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Release of constraints on nest-site selection in burrow-nesting petrels following invasive rat eradication

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Abstract Introduced mammals have been eradicated from many offshore islands around the world, removing predation pressure from burrow-nesting seabirds and other affected wildlife. Nest-site selection in procellariiform seabirds is mediated by nesting habitat characteristics and social information, although it is unclear if, or how, nest-site selection will affect post-eradication colony growth. Using a Bayesian hierarchical modeling approach we assessed how nest-site selection differs among burrow-nesting seabird colonies at different stages of recovery after Pacific rat (*Rattus exulans*) eradication. We compared nest-site selection in a community of seven procellariiform species among six offshore islands in northeastern New Zealand: four designated rat-free over a continuum within the last 26 years, an island which never had rats, and an island with rats present. We hypothesized that, immediately after eradication, birds would be constrained to nesting habitat where they were less vulnerable to predation, and as time since eradication increased birds would eventually spread to new habitat. We found a positive relationship between mean burrow density and time since rat eradication. Soil depth was the most important predictor of burrow presence, abundance, and occupancy in plots among islands, with more burrows found in deeper soil. We found that the relationships between habitat covariates and nest-site selection decreased with increasing time since eradication. The probability of a covariate having a significant effect on nest-site selection decreased with increasing time since eradication and decreasing variability in the covariate across an island. Our results suggest that the eradication of rodents reduced constraints on petrel nesting distribution and that nest-site selection in burrow-nesting petrels may be influenced by burrow density, where selection of particular nesting habitat characteristics may be relatively more important in small recovering populations. We conclude that colony expansion immediately after predator removal is complex, influenced by numerous interacting factors, but may be partly limited by the availability of suitable nesting habitat.

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Introduction

According to the fossil record, burrow-nesting petrels (order: *Procellariiformes*) once nested in abundance throughout the New Zealand archipelago (Holdaway et al. 2001). However, with the arrival of humans, petrels were largely extirpated from the mainland due to the combined effects of disturbance, habitat alteration, and predation by introduced mammalian predators (Jones 2000; Taylor 2000). Globally, the most widespread of invading predators are rodents, which affect seabirds directly, through predation (Atkinson 1985; Burger and Gochfeld 1994; Jones et al. 2008), and indirectly, by altering vegetation at nesting sites (Campbell and Atkinson 1999; Grant-Hoffman et al. 2009). Rodents have invaded over 40 % of islands in the New Zealand archipelago over the past 800 years (Towns et al. 2011), which has limited the availability of predator-free, unaltered nesting habitat.

Over the past 50 years, rodents and other vertebrate predators have been eradicated from over 90 islands in New Zealand; representing approximately 30,000 ha of newly predator-free nesting habitat (Clout and Russell 2006; Towns 2011). One of the main goals of eradication is to facilitate the re-colonization and colony expansion (hereafter "recovery") of affected burrow-nesting seabird populations (Jones et al. 2011). Evidence suggests that some seabird species have recovered on a number of islands after predator eradication (Buxton et al. 2013a; Jones 2010; Towns et al. 2006; Veitch et al. 2011). However, the key factors driving patterns of recovery has received relatively little research attention (Buxton et al. 2014).

The process of re-colonization and re-distribution of seabird species after rodent eradication is complex, with multiple ecological, behavioural, and anthropogenic drivers (e.g. natal philopatry, late age at first breeding, slow population dynamics; Buxton et al. 2014). Nesting habitat selection and availability could play a significant role in seabird recovery (Major et al. 2011). Nest site placement is a key reproductive decision for long-lived seabirds and is partly responsible for population regulation (Cody 1985; Forbes and Kaiser 1994). Depending on species' habitat requirements relative to availability, some sections of a newly predator-free island may not support recovery as well as others. Moreover, factors influencing nest locations are likely to differ among islands relative to predator invasion and eradication histories.

Breeding bird densities are generally higher in better quality habitat (Rosenzweig 1981; Stenhouse and Montevecchi 2000). Abiotic and biotic factors that determine nesting habitat quality for burrow-nesting seabirds include: soil type, which must be soft enough to excavate but strong enough to avoid collapse; canopy and understory 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 (Bancroft et al. 2005; Burger and Gochfeld 1991; Rodway et al. 1998; Springer 1991; Thompson and Furness 1991; Whitehead et al. 2014). In addition to these habitat characteristics, social factors are expected to influence nest-site selection. Most seabirds are colonial animals, and large colonies are highly attractive to sexually mature birds searching for nesting sites (Wittenberger and Hunt 1985). Evidence suggests that colonies act as "information centers", indicating high quality habitat (Doligez et al. 2003; Forbes and Kaiser 1994). Consequently, a potential nest site with relatively low quality habitat may be preferred if other breeding birds are present (Oro 2008; Stenhouse and Montevecchi 2000).

The presence of introduced predators can shape seabird nesting distribution by extirpating them from areas accessible to predators; thus limiting seabird nesting to refugia (e.g. cliffs or rocky tali; Buxton et al. 2013a; Drummond and Leonard 2010), or to habitats unsuitable for predators (Catry et al. 2007). Nest sites may also persist in areas where seabirds nest in high densities, where high numbers of birds are able to swamp the effects of predation (Cuthbert 2002; Jones 2003; Lyver et al. 2000; Regehr et al. 2007). When introduced predators are removed from an island, nesting habitat use will likely be governed by processes linked to the former presence of predators, until seabird populations begin to recover. As recovery proceeds and greater numbers of birds recruit into a newly-predator-free space, small remnant colonies are likely to be attractive initially (Danchin et al. 1998; Kildaw et al. 2005). As these sites become saturated through crowding, the "ideal-free" and "ideal-despotic" models (Fretwell and Lucas 1969; Fretwell 1972) predict that competition will eventually force recruits into new habitat.

In this study, we examined nest-site selection by burrow-nesting petrels along a chronosequence of

islands off the northeastern coast of New Zealand that vary in the presence, absence, or time since eradication of Pacific rats (*Rattus exulans*). Research suggests that Pacific rats suppress seabird population size by reducing breeding success (Towns 2009). We measured burrow presence, abundance, and occupancy in plots placed along linear transects to develop a nest-site selection model that addresses three questions. First, what habitat characteristics influenced nest-site selection along the chronosequence? Second, after accounting for the effect of habitat, did the presence of other nests influence nest-site selection? Third, how did time since rat eradication and other island-specific (e.g. nesting habitat availability) variables affect nest-site selection? After rat eradication, petrels will likely be initially attracted to remnant colonies, until crowding eventually forces recruits into new habitat. Thus, we predict that the presence of other nests will have greater influence on nest-site selection on islands with less time since rat eradication. We further predict that on islands with more time since eradication, there will be weaker selection for specific nesting habitat.

