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Breeding habitat of the Cook's Petrel (*Pterodroma cookii*) on Little Barrier Island (Hauturu): implications for the conservation of a New Zealand endemic

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Abstract. Cook's Petrel (*Pterodroma cookii*), a trans-equatorial migrant endemic to the New Zealand archipelago, is today endangered and restricted to island habitats at the northern and southern extents of its former range. To improve the limited knowledge of the breeding habitat of this species, we combined an island-wide survey, the mapping capabilities of geographic information systems, and logistic and autologistic analyses to examine burrow distribution and habitat use of the world's largest population of Cook's Petrel, on Little Barrier Island (Hauturu). Our results show that, on this island, Cook's Petrel breeds predominantly above 300 m above sea level, on steeper slopes, closer to ridge tops, and in unmodified forest habitats with low and open canopies and greater numbers of large stems compared to the available terrain and habitat. Within these habitats above 300 m, densities of burrows are 0.04 burrows m⁻². Through comparisons with habitat data from two low-altitude colonies, we conclude that the current distribution of this population is a result of habitat selection and historical human-mediated impacts. We suggest that mature forest habitats, close proximity to ridge tops, and steep slopes are key habitat requirements for this species. A large amount of suitable habitat is available for Cook's Petrel on Little Barrier Island and the recent removal of introduced predators is expected to result in an expansion of this population. The results of the current study provide useful information to aid in the restoration of former colony sites on other islands and the New Zealand mainland.

Introduction

The conservation of threatened species requires a detailed understanding of their basic biology, distribution and use of habitat (Guisan and Zimmermann 2000; Araújo *et al.* 2002). Such data provide a base for the assessment of the status and threats to existing populations, the planning of future management actions, and ongoing monitoring of population status and recovery (Caughley 1994; Jones 2001). When endangered taxa occupy remote, rugged habitats the collection of these basic biological data can be problematic given logistical and funding constraints.

Gadfly petrels (Pterodroma spp.) are a group of small to medium-sized, predominantly burrow-nesting Procellariiformes with breeding largely restricted to islands as a result of their vulnerability to terrestrial predators, particularly introduced species (Brooke 2004). These seabirds are important drivers of terrestrial communities by acting as links between oceanic and terrestrial food webs (Markwell and Daugherty 2002; Hawke and Holdaway 2005) and they have the potential to be used as natural indicators for the investigation of climatic and oceanic processes resulting from global climate change (Moller et al. 2000). Human impacts at breeding colonies (Atkinson 1985; Cooper et al. 1995; Probst et al. 2000) and processes such as marine pollution (Ludwig et al. 1998) threaten many species of gadfly petrels. Unfortunately the small to medium size of gadfly petrels, their predominantly nocturnal activity at breeding sites, and distribution in remote, rugged island habitats has resulted in a lack of basic data for many species (Taylor 2000).

The New Zealand archipelago is a world hotspot for petrel diversity (Taylor 2000) and gadfly petrels were formerly a ubiquitous element of the mainland avifauna (Holdaway et al. 2001). One of the most abundant members of this group was the Cook's Petrel (Pterodroma cookii), an endemic trans-equatorial migrant. Bone deposits indicate that, before human arrival (>800 years before present), Cook's Petrel bred throughout New Zealand in the coastal and interior ranges of the North and South Islands (Worthy and Holdaway 2002). Today, as a result of human settlement of the New Zealand archipelago and exposure to introduced predators, Cook's Petrel is endangered and restricted to breeding sites at the northern and southern extremes of its former range, on Little Barrier Island (Hauturu) and Codfish Island (Whenua Hou) more than 1000 km apart (Taylor 2000). Until recently a population bred on Great Barrier Island (Aotea) 3 km east of Little Barrier Island. However, only 12 scattered burrows have been found in the last 25 years (Imber et al. 2003a) and this colony is considered effectively extinct owing to predation by feral Cats (Felis catus), Black Rats (Rattus rattus), Pacific Rats (Kiore) (R. exulans) and feral Pigs (Sus scrofa). The current lack of basic biological information for Cook's Petrel constrains effective conservation strategies. Although Imber et al. (2003a) studied the breeding biology of this species, there are few data on the distribution, use of habitat and size of populations for the Cook's Petrel owing to the rugged nature of breeding locations.

