large proportion of suitable habitat on Mauitaha, Taranga and Ohinau (Pacific rats still present, removed in 2011, and removed in 2005, respectively) that was not occupied with burrows. When habitat covariates were included in a model comparing burrow density with time since eradication, model fit increased, while the relationship between burrow density and time since eradication was still strong. We infer that, although nesting habitat is important in determining the distribution and density of petrel burrows, time since rat eradication still contributed to the final pattern of observed burrow distribution. We therefore conclude that although there may be interactive effects between colony recovery and nesting habitat quality, and that habitat should not be ignored, the effects of habitat are not necessarily enough to restrict increases in colony growth after eradication (Major et al. 2011; Buxton et al. 2015).

Potential caveats

Although we found a strong relationship between burrow density and colony area with time since rat eradication, caution must be taken when inferring a causal relationship with Pacific rat removal (Craig 1983; Jones 2001). Current distribution of burrow-nesting petrels on restored islands is likely to be shaped by a set of interacting variables including other introduced species (e.g. European rabbits), habitat modification, history of human harvesting, and historical distribution. We emphasise that, in this study, we use patterns of burrow distribution along the chronosequence of islands as a proxy for potential colony expansion after restoration, not as a direct indication of population recovery after rat removal.

In this study we use burrow density as a proxy for petrel abundance, as it has been shown to provide a temporally and spatially stable index of bird numbers (Rayner et al. 2007). Other indices, for example burrow occupancy assessed with infrared burrow cameras (Lyver et al. 1998), vary widely with season, at-sea conditions, and are associated with detection error (Sutherland & Dann 2012). However, burrow density alone may not be appropriate as a comprehensive index of population size, and more research is needed to examine the relationship between abundance and burrow density.

Finally, we did not distinguish between species in our analyses, despite the fact that grey-faced petrels and flesh-footed shearwaters were the most abundant species on islands (Buxton et al. 2013). Both species are relatively large and are thought to be less severely affected by the presence of Pacific rats (Priddel et al. 2006), in contrast to less common species, such as Pycroft's petrel and little shearwaters, which are known to have almost complete nest failure in the presence of Pacific rats (Pierce 2002). We are unsure how the varying abundances

of each species of different sizes affected results. Further research should focus on the differences or similarities in recovery dynamics of various burrow-nesting seabird species.

Conservation implications

Increase in burrow density and increase in burrowed area have several significant restoration and management implications. Because of seabirds' role as ecosystem engineers, the growth of burrow-nesting petrel colonies can provide important insights into island ecosystem recovery (Mulder et al. 2009; 2011). Burrow excavation alone alters the physical and chemical properties of soil, increasing porosity and the rate of soil-forming processes, and results in stronger and drier soil (Bancroft et al. 2005b). Thus, an increase in burrow density and distribution after rat eradication may reflect a rapid change in soil dynamics. It has been postulated that a burrow density of 0.3–1 burrow/m² is needed to promote ecosystem recovery to never-invaded levels (Townes et al. 2009; Jones 2010a). We found that mean burrow density on restored islands was less than half (<0.1 burrow/m²) that on the never-invaded Ruamaahuanui (>0.2 burrow/m²). Thus, although increases in the number of burrows after rat eradication may seem rapid, burrow densities on restored islands have probably not yet reached a level where seabird-dominated ecosystem functioning is possible (Jones 2010b).

The increase in burrow density observed in our study, without active intervention, raises the question: in which cases and to what extent should managers actively work to facilitate seabird recovery (Holl & Aide 2011; Jones & Kress 2012; Buxton 2014)? Our data contradict the idea of slow or non-existent petrel recovery and instead suggest that island managers should carefully consider when the benefits of active restoration outweigh the cost. Several techniques, such as vocalisation playback and chick translocation, have been developed to actively anchor seabirds into new habitat (Parker et al. 2007; Miskelly et al. 2009; Buxton & Jones 2012; Jones & Kress 2012). In order to actively speed petrel recovery on islands with remnant colonies, the most effective strategy may be to lure birds into new habitat, which they would only otherwise inhabit passively after filling remaining patches.

Despite our study having potential caveats, our data confirm that much valuable information can be ascertained from monitoring the passive recovery of seabirds after predator removal to guide ecological understanding and restoration. Generally, invasive predator eradication projects have been undertaken without adequate consideration of ecosystem-level goal-setting or pre-eradication data collection. Thus, many projects lack the capacity to reliably assess success, notably the impact of predator removal on seabirds (Phillips 2010). Our results can be used to guide potentially effective monitoring strategies. For example, our data show that an increase in colony density and extent are expected after eradication, which suggests that post-eradication monitoring should target areas that are already burrowed at the time of eradication, but also non-burrowed areas where colonies may spread in the future.

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Supplementary Material

Additional supporting information may be found in the online version of this article.

Appendix S1. Median effect sizes and 95% CI of habitat covariates and time since Pacific rat eradication

Appendix S2. Ranking of multivariate varying intercept models

Appendix S3. Median effect sizes and 95% CI from the top multivariate model predicting petrel burrow presence

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