Methods

Study area and species

We assessed nest-site selection on five islands representing 0–24 years of recovery after Pacific rat eradication and one island that was never invaded by rats. Korapuki, Kawhitu and Ohinau had Pacific rats and European rabbits (*Oryctolagus cuniculus*) eradicated in 1987, 1991, and 2005 respectively, and Taranga had Pacific rats removed in 2011; while Ruamaahuanui never had introduced predators and Mauitaha is still inhabited by Pacific rats (Table 1). All islands are within 7–13 km of New Zealand's North Island in the Hauraki Gulf, and have similar climate and geology (Fig. 1). Furthermore, all islands have similar disturbance and habitat modification histories, with extensive burning and terracing by Māori (indigenous peoples of New Zealand; Edgar 1962; Sladden and Falla 1928). However, all islands have been protected as nature reserves and have remained relatively undisturbed since the mid-nineteenth century.

We considered nesting habitat selection of seven species of burrow-nesting seabirds in the order

Table 1 Six islands off the northeastern coast of New Zealand's North Island surveyed for burrow-nesting seabird nesting habitat using plots placed along transects

Island	Area of island (ha)	Time since eradication	Species eradicated	Petrel species present	Year surveyed	Month surveyed	Transects	Plots
Mauitaha	22	0	Pacific rat	GFPE, LISH, PYPE, FLSH, FFSH	2011/2012	December/October	31	68
Taranga	470	1	Pacific rat	GFPE, LISH, PYPE, FLSH	2011/2012	November/October	61	120
Ohinau	32	7	Pacific rat, European rabbit	GFPE, LISH, FFSH	2012	October	33	100
Kawhitu	100	21	Pacific rat, European rabbit	GFPE, LISH, PYPE, CDPE	2012	November	35	132
Korapuki	18	26	Pacific rat, European rabbit	GFPE, LISH, PYPE, CDPE, SOSH	2012	December	41	101
Ruamaahuanui	21	n/a	n/a	GFPE, LISH, PYPE, FLSH, CDPE	2010	November	n/a	76

Each island differs in the presence (0), absence (n/a), or time since Pacific rat eradication. Petrel species nesting on islands include grey-faced petrel (GFPE), little shearwater (LISH), Pycroft's petrel (PYPE), fluttering shearwater (FLSH), flesh-footed shearwater (FFSH), common diving petrel (CDPE), and sooty shearwater (SOSH)
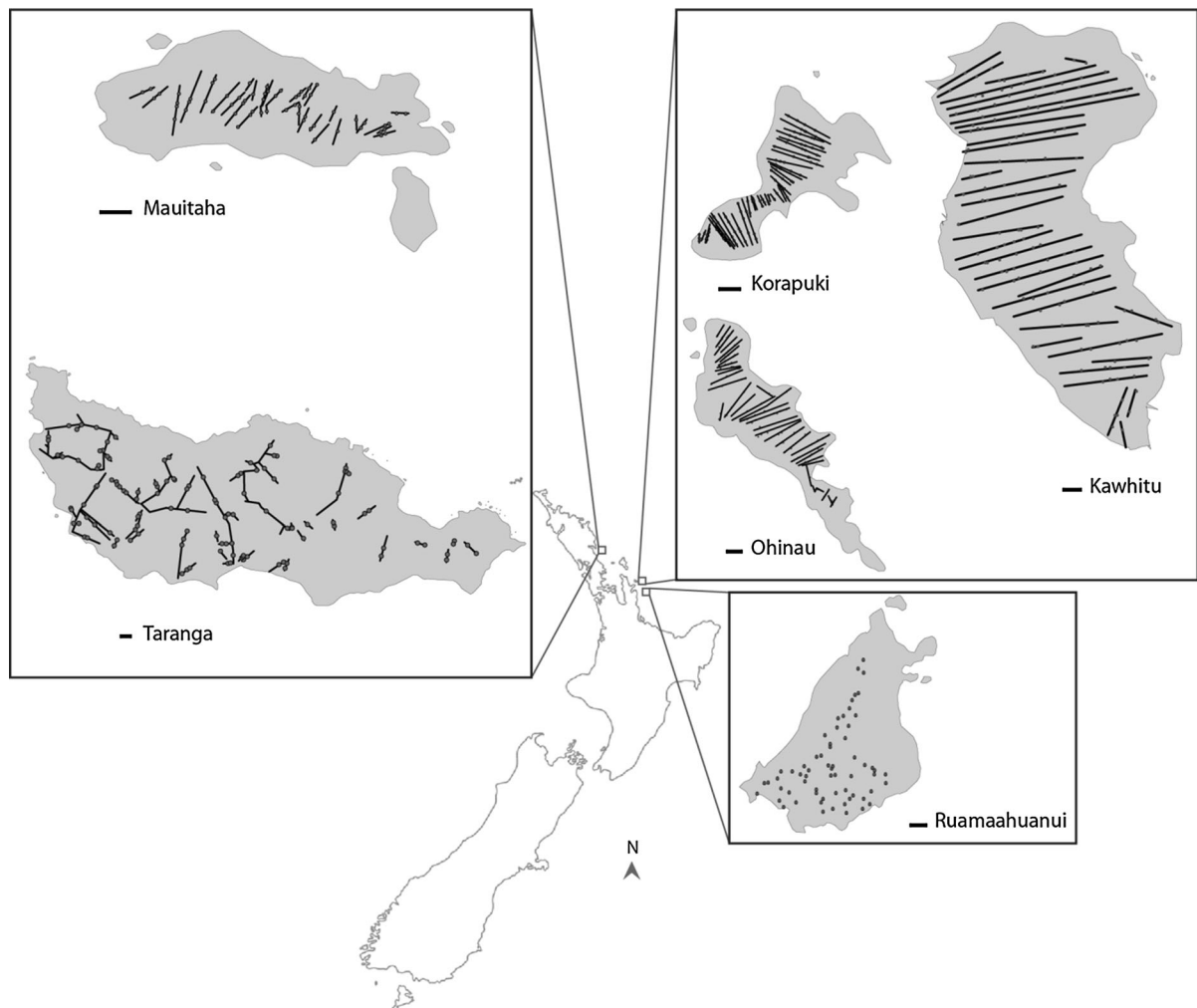
Fig. 1 Distribution of habitat plots along search transects on study islands off the northeast coast of the North Island, New Zealand. On Taranga, transects were restricted to cut tracks due to rugged terrain; no transects were placed on Ruamaahuanui due to the high density of burrows. *Black lines* to the left of island names indicate 100 m scale. Distance between islands relative to each other is not to scale

Procellariiformes: 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*) (Table 1). Grey-faced petrel, little shearwater, and common diving petrel are winter breeders, where courtship and burrow cleaning occur in March or April, laying in July or August, and fledging in late December to January (Miskelly 2013). Fluttering shearwater, flesh-footed shearwater, sooty shearwater, and Pycroft's petrel clean burrows from September to

October, lay in November to December, and fledging occurs from March to May (Miskelly 2013). Limited available information suggests that burrows of all species tend to be sympatric, with no heterospecific separation of physical habitat characteristics, and different species sometimes occupying burrows of others (Buxton 2014; Hicks et al. 1975; Pierce 2002). Because of this and the low observed burrow occupancy of each species (see below), to increase power we combined all procellariiform species in our analyses. We surveyed islands when all petrel species were at some stage of the breeding cycle (courtship, laying, incubation, or chick rearing; Table 1).