On Codfish Island (14 km²), the population of Cook's Petrel was estimated at 20000+ pairs, covering a large proportion of the island, when discovered in 1934 (Stead 1936). Predation by introduced Weka (Gallirallus australis) (eradicated 1984) and Pacific Rat (eradicated 1998) (Imber et al. 2003a) reduced this population to $\sim 1000+$ pairs (Taylor 2000). The much larger Little Barrier Island (30 km²) is now the most important breeding location for Cook's Petrel in the world, with a roughly estimated population of 50000+ pairs breeding above 300 m altitude (Taylor 2000). Although protected as a nature reserve since 1894, habitat modification through human settlement and introduced mammals have had severe effects upon this population (Imber et al. 2003a). First Maori and then European settlement resulted in logging and burning of the lower slopes of Little Barrier Island (Hayward 1982) followed by grazing of these areas by European Cattle (Bos taurus) and Sheep (Ovis aries)(Hamilton 1961). Feral Cats and Pigs were introduced in the late 1800s and the Pacific Rat before European arrival (Hamilton 1961). Although Pigs were removed in the early 1900s, Cats and Rats remained until successful eradications in 1980 and 2004 respectively.

Given the conservation status of Cook's Petrel, the importance of Little Barrier Island as the world's major breeding site for this species, and the lack of information available, there is a critical need to quantify the species' breeding habitat on this island. Such data would provide a benchmark for monitoring of the population (likely to change following eradications of predators) and provide the initial information needed to develop an accurate estimate of population size. Such data could also be used in the establishment of other colonies of this species through seabird translocation techniques developed in New Zealand (Gangloff and Wilson 2004). In the current study we combine seabird census techniques, a rigorous survey methodology, and the mapping capabilities of geographic information systems (GIS) in the first detailed assessment of the breeding habitat for Cook's Petrel. The key objectives of this study were to: (1) determine the distribution and density of Cook's Petrel; (2) characterise the habitats used for breeding; and (3) ascertain the potential for population expansion.

Methods

Study area

Little Barrier Island is an extinct volcanic island in the Hauraki Gulf near Auckland, New Zealand (Fig. 1). The lower slopes of the island experience a warm subtropical climate whereas at higher altitudes a frequent capping of cloud cover supports wet cloud-forest communities. The island is $\sim 30 \text{ km}^2$ in area and rises to a series of central peaks, the highest being 710 m above sea level (asl). From these central peaks a series of steep ridges run axially outwards towards the coast, dividing deep forested valleys (Fig. 1) (Hamilton 1961).



Fig. 1. Map of Little Barrier Island showing its position within New Zealand, the location of the stratified survey plots (n = 194), forest types, the 300-m altitude contour and strata boundary (white line), plots with 0, 1, 2, 3 burrows present, and the low-altitude Valley (V) and Tirikakawa (T) colonies.

Little Barrier Island's mountainous terrain and thickly forested slopes support over 350 native species of plants and several threatened bird species. The forest follows an altitudinal gradient (Fig. 1). Broadleaf forests dominate near the coast, with Northern Rata (Metrosideros robusta) and Tawa (Beilschmiedia tawa) occurring on the slopes, and mixed Kauri (Agathis australis) forest occurring extensively on ridges from 50 to 500 m. Further up, forests of Towai (Weinmannia silvicola) and Tawa dominate, in turn giving way to summit vegetation dominated by Quintinea (Quintinea acutifolia), Tawari (Ixerbia brexioides) and Southern Rata (Metrosideros umbellata). Although much of the island's original forest cover remains intact at higher altitudes, the large areas of lowland forest, which were cleared for timber and farming, now comprise dense pioneer growth of Manuka (Leptospernum scoparium) and Kanuka (Kunzea ericoides) (see Fig. 1, regenerating forest) in varying stages of transition to broadleaf and Kauri forest communities (Hamilton 1961).

Cook's Petrel survey

Observations of previous authors (Turbott 1947; Oliver 1955; Imber et al. 2003a) indicated that the distribution of Cook's Petrel on Little Barrier was disjunct along an altitudinal gradient, with birds breeding above 250-350 m asl. Consequently we selected two *a priori* strata, below 300 m (comprising 20 km² of the surface area of the island) and above $300 \text{ m} (15 \text{ km}^2)$, for the purposes of this study. Using a GIS (Arcview 9.0 TM, Esri Inc., USA) and digital elevation model (see GIS-based data, below, for details) of Little Barrier Island, the strata were partitioned and centres of survey plots generated using randomly selected coordinates within each stratum. With no prior knowledge as to the time required for conducting survey work in the rugged terrain, 104 plots were randomly generated within each stratum (208 total) as a sampling goal (Fig. 1). To minimise spatial autocorrelation in burrow counts a minimum distance rule of 100 m between sites was applied.