Habitat surveys

To distribute habitat surveys across the entire surface of our study islands, we randomly placed plots along evenly spaced transects. A mean of 35 transects ran from coast to coast, perpendicular to the long axis of each island, resulting in a distance of 10–40 m between transects depending on island size (Fig. 1; Table 1). We surveyed all island area, except for slopes >60° due to unsafe access and a low probability of encountering burrows (Fig. 1; Whitehead et al. 2014). Because of the steep terrain on Taranga, transects were shorter and constrained by proximity to existing tracks. The transect method was not employed on Ruamaahuanui because of high burrow density and thus high risk of burrow collapse. Instead, we used burrow count surveys from existing plots that had been allocated randomly as part of a previous study (Whitehead et al. 2014).

We surveyed between one and six 3 m-radius circular plots at randomly-assigned distances along each transect. Each plot center was marked with a handheld Global Positioning System (GPS 60CSx Garmin, Kansas, USA) and a metal stake and the boundaries delineated using a transect tape. Within each plot we counted all burrow entrances where the midline of the entrance fell within the plot limits. We assessed occupancy using an infrared burrow camera (burrowscope; Sextant Technology Ltd., Wellington, New Zealand) on all islands except Ruamaahuanui. We also recorded key habitat variables selected based on studies of other burrow-nesting seabirds (Catry et al. 2003; Charleton et al. 2009; Rayner et al. 2007; Schulz et al. 2005; Scott et al. 2009) and on preliminary surveys of our study sites. These were:

1. *Aspect* categorical north, south, east or west slope direction, measured using hand-held compass pointed towards the nearest coast from the plot center;
2. *Slope* measured using a hand-held inclinometer from the highest point of the plot to the lowest (down-slope) point;
3. *Topography* broad feature class (ridge crest, slope face, valley bordered by higher ground, or flat terrace) and elevation, read using a handheld GPS;
4. *Soil depth* measured using a 1 m stainless steel rod at the center point of the plot. The rod was driven into the soil as far as possible until an obstruction

was hit (or until the rod was buried). If the rod was blocked by a root at a shallow depth or a burrow was at the center of the plot, the spike was moved 30 cm away in a random direction until the obstacle was avoided.

5. *Soil strength* measured using a penetrometer (New Zealand Soil Bureau Inc. Wellington, New Zealand) at the center of the plot;
6. *Ground cover* the percent cover in five categories (<1 % = 1, 1–25 % = 2, 25–50 % = 3, 50–75 % = 4, 75–100 % = 5) was estimated for the following: bare ground (exposed substrate), rock (defined as larger than 5-cm diameter), and vegetation under 135 cm height;
7. *Stem count* species and number of stems between 2.5 and 10 cm in diameter at chest height (dbh);
8. *Canopy species and percent cover* visual percent cover was estimated in five categories (same as above) for each main canopy species (tree species >5 m).

Statistical analyses

Not all sites were expected to have burrows, and not all burrows were expected to be occupied. Consequently, inference on nest-site selection was made at three levels: (1) whether one or more burrow entrances were present; (2) the number of nests; and (3) the number of occupied nests (all species combined). To maximise inference, we developed a Bayesian hierarchical model to incorporate these three levels. To assess the effect of social attraction to nest-site locations while controlling for habitat, we examined the spatial autocorrelation of model residuals at each of the three data-sampling levels. If residual autocorrelation existed, a spatial covariance error structure would be incorporated into the model (Banerjee et al. 2004; Wagner and Fortin 2005). We used the spatial scale and intensity of autocorrelation to indicate the distance and degree to which nest-site selection was influenced by the presence of other nests. To examine differences in nest-site selection with increasing time since eradication, we examined model outputs from the first level of inference (the presence or absence of burrows). First we compared the proportion of habitat covariates selected for with time since eradication, using generalized linear mixed models (GLMM), based on the assumption that a greater number of

variables associated with burrow presence could indicate birds were being more selective. Second, to test the changing strength of nest-site selection with increasing time since eradication, we compared model fit across islands.

All statistical analyses were performed in R version 2.14.2 (R Development Core Team 2012).

Model parameterization

We used two-way indicator species analysis (TWIN-SPAN) prior to modelling to reduce the 25+ canopy and stem species into simple vegetation classes. This is a divisive clustering method that separates vegetation into classes based on the abundances and associations between plant species (Hill 1979; Whitehead et al. 2014). By combining data from plots on all islands, we were able to define seven canopy classes and five stem classes comparable among islands. Next, all categorical covariates (aspect, topography, canopy and stem vegetation classes) were transformed into dummy variables by setting one class as a reference class with a coefficient of zero (Hardy 1993). Finally, we computed a Spearman's correlation matrix to assess multicollinearity among explanatory variables. We omitted one of each covariate randomly when correlation coefficients (r_s) were $\geq$0.5. We did not include interaction terms, because models would be over-parameterized and thus be unlikely to converge (Ginzburg and Jensen 2004).

To ensure that resulting parameter estimates would be comparable, all variables were scaled by subtracting the mean and dividing by one standard deviation (Schielzeth 2010).

Hierarchical modeling approach

To examine the relationships between burrow presence, abundance, and occupancy with habitat covariates we adopted a Bayesian hierarchical framework (Fig. 2), implemented with Markov chain Monte Carlo (MCMC) methods. We used Bayesian inference as it allows for parameter uncertainty, which can be substantial when modeling patchy and spatially-varying processes, such as nest-site selection (Banerjee et al. 2004). Because we were interested in similarities and differences in nest-site selection among and between islands, we selected a hierarchical approach,
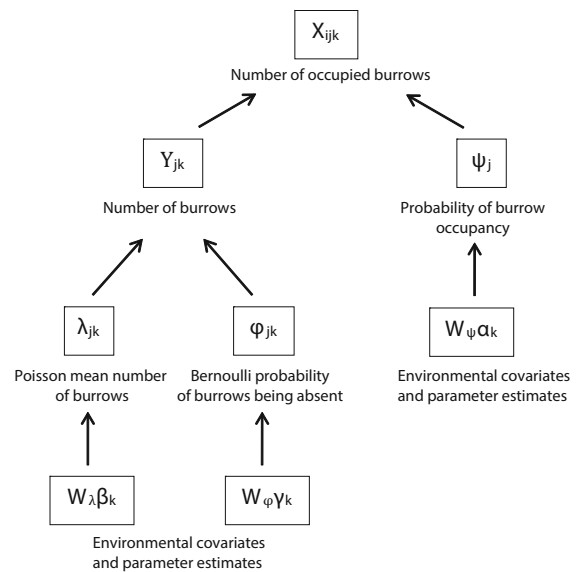
Fig. 2 Bayesian hierarchical model describing the effect of habitat variables (*W*) and parameter estimates (α, β, and γ) on the number of occupied burrows and the number of burrows in each plot *j* on each island *k*

which is ideal for aligning complex data from various sources (Cressie et al. 2009; Ellison 1996).