Fieldwork for the island-wide survey was conducted between November 2004 and March 2005 during the breeding season of Cook's Petrel. Each plot, the centre of which was defined by the randomly generated coordinates, was visited using a map and handheld GPS. In cases where only the general vicinity of the plot (within 30 m) could be reached owing to canopy-affected GPS signal, a plot centre was establish by measuring 20 m from the current location in a random direction (using a random number table). From the centre of each plot, a tape (held in the centre by one person) was used to establish a 3-m radius. The other person held the end of the tape and counted all Cook's Petrel burrows within the 28.27 m² plot. The burrows included in the count had a tunnel length >0.5 m (one arm-length) and were considered to have been in use by breeding birds within the previous two seasons if there were obvious signs of use (guano, feathers, fresh digging and or scratch marks) (Catry et al. 2003; Schulz et al. 2005). Additionally, only burrows with an entrance diameter <140 mm were counted to avoid including burrows of the much larger Black Petrel (Procellaria parkinsoni), which weighs ~700 g and is the only other petrel breeding in forests of Little Barrier Islands on summit ridge tops, though the population is only small (200+ pairs) (Imber et al. 2003b). Where burrowing activity had

Habitat data

The following habitat variables were recorded within each plot:

- (1) Canopy cover, understorey cover and ground cover visually estimated in four classes (1 = 0-25%, 2 = 26-50%, 3 = 51-75%, 4 = >75%) at plot centre.
- (2) Canopy height (in m) measured using a laser range finder (Haglof Lazer Pro. Haglof Inc., Madison, MS, USA) at plot centre.
- (3) Number of stems within the plot between 1 and 20 cm diameter at breast height (dbh).
- (4) Number of stems within plot > 20 cm dbh.
- (5) Slope (in degrees) measured using a hand-held inclinometer at plot centre.
- (6) Aspect (in degrees) measured using a hand-held compass at plot centre.

GIS-based data

A GIS-based digital elevation model (DEM), derived from the New Zealand Map 260 Series (Land Information New Zealand, Wellington) and from additional spot-height data provided by Land Information New Zealand (Wellington), was used to obtain topographic data for each plot. We calculated the altitude and three-dimensional (3D) distance from the nearest ridge top to each of our plots in metres.

To calculate a raster for 3D distance from ridge top, the Euclidian distance from each raster cell to the closest point on the nearest ridge was calculated using the Arctoolbox extension and command-line interface of ArcView 9.0 (ESRI Inc., Redlands, CA, USA). The ridgeline was interpreted by eye through examining the DEM slope contours at high spatial resolution. The difference between the altitude of each cell and the nearest ridge-top location was calculated and 3D distance obtained by taking the square root of the squared and summed values for the two-dimensional distance and the altitudinal difference for each cell. We obtained forest-type data from a digitised version of the vegetation map (scale 1:15840) presented in Hamilton (1961). From the original 22 vegetation categories presented in Hamilton (1961), we identified six dominant forest types (Fig. 1) occurring across the altitudinal gradient from coastline to summit. These forest types were:

- Coastal broadleaf forest (sea level to 100 m asl): dominated by Pohutukawa (*Metrosideros excelsa*), Puriri (*Vitex lucens*), Taraire (*Beilschmiedia taraire*), Karo (*Pittosporum crassifolium*), Houpara (*Pseudopanax lessonii*), Whau (*Entelea arborescens*) and Coprosma spp.
- (2) Regenerating forest (sea level to 300 m asl): dominated by regenerating Manuka and Kanuka at various stages of succession from shrubland to closed-canopy forest, with young Northern Rata, Tawa and Kauri emergents. This pioneer forest replaces mixed Kauri and mid-altitude forest on ridges and valley floors respectively.
- (3) Mixed Kauri forest (50–450 m asl): Kauri dominated forest occurring primarily on ridge tops with Northern Rata, beech (*Nothofagus* spp.) and Miro (*Prumnopitys ferruginea*) as important elements.