We used MCMC, Gibbs sampling, and Metropolis algorithms to generate posterior parameter distributions (Gelman et al. 2004). Posterior distributions from MCMC functions, given the data and priors, yielded medians and 95 % credibility intervals (CI) for each habitat parameter. Because little information was available about habitat selection of burrow-nesting seabirds between islands, we used non-informative prior distributions (Gelman and Hill 2007). To ensure convergence and minimize autocorrelation between chains, we ran 90,000 iterations with a burn-in of 10,000 and a thinning rate of 40.

We used packages MASS and mvtnorm to write model code (Online Resource 1; Genz et al. 2012; Venables and Ripley 2002).

Modelling burrow entrance density

Plots were placed randomly along transects, resulting in the inclusion of large amounts of plots with no burrow entrances. We therefore used a zero-inflated Poisson (ZIP; Martin et al. 2005) model with two states: a state in which burrows were present at a site and a state in which burrows occurred with varying levels of abundance (Fig. 2; Welsh et al. 1996). This

approach allowed us to estimate the probability that burrows were present in a particular habitat, and given their presence, estimate the mean number of burrows (Dagne 2004). The model took the form:

$$Pr(Y_{jk} = y) = \varphi_{jk}\delta_{jk} + (1 - \varphi_{jk})\frac{\lambda_{jk}^{y}e^{-\lambda_{jk}}}{y!} \qquad (1)$$

where Y_{jk} was the number of burrows, λ_{jk} was the Poisson mean number of burrows, φ_{jk} was the Bernoulli probability of no burrows, and δ_{jk} was an indicator of burrow absence (i.e. equals 1 when $Y_{jk} = 0$) in plot j on island k. Equation (1) can be broken down depending on the value of Y_{jk}:

$$(Y_{jk} = 0) = \varphi_{jk} + (1 - \varphi_{jk})e^{-\lambda_j k}$$
$$(Y_{jk} = y) = (1 - \varphi_{jk})\frac{\lambda_{jk}^{y}e^{-\lambda_j}k}{y!}, \quad y > 0.$$

The Bernoulli probability of the absence of burrows (φ_{jk}) and the Poisson mean number of burrows (λ_{jk}) were linear predictions of covariates:

$$logit(\varphi_{jk}) = \sum_{l=1}^{L} \alpha_{kl}W_{kl}, \qquad (2)$$

$$ln(\lambda_{jk}) = \sum_{l=1}^{L} \alpha_{kl}W_{kl}, \qquad (3)$$

where W_{kl} were individual environmental covariates l for models on island k, and α_{kl} were the associated parameters. The α_{kl} came from a prior distribution with mean $M_{\alpha l}$ and variance $\sigma_{\alpha l}^2$:

$$\alpha_{kl} \sim Normal(M_{\alpha l}, \sigma_{\alpha l}^2) \qquad (4)$$

$$M_{\alpha l} \sim Normal(0, 1000) \qquad (5)$$

$$\sigma_{\alpha l}^2 \sim InverseGamma(0.1, 0.1). \qquad (6)$$

Posterior distributions were interpreted by generating median α_{kl} values with 95 % credible intervals for each habitat variable on each island for both φ_{jk} (probability of a burrow being absent) and λ_{jk} (mean number of burrows).

Modeling burrow occupancy

Our observed measures of burrow occupancy are likely to be associated with an unknown detection

probability (Hamilton 2000), but we assume the detection probability to be non-variant over habitat conditions. We modeled the number of "occupied" burrows X_{ij} among present burrows Y_{jk} in each plot j on each island k as a binomial process:

$$X_{jk} \sim Binomial(\psi_{jk}, Y_{jk}), \quad Y_{jk} > 0 \qquad (7)$$

where ψ_{jk} was the probability of finding a bird in a burrow in plot j (note: ψ_{jk} is equal for all burrows in plot j). Similar to Eq. (2), the probability of an occupied burrow ψ_{jk} was modelled as:

$$logit(\psi_{jk}) \sim \sum_{l=1}^{L} \alpha_{kl}W_{kl} \qquad (8)$$

where W_{kl} were the environmental covariates l for models on island k, α_{kl} were the associated parameters, and prior distributions of α_{kl} were similar to Eqs. (4–6). Posterior distributions for each habitat variable on each island were interpreted by generating median α_{kl} values with 95 % credible intervals.

Model selection

To reduce the number of variables in the final multivariate model, we first ran a series of univariate models, with each habitat covariate included separately. To compare between habitat variables, we calculated deviance information criterion (DIC):

$$DIC = p_D + \overline{D}, \qquad (9)$$

where the mean deviance $\overline{D}$ was averaged over all MCMC simulations and penalized for the effective number of parameters p_D (Spiegelhalter et al. 2002). The number of parameters is not clearly defined for multilevel models and is unstable, even from simulations that have converged (Gelman and Hill 2007). Thus, when interpreting DIC values we also visually inspected the diagnostic plots to assess model fit (Wheeler et al. 2010).

To construct biologically plausible multivariate models, we selected habitat covariates with a combination of the lowest DIC values and those whose 95 % credible intervals did not overlap zero on at least one island.

Spatial autocorrelation

A variogram of multivariate-model residuals for each island was constructed to determine if adjacent plots

were more similar than those separated by large distances (i.e. spatial autocorrelation; Legendre 1993). Distance classes were calculated from the eastings and northings of plot centers (GeoR package; Ribeiro and Diggle 2001). We interpreted the distance (if any) at which residuals were no longer autocorrelated as the "range", or distance class on the x-axis, at which a "sill", or asymptote, is reached. We estimated variogram model parameters (range and sill) by maximum and restricted-maximum likelihood methods, and fitting of ordinary and weighted least squares. If a sill in the semivariance was not reached within a range of 20 m (suggesting spatial autocorrelation up to 20 m), we calculated and plotted Moran's I values. Using normal approximation, we tested whether Moran's I values differed significantly from 0, indicating dispersion or correlation of model residuals among distance classes (spdep package; Bivand et al. 2013).

Post-hoc comparison of nest-site selection among islands

To examine how selectivity for nesting habitat differed with time since eradication and other island factors, we compared outputs from the Bernoulli burrow absence model component (φ_{jk}; Eq. 2) using binomial GLMM (lme4 package; Bates et al. 2012). For each of the habitat covariates on each island, we used 95 % CI from the posterior parameter distributions of univariate and multivariate models to construct a binary dependent variable. Parameter estimates of habitat covariates whose 95 % CI did not overlap zero were scored as 1, as this likely indicated that petrels "selected" or "avoided" this particular habitat. Conversely, habitat covariates whose CI overlapped zero were scored as 0, as this likely indicated no selection or avoidance. This resulted in a dataset with a sample size of 108 for the univariate model (6 islands × 18 covariates) and 36 for the multivariate model (6 islands × 6 covariates). We tested the effect of the following independent variables on the probability of habitat covariates being selected or avoided: (1) number of years since Pacific rat eradication (where Ruamaahuanui, which never had predators introduced, was set to 100); (2) the historical presence of European rabbits; (3) the mean value of each habitat covariate on each island center-scaled among islands; and (4) the coefficient of

variation (standard deviation/mean) of each habitat covariate on each island. Categorical island and habitat variables were included as random factors. We assumed that a greater number of habitat covariates whose CI did not overlap zero indicated that birds were being more selective.

Comparing model fit

We assessed model fit following the procedure described by Kesler and Haig (2005) and Bourgeois and Vidal (2007), by comparing the predicted probability of burrow presence between occupied and unoccupied plots. Predicted probabilities of burrow presence were calculated by taking $1 - \varphi_{jk}$ (Eq. 2) from the top multivariate ZIP model. If unoccupied plots had similar predicted probabilities of burrow presence to occupied plots, this suggested that suitable nesting habitats remain unoccupied, or rather, the island had not been fully re-colonized (Anderson et al. 2013). Conversely, if occupied plots had higher predicted values than unoccupied it suggested that breeding birds were nesting in, and potentially saturating, specific habitat types before using plots with lower predicted values. To quantify model fit we calculated area under Receiver Operator Characteristic curves (AUC) based on accuracy of predictions (PresenceAbsence package; Freeman and Moison 2008). 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 (Oppel et al. 2012).

## Results

Between 2010 and 2012 we surveyed a total of 597 habitat plots on 196 transects (Table 1). Burrow density was related positively to the number of years since Pacific rat eradication ($Z_1 = 9.883$, $P < 0.001$, Fig. 3). However, time since eradication explained <40 % ($R^2 = 0.37$) of variation in burrow density between islands.

Nest-site habitat characteristics

We found two pairs of habitat covariates with correlation coefficients ≥0.5 (slope and "face"
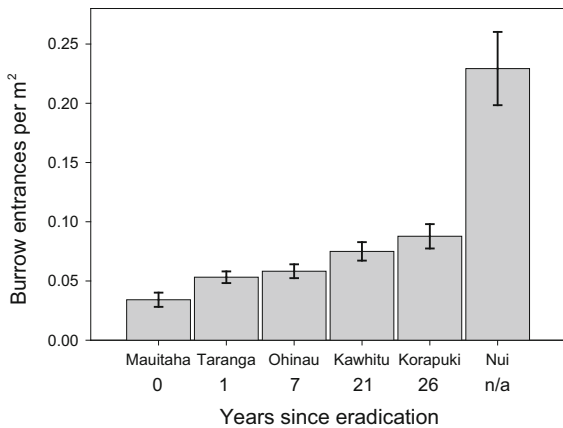
Fig. 3 Mean density of burrow entrances on study islands off the northeast coast of the North Island of New Zealand with time since Pacific rat eradication. Mauitaha is still inhabited by Pacific rats; Ruamaahuanui (Nui) never had mammals introduced and all other islands ordered from *left* to *right* by increasing time since eradication. *Error bars* indicate standard error

topography category, R = 0.56; total canopy cover and total understory vegetation cover, R = 0.50). We removed the "face" topography category and total understory vegetation cover from further analysis.

TWINSPAN analysis revealed seven canopy classes: pohutukawa (*Metrosideros excelsa*), kanuka (*Kunzea ericoides*), kohekohe (*Dysoxylum spectabile*), nikau (*Rhopalostylis sapida*), tawa/taraire (*Beilshmiedia tawa/B. tarairi*), mapou (*Myrsine australis*), and māhoe (*Melicytus ramiflorus*); and five smaller stem classes (2.5–10 cm at breast height): mapou, māhoe, karamū (*Coprosma macrocarpa*), kawakawa (*Macropiper excelsum*), and karo (*Pittosporum crassifolium*). The canopy species nikau, kohekohe, and tawa/taraire and small stem species kawakawa and karo were observed on ≤3 islands in low abundance among plots and were thus removed from further analysis. The dummy variable for gully topography also occurred with low frequency among plots and was removed from further analysis.

Among islands, univariate ZIP models and univariate observed occupancy models indicated that soil depth was the most influential factor determining the presence $(1 - \varphi)$, density, and occupancy of burrows (Online Resource 2, Tables 2.1, 2.2), which all increased with increasing soil depth. We constructed 2 multivariate models (ZIP burrow count and observed occupancy model) using habitat covariates selected

from univariate models (see methods and Online Resource 2, Tables 2.3, 2.4).

In the top multivariate ZIP models, on at least one island, the expected probability of burrow presence $(1 - \varphi)$ increased with western aspect, slope, soil depth, rock cover, and the presence of karamū and māhoe stems (Fig. 4a); and burrow counts (Y_{jk}) increased with western and southern aspect, slope, soil depth, rock cover, and the presence of karamū stems (Fig. 4b). On three islands (Taranga, Korapuki, Ruamaahuanui), burrow count decreased with the number of stems, while on Mauitaha burrow count increased in the presence of large stems. On Kawhitu, burrow count increased in the presence of māhoe stems, while on Korapuki and Ruamaahuanui burrow count decreased with the presence of māhoe stems. Overall, burrows were more likely to be found on steeper slopes, in deeper soil, with more rock cover, in the presence of māhoe stems. The top multivariate ZIP model predicting burrow presence had an AUC = 0.77 ± 0.02 and predicting burrow count had an AUC = 0.70 ± 0.02.

In the top multivariate observed occupancy models, on at least one island, probability of "observed" burrow occupancy (X_{jk}) increased with soil depth and māhoe in the canopy, and decreased with western aspect, increasing rock cover, and with the presence of kanuka and mapou stems (Fig. 4c). The top multivariate occupancy model had an AUC = 0.74 ± 0.03.

Spatial autocorrelation

We found little evidence of spatial autocorrelation. For most islands, variograms of φ, λ, and Ψ residuals (Eqs. 2, 3, and 8) reached a sill at a range of ≤ 10 m (Online Resource 3, Figs. 3.1, 3.3, 3.5) and Moran's *I* values did not differ significantly from 0 (except at 100 m on Mauitaha, Online Resource 3, Fig. 3.6), indicating no spatial autocorrelation at distances greater than 10 m. The majority of our plots (∼90 %) were ≥10 m apart, thus we did not consider spatial autocorrelation to be a statistical issue in our analysis. We found weak evidence of spatial autocorrelation on Taranga and Mauitaha only. The φ and λ residuals on Taranga did not reach a sill until ∼20 m (Online Resource 3 Figs. 3.1 and 3.3), while the Ψ residuals on Mauitaha did not reach a sill until ∼30 m (Online Resource 3, Fig. 3.5).
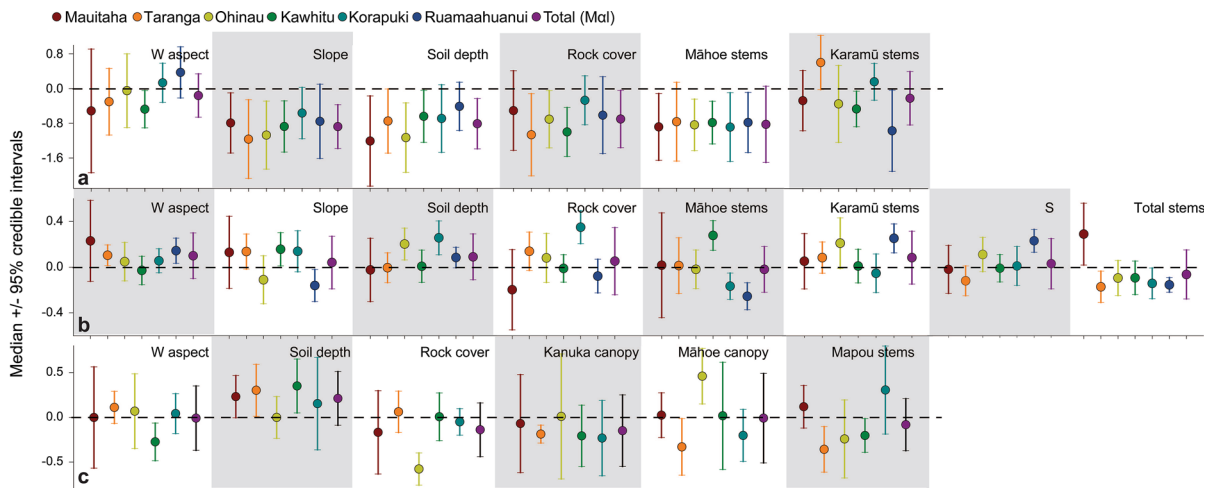
Fig. 4 Median effect sizes and 95 % credibility intervals of habitat covariates from multivariate models predicting **a** petrel burrow absence, **b** abundance, and **c** occupancy on six islands in northeastern New Zealand. Mauitaha is still inhabited by Pacific rats; Ruamaahuanui never had rats introduced and all other islands are ordered from left to right by increasing time since rat eradication. Habitat variables were selected based on low deviance information criterion values and credible intervals not overlapping 0 on ≥1 island from univariate models. Total values represent medians among islands [$M_{\alpha l}$ Eq. (5)]