- (4) Mid-altitude forest (100–500 m asl): Northern Rata and Tawa dominated forest occurring in valleys at lower altitude and on ridges and in valleys at higher altitude.
- (5) High-altitude forest (300–600 m asl): wet cloud-forest communities dominated by Towai and Tawa.
- (6) Summit forest (600–710 m asl): low growing, cool, wet and windswept summit community dominated by Quintinea, Tawari and Southern Rata.

All data were manipulated in raster format using a cell resolution of 5.32×5.32 m, or 28.27 m², the same area as our survey plots. Analyses were conducted using ArcView and the ArcView spatial analyst extension (ESRI Inc.).

Low-altitude colonies of Cook's Petrel

Although not captured during our island-wide survey, two small colonies of Cook's Petrels below 300 m (Fig. 1) were revealed as important comparative components in an investigation of the habitat use of this species at high and low altitudes on Little Barrier Island and historical impacts on this distribution. Both colonies are ~100 m asl. The first (Valley Track site) is the site of a long-term Department of Conservation Cook's petrel breeding study and known to us prior to commencement of survey work. The second site (Tirikakawa site) was discovered while moving between survey plots during our fieldwork in December 2004. Habitat data were collected from these colonies in December 2005 by first ascertaining the spatial extent of each colony by searching and locating all burrows. We then established a $15 \times$ 15 m grid over the entire area and collected data from plots established at each grid intersection using the same protocols as our island-wide survey. Habitat data from 24 and 18 plots were collected from the Valley and Tirikakawa sites respectively.

Statistical analyses

Datasets were examined for normality and transformations applied where necessary. Transformed variables are indicated with a prefix in the Results. To incorporate the nominal categorical variables of aspect (N, S, E, W) and forest type (six categories) into our multivariate analysis, the categories of each variable were transformed into binary variables (1 if applicable to the plot location, 0 if not) and included separately.

Analyses of burrow counts within forest types were conducted using Kruskal-Wallis analysis of variance (ANOVA). To investigate patterns of habitat use by Cook's Petrel we used autologistic and logistic regression models. Autologistic regression is a form of logistic regression (binomial distribution and log link function) incorporating an autocovariance term to account for spatial dependency in the response variable (Smith 1994). By accounting for spatial dependency we hoped to minimise bias to predictor variables and accurately classify habitat characteristics influential in the distribution of Cook's Petrel (Klute et al. 2002). The modelling procedure involved running mixed nominal logistic regression models incorporating autocovariate variables of different neighbourhood size. The autocovariate variables for our models were quantified using an inverse-distance-weighted calculation from Augustin et al. (1996). The most appropriate neighbourhood size for each autocovariate was selected by comparing the variable significance and model predictive power across a range of potential neighbourhood sizes, ranging from 100 m to 3000 m in increments of 100 m.

We conducted our analyses at two levels. The first level incorporated the island-wide dataset with two models analysing habitat differences between (1) sites in low-altitude (below 300 m) and high-altitude (above 300 m) strata (stratum as the binary dependent variable), and (2) sites with and without Cook's Petrel burrows (burrow presence or absence as the dependent variable). This approach provided a means of investigating patterns of habitat use by Cook's Petrel on the island beyond circumstantial association with altitudinal habitat gradients. The second level of our analyses focused upon modelling habitat differences between sites where Cook's Petrel burrows were present or absent using the above-300 m dataset only.

Principal components analysis (PCA) was conducted upon the datasets for each level of analysis to reduce the number of habitat variables to a smaller set of uncorrelated components. The resulting components, presenting measures of the relationships within the data, were screened and those with eigenvalues greater than one were included in the analyses. Using this criterion the first nine components from the analyses of both the island-wide and above 300-m datasets were included. These components were then used, in conjunction with the autocovariate variables, as predictor variables in autologistic models. Model selection was conducted through examination of the strength of the model fit and individual predictor tests (Wald's χ^2 statistics and R^2 values) and discrimination ability was examined using receiver operating curve plots. These plots relate the proportions of correctly and incorrectly classified observations over a range of threshold levels. Models with no discrimination ability have an area under the curve of 0.5, whereas those with a perfect discrimination ability have an area of 1 (Pearce and Ferrier 2000).

The small sample size (only two sites) prevented similarly complex analyses examining the differences between the two low-altitude colony sites and other locations. However, to compare habitat data between plots at these sites, plots at similar low altitudes without Cook's Petrel burrows (< 200 m: n = 90) and plots where Cook's Petrel burrows were present, we averaged observations from all plots at the low-altitude sites and compared these values in conjunction with their 95% confidence interval values.