Table 2 Model outputs from a generalized linear mixed regression examining variables affecting the number of nesting habitat variables selected for by burrow-nesting petrels (based on the presence/absence component of univariate and multivariate Bayesian hierarchical nesting habitat selection models)

|	Parameter estimates $\pm$ SE	Z value	P value	R^2m	R^2c
Univariate models					
Years since eradication	-0.04 ± 0.01	-2.53	0.02*	0.45	0.47
Scaled habitat abundance	0.30 ± 0.29	1.03	0.30		
Coefficient of variation	-0.02 ± 0.15	-0.13	0.90		
Rabbits	0.75 ± 0.56	1.34	0.18		
Multivariate models					
Years since eradication	-0.02 ± 0.52	-0.04	0.97	0.64	0.67
Scaled habitat abundance	-0.64 ± 0.65	-0.90	0.32		
Coefficient of variation	-1.56 ± 0.92	-1.88	0.05*		
Rabbits	1.00 ± 0.98	1.02	0.31		

Independent variables include the number of years since Pacific rat eradication, the center-scaled mean value of each habitat covariate, the coefficient of variation of each habitat covariate on each island, and the historical presence of rabbits. R^2m indicates marginal R^2 values; R^2c indicates conditional R^2

* Statistical significance

Nest-site selection among islands

We examined inter-island factors affecting the number of selected nesting habitat covariates using 95 % CI from a multivariate burrow absence model (Eq. 2) and found a significant effect of the coefficient of variation (standard deviation/mean habitat variable; $n = 36$, $P = 0.05$; Table 2; Fig. 5a). When coefficients of variation on an island were high (i.e., habitat was variable—high standard deviation and a low mean) fewer habitat covariates were selected for. When we examined factors affecting the number of nesting habitat variables selected for using 95 % CI from univariate burrow absence models we found a significant effect of time since rat eradication ($n = 108$, $P = 0.021$; Table 2; Fig. 5b). Fewer habitat
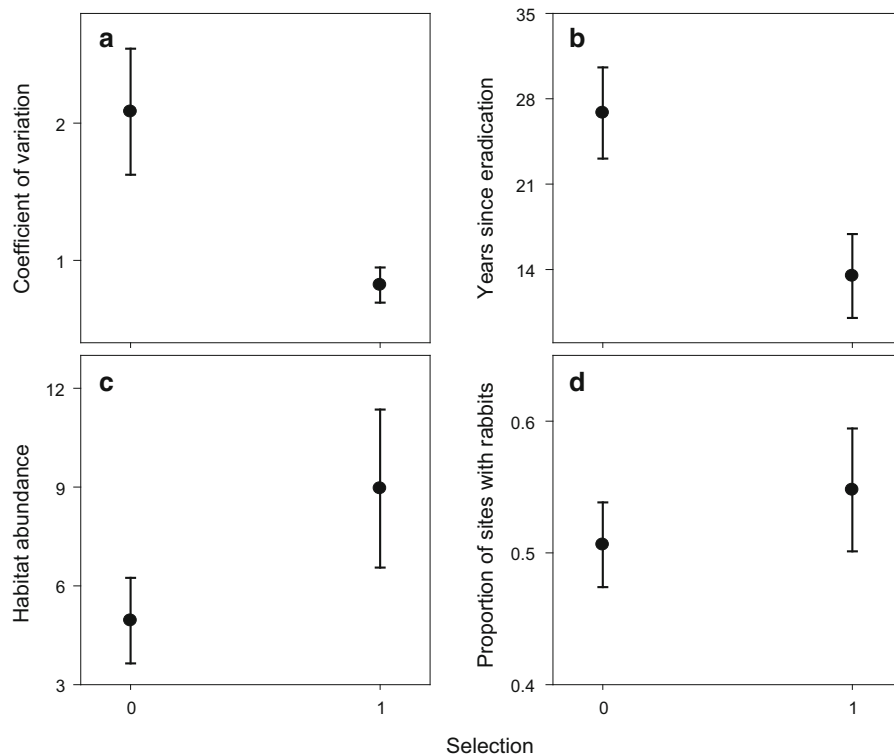
Fig. 5 Post-hoc analysis of a nest site selection model on six islands in north-eastern New Zealand. We compared the proportions of habitat covariates "selected" (95 % credible intervals not overlapping zero, scored as 1) or "not selected" (95 % credible intervals overlapping zero, scored as 0) with

a the coefficient of variation of each habitat covariate on each island, **b** the number of years since Pacific rat eradication, **c** the mean value of each habitat covariate, and **d** the historical presence of rabbits. *Error bars* indicate standard error

covariates were selected for (higher proportion of covariates whose CI overlapped 0) on islands with more time since rat eradication. We found no effect of the historical presence of rabbits or the mean value of each habitat covariate on the number of nesting habitat variables selected (all $P > 0.182$, Fig. 5c, d).

Model fit

On both Ohinau and Mauitaha (Pacific rats removed in 2005 and Pacific rats still present, respectively; Fig. 6), we found that predicted probabilities of burrows being present were higher in plots with burrows present, suggesting that birds were nesting in specific habitat types on these islands. On all other islands there was no clear difference between predicted probabilities in plots with burrows present or absent, suggesting model habitat covariates did not influence nest-site selection. AUC values indicated better model fit on islands with

less time since eradication (AUC ± standard deviation: Mauitaha—rats present—0.70 ± 0.07; Taranga—rats removed 2011—0.62 ± 0.06; Ohinau—rats removed 2005—0.70 ± 0.05; Kawhitu—rats removed 1991—0.53 ± 0.05; Korapuki—rats removed 1986—0.52 ± 0.06; Ruamaahuanui—rats never introduced—0.54 ± 0.11), which is reflected in Fig. 6, where predicted probabilities decreased with time since eradication. This suggests that as time since eradication increased, birds were more likely to nest in less specific habitat.

Discussion

We examined burrow-nesting petrel nest-site selection on four islands with different times since Pacific rat eradication, an island with rats present, and an island which never had rats. Although the structure of the
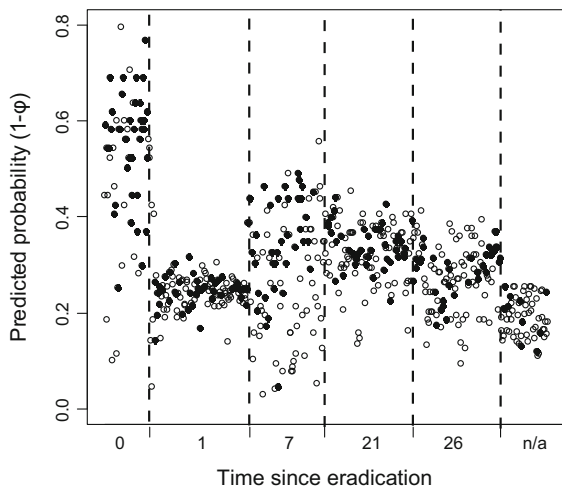
Fig. 6 Predicted probabilities from a model describing the effects of habitat variables on burrow presence $(1 - \varphi)$ in plots with burrows present versus plots with no burrows on islands in north-eastern New Zealand with different times since Pacific rat eradication. Low predicted probabilities in plots with burrows absent (*white dots*) and high predicted probabilities in plots with burrows present (*black dots*) indicate good model fit and suggest that birds nest in specific habitat types

data and results were complex, with numerous interacting variables, our analyses indicated that nest-site selection is island-specific, depending on both restoration history and habitat availability.

Nest-site selection among islands

For burrow-nesting seabirds, selection of appropriate nesting habitat will affect burrow quality and thus influence reproductive success. Substrate characteristics, such as soil properties, can affect the excavation, stability, and thermal properties of a burrow (Dalsted et al. 1981; Stokes and Boersma 1991). We found that soil depth was the most important factor predicting the presence, abundance, and occupancy of burrows across all study islands. Soil depth is an important nesting habitat feature for many species of petrel, as they tend to dig long, multi-cavity burrows (Charleton et al. 2009; Gaze 2000; Schramm 1986; Schulz et al. 2005). Rock cover also arose as important in all models, with burrows more likely to be found in plots with large boulders present. Burrow collapse is less likely under boulders (Brandt et al. 1995). However, burrow occupancy was lower in plots with more rock cover (although only significant on one island),

possibly due to the poor insulating properties of volcanic boulders (Brandt et al. 1995).

We found that burrows were more likely to be present in steeper terrain. On slopes, burrows open horizontally, whereas on terraces, openings face upwards, allowing water to enter more readily (Stokes and Boersma 1991). Furthermore, because most petrels have high wing-loading, slope is thought to increase take-off and landing capability by creating updrafts that increase lift (Rayner et al. 2007; Schulz et al. 2005; Scott et al. 2009). However, we found that slope affected burrow abundance on only one island, and had no effect on burrow occupancy. We speculate that slope may have a weaker effect on nest-site selection on heavily forested islands, such as our study islands. Updrafts generated from wind striking a hill may not be as effective at creating lift when large trees are present. Furthermore, to take advantage of lift, it would be necessary for birds to gain the necessary height and clearance to depart the colony by walking to large rocks or clear areas, or by climbing trees. However, lift may still be an important feature in habitat selection. On some islands, we found a higher likelihood of finding burrows and higher abundance of burrows on southerly and westerly aspects (Fig. 4), which face the prevailing south-westerly winds of northern New Zealand (National Institute of Water and Atmospheric Research). Slopes facing prevailing winds generate lift during take-off and drag during landing (Warham 1990).

Finally, canopy and stem species affected burrow presence, abundance and occupancy varyingly among islands. Generally, burrows were more likely to be present when māhoe stems were present. Burrows tended to be more abundant in areas with karamū stems and more occupied in areas without kanuka in the canopy. These associations could be due to a combination of the following factors: (1) all study islands were burned in recent history by Māori and evidence suggests that kanuka is a common pioneering species, whereas māhoe and karamū are secondary successional immigrants (Atkinson 2004). Thus, islands or sites with more māhoe and karamū may represent areas with more time to recover after fire disturbance, suggesting that the relationship between petrel burrows and plant species may be correlated (due to longer recovery times) rather than causative; (2) some species, such as kanuka, have thick, interlocking root systems which may be difficult for petrels

to penetrate (Bergin et al. 1995); (3) plant species may be associated with soil properties; for example, māhoe grow exclusively in well-drained, fertilized soils, also preferred by burrow-nesting petrels (Dawson and Lucas 2011); and (4) the density of the canopy and understory may affect the accessibility of a nest site (Whitehead et al. 2014). For example, young mapou tend to form dense stands; thick understory could make it more difficult for petrels to safely reach burrows.

Social attraction and nest-site selection

Petrels are colonial animals, nesting in large social groups (Warham 1990). Evidence suggests that for colonial animals, "social attraction" is among the most important drivers of habitat selection, where the presence, density, and reproductive success of established breeders indicate habitat quality (Danchin et al. 1998; Forbes and Kaiser 1994; Kildaw et al. 2005). However, we found little evidence for spatial autocorrelation, indicating that the presence of other nests did not influence nest-site selection. This suggests that petrels are not selecting habitat based on the presence of other birds (Bayard and Elphick 2010). However, our plots were generally separated by relatively large (>20 m) distances, compared to distances separating burrows still considered to be in the same colony (~8 m; R. Buxton unpub. data), which may have resulted in the lack of observed spatial autocorrelation. Although not statistically significant, we found weak support for spatial autocorrelation on Mauitaha and Taranga, islands with Pacific rats present and removed in 2011, respectively. The low nest density and high habitat-mediated nest-site selection on these islands suggests that birds may be clustering more in the presence of rats, a pattern which has been observed in other seabird species (Cuthbert 2002; Regehr et al. 2007).