Data are shown as means \pm standard errors, and the threshold of significance for all analyses was set at $\alpha = 0.05$. Autocovariates were calculated using the software R, 1.9.0 (<u>Ihaka and Gentleman 1996</u>), whereas all other analyses were conducted using JMP 5.1 (SAS Institute Inc., Cary, NC, USA).

Results

The average values, ranges and standard errors for all variables recorded from plots during the island-wide survey are shown in Table 1.

General distribution and densities of Cook's Petrel burrows

During the 12 weeks of our island-wide survey we visited 194 sites (of a targeted 208), 90 within the below 300 m stratum and 104 in the above 300 m stratum (Fig. 1). No Cook's Petrel burrows were found in plots below 300 m. Above 300 m, 57 plots contained Cook's Petrel burrows (ranging from 1 to 3 per plot) with a mean density of 1.89 burrows plot⁻¹ (0.07 burrows m⁻²) in plots containing burrows, and 1.11 burrows plot⁻¹ (0.04 burrows m⁻²) across all plots.

Presence within different forest types

At an island-wide scale the distribution of Cook's Petrel burrows differed significantly between the six forest types (Kruskal–Wallis ANOVA, P = < 0.0001). Burrows were not found in plots within any forest type below 300 m (regenerating (n = 55), coastal broadleaf (n = 5), mixed Kauri (n = 6) and midaltitude (n = 24) forests). Above 300 m, plots in mixed Kauri (n = 14) and mid-altitude forests (n = 38) had similar numbers of burrows, as did plots in high-altitude (n = 36) and summit forest (n = 16). There was, however, a difference between these two groups: high-altitude $(1.47 \text{ burrows plot}^{-1} \pm 0.18)$ and summit forest (1.69 ± 0.28) had significantly more burrows per plot than mixed Kauri (0.57 ± 0.25) and mid-altitude (0.52 ± 0.14) forests (Kruskal–Wallis ANOVA, P = < 0.001).

Multivariate habitat analyses

Island-wide analysis

The first nine components selected using PCA on the islandwide dataset explained 74% of the total variance. Selected island-wide strata and island-wide presence/absence models are shown in Table 2.

For the island-wide stratum and presence/absence models, principal component 1 (PC1), principal component 2 (PC2) and an auto-covariance term with a neighbourhood size of 1000 m were the most significant predictor variables. The strata model proved a stronger fit (Wald's $\chi^2 = 216.72$, d.f. = 3, P < 0.0001, $R^2 = 0.81$) than the presence/absence model (Wald's $\chi^2 = 118.28$, d.f. = 3, P < 0.0001, $R^2 = 0.50$, Table 1). Both models show strong discrimination with ROC values of 0.99 for the stratum model and 0.93 for the presence/absence model.

PC1 comprised 14.7% of the total variance and was strongly negatively correlated with regenerating forest types (r = -0.83) and positively correlated with altitude (r = 0.79), slope (r =0.66) and canopy cover (r = 0.53) (Table 3). Individual predictor tests revealed PC1 as significant for both the strata (Wald's $\chi^2 = 16.64$, d.f. = 1, P < 0.0001) and presence/absence models (Wald's $\chi^2 = 19.77$, d.f. = 1, P < 0.0001), although providing a stronger fit for the presence/absence model, with a higher χ^2 significance. PC2 comprised 11.3% of the variance in the data and was negatively correlated with summit forest types (r = -0.57) and positively correlated with canopy height (r = 0.65) and distance to ridge top (r = 0.59). In individual predictor tests this component was significant for both the stratum model (Wald's $\chi^2 = 9.12$, d.f. = 1, P = 0.003) and presence/absence model (Wald's $\chi^2 = 4.37$, d.f. = 1, P = 0.037).

Autologistic models of stratum membership and burrow presence and absence revealed that the probability of occurrence of Cook's Petrel burrows was increased in higher altitude areas, where regenerating forest was limited, and on steeper slopes with reduced canopy cover (PC1). In addition, the availability of summit forest habitats, with lower canopy heights and shorter distances to the ridge tops was also influential (PC2). The two models revealed strong correlations between islandwide habitat gradients (indicated by the stratum model) and the habitat use of Cook's Petrel (indicated by the island-wide presence/absence model). However, the stronger significance of PC1 as a predictor in the island-wide presence/absence model in comparison with the island-wide stratum model suggests species-specific patterns beyond random association with altitudinal habitat gradients. These patterns appear to be related to the dichotomy between low-altitude, human-impacted habitats (regenerating forest) and topographic and floristic components above 300 m (altitude, slope and canopy height).