Effect of time since rat eradication

Although we lack the ability to assume a causal effect of time since Pacific rat eradication, we found a distinct pattern of increasing burrow density along the chronosequence of islands that we use as a proxy for colony expansion or "recovery" after disturbance (Fig. 3). Low burrow densities on Mauitaha (0.03 ± 0.01 burrows/m^2), where Pacific rats are still present, and Taranga (0.05 ± 0.01 burrows/m^2), from

where they were eradicated only 2 years prior to our surveys, are comparable to those on other predator-invaded islands in New Zealand (e.g. 0.04 Cook's petrel *Pterodroma cookii* burrows/m^2 on Hauturu-Little Barrier Island; Rayner et al. 2007). Burrow densities on Korapuki and Kawhitu (0.09 ± 0.01 and 0.08 ± 0.01 burrows/m^2), islands with over 20 years since rat eradication, were significantly lower than on predator free islands (e.g. Ruamaahuanui 0.23 ± 0.03 burrows/m^2, Ruamaahuaiti 0.21 ± 0.04, and Hongiora 0.76 ± 0.07; Whitehead et al. 2014). However densities were comparable with those on other islands with similar times since predator eradication (e.g. Moutohorā 0.07 ± 0.01; Whitehead et al. 2014). Although this relationship was striking, caution must be taken when inferring a causal relationship with Pacific rat removal (Craig 1983; Jones 2001). For example, 13 years after Pacific rats were removed from Middle Chain Islands, burrow density was 0.04 ± 0.01 burrows/m^2 (Whitehead et al. 2014). 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, historical distribution, and species-specific behaviour and biology.

Nest-site selection between islands

We found differences in petrel nest sites between islands, including a negative relationship between the number of habitat covariates selected for on an island and time since rat eradication (Fig. 5a). This suggests that as time passes after rat eradication and burrow density increases, birds may reduce selectivity of nest-site locations and occupy new nesting habitat.

We hypothesized that the presence of Pacific rats may have restricted petrel nest-site selection to patches of habitat where: (1) they could escape predation; (2) density was high before rat invasion (e.g. high quality habitat) and predation was swamped (Lyver et al. 2000; Regehr et al. 2007); (3) micro-habitat was used infrequently by predators; or (4) alternative food resources were available for predators (Rayner et al. 2007). On islands lacking other predators, Pacific rats can move large distances, populations have been found in a range of habitat types (Moller and Craig 1987), and few micro-habitats lack rats completely (Newman and McFadden 1990). Thus, we find

the first explanation the least likely. For colonial seabirds, predation is generally inversely density-dependent, i.e. where small colonies are often extirpated and dense colonies are able to swamp predation effects (Cuthbert 2002; Lyver et al. 2000; Oro et al. 2006). Thus, colonies persisting on islands with rats or recently rat-free islands likely remain in locations where per-capita predation rates were low: either in areas where productivity and density were high or where predators were less abundant. Regardless, on islands with fewer than 8 years since rat eradication, our nesting habitat models had better fit, indicating high selectivity for nest-site locations in specific areas.

When rats are removed, if populations begin to grow, persisting colonies may be initially attractive to new recruits. Although we found no significant spatial autocorrelation <100 m, islands with less time since eradication showed greater autocorrelation, suggesting a more clustered burrow distribution. Once remnant areas become crowded, new recruits may be forced into new nesting habitat, thus lowering the number of habitat covariates selected for as time increases after eradication. Our data confirmed that islands with more time since eradication had no spatial autocorrelation, fewer habitat covariates were selected for, and habitat covariates had weaker effects on nesting habitat selection. An increase in burrow density and decrease in habitat constraints after rat eradication may reflect differential recruitment and the influence of density dependence.

Although nesting habitat models on Taranga (1 year since Pacific rat eradication) had better model fit than islands with more time since eradication, predicted probability of burrow presence in plots with burrow present and absent showed a similar pattern to that of a predator-free island (Fig. 6). We speculate that the discrepancy in probability of burrow presence may be due to Taranga's size (470 ha), which is four times larger than other islands. Larger islands contain a greater abundance and variation in habitat types (Kohn and Walsh 1994), which may result in lower predicted probabilities from nesting habitat models.

Nest-site selection was also related to variability in habitat measures across an island (coefficient of variation, Fig. 5b), with fewer habitat covariates selected for when habitat was patchy and limited. In other words, if there was a lower mean of nesting habitat (e.g. shallower soil, more gradual slopes) on an island, there were fewer habitat covariates selected for, i.e. birds were less selective.

Potential biases

The influence of burrow-nesting seabirds on their habitat is a potentially confounding factor in our analyses (Mulder et al. 2011). Not only will the availability of suitable nesting habitat influence the distribution of seabirds, but in turn, the distribution of seabirds will influence habitat. For example, the combination of burrowing and below-ground activity can result in root damage, decreased stability of trees and shrubs, and reduced seedling survival, thus altering plant community composition in heavily burrowed areas (Smith et al. 2011). Furthermore, burrow building alters soil porosity and soil-forming processes, resulting in stronger and drier soil (Bancroft et al. 2005). This circular feedback process between seabirds and island habitat is likely to be difficult to tease apart, especially in recovering populations. However, in recovering petrel populations on islands with low burrow abundance, it is unlikely that burrow densities have reached a point in which habitat is altered significantly.

Furthermore, we combined all species in our analysis of burrow distribution and occupancy. However, grey-faced petrels were by far the most abundant species on all islands, except for Ohinau, where flesh-footed shearwaters were most common (Buxton et al. 2013b). Both species are relatively large (mean weight: grey-faced petrel 550 g and flesh-footed shearwater 700 g) and are thought to be less severely affected by the presence of Pacific rats (Priddel et al. 2006). Uncommon species, such as Pycroft's petrel (150 g) and little shearwaters (240 g), are known to have lower productivity, even to the point of total nest failure, in the presence of Pacific rats (Pierce 2002). Furthermore, different species may have different rates of recovery due to differences in intrinsic demographic rates and meta-population dynamics (Buxton et al. 2014). Thus, we are unsure of how the varying abundances of each species of different sizes affected our results. Further research should focus on the differences or similarities in recovery dynamics of various burrow-nesting seabird species.

Conclusions and conservation implications

Our results suggest that nest-site selection, particularly the need for deeper soil, is important among recovering petrel colonies. However, our results also indicate that birds can expand into new habitat, suggesting that

the importance of nesting habitat characteristics may decrease as colonies grow. Thus nesting habitat suitability may be relatively more important in small populations; highlighting the importance of these habitat characteristics for petrel population recovery, both within islands and among islands.

Burrow-nesting seabird systems are complicated, including complex intra-island metapopulation dynamics and problematic nest-occupancy detection. Because of their ability to draw inference from composite systems, we propose that hierarchical Bayesian modelling may be the most capable method to address these complexities.

In New Zealand, island habitat is not homogenous, but instead includes both whole islands and within-island areas that vary in their quality as nest sites for petrels. Thus not all islands and areas within islands have the same petrel restoration potential. Our results can be useful to delineate suitable habitat patches for petrels at restoration sites, including those with deep soil, aspects that face prevailing winds, and steeper slopes.

Historically, removing introduced mammalian predators has been used to both enhance seabird productivity and prevent the extinction of threatened populations (Rauzon 2007). Because predator eradications have become increasingly successful and common, we propose that they represent not only an effective conservation technique, but also a means to study recovery biology. In this way, strategies to restore seabird populations can be developed based on an iterative adaptive management framework (Westgate et al. 2013). Suitable nesting habitat is a fundamental requirement for burrow-nesting species, affecting fitness through reproductive success. Thus, an accurate assessment of the importance and availability of suitable nesting habitat should be an integral part of petrel restoration strategies.

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