The spatial autocovariate term (1000-m neighbourhood) that provided the best fit to both island-wide models, was significant in the stratum model (Wald's $\chi^2 = 15.43$, d.f. = 1, P < 0.0001) and the presence/absence model (Wald's $\chi^2 = 8.37$, d.f. = 1, P = 0.003). The size of the neighbourhood selected for the autocovariate term (1000 m) and visual examination of the distribution of plots with burrows present, suggests that spatial autocorrelation present in these data was a result of the occurrence of burrows above 300 m, clustered in areas close to ridge tops, and surrounded by empty plots below 300 m.

Above-300 m analysis

The first nine components selected from the PCA on the above-300 m dataset explained 73% of the total variance. Modelling presence or absence of Cook's Petrel burrows above 300 m using these components resulted in a highly significant logistic model (Wald's $\chi^2 = 0.29$, d.f. = 2, P < 0.0001, Table 2) with principal component 1 (PC1) and principal component 7 (PC7) being significant predictors of burrow presence. The modelling process failed to select a significant autocovariate at

Table 1. Summary of the raw habitat data of presence or absence of Cook's Petrel burrows used in principal components and autologistic analysesData displayed for plots with burrows present (only present in above 300-m stratum) and burrows absent (both strata and above 300-m stratum only). Excludes
forest type. Canopy cover, understorey cover and ground cover measured in four classes: 1 = 0-25%, 2 = 26-50%, 3 = 51-75%, and 4 = >75%

Variable	Burrows present $(n = 56)$		Burrows abs	Burrows absent, both strata ($n = 138$)			Burrows absent $>300 \text{ m} (n = 47)$		
	Mean	Range	S.E.	Mean	Range	S.E.	Mean	Range	S.E.
Canopy cover class	2.71	1–4	0.14	2.38	1–4	0.10	2.85	1–4	0.17
Understorey cover class	2.40	1–4	0.16	2.24	1–4	0.08	2.48	1-4	0.13
Ground cover class	1.89	1–4	0.12	1.99	1–4	0.09	2.25	1-4	0.16
Canopy height (m)	11.20	4–26	0.66	10.96	1-30	0.56	12.17	1-30	0.93
Number of stems 1–20 cm dbh	26.78	0–60	1.85	24.37	3-60	1.07	26.60	5-60	2.08
Number of stems >20 cm dbh	1.07	0–4	0.14	0.79	0–4	0.08	1.04	0–3	0.14
Slope (°)	36.26	10-60	1.53	24.47	1-52	1.07	30.28	1-52	1.72
Altitude (m)	509.56	316-687	12.31	273.21	55-655	11.16	417.13	301-655	13.31
Distance to ridge (m)	62.20	1-329	8.45	90.13	0-455	8.85	99.04	1-348	13.59
Aspect (°)	48.15		62.90	48.13		79.38	48.15		79.30

any neighbourhood size suggesting a lack of spatial dependence in these data. This model demonstrated a reasonable ability to discriminate between plots with burrows present and absent, with a ROC value of 0.75.

PC1 (Wald's $\chi^2 = 13.54$, d.f. = 1, P < 0.001) comprised 14.36% of the total variance and was negatively correlated with altitude (r = -0.90), summit forest (r = -0.69), and positively correlated with mid-altitude forest (r = 0.65), canopy height (r = 0.60) and distance to ridge (r = 0.52) (Table 3). PC7 (Wald's $\chi^2 = 4.5$, d.f. = 1, P = 0.037) explained 6.32% of the variance and was correlated with stems greater than 20 cm dbh (r = 0.66) (Table 3). This logistic model suggested that above 300 m Cook's Petrel burrows are more likely to occur in high-altitude, low-canopy habitats with shorter distances to the ridgeline (PC1). In addition, the structural composition of the forest (size of woody stems) appeared important, with the likelihood of burrow presence increasing with increasing trunk size and density (PC7).

Habitat characteristics at two low-altitude Cook's Petrel colonies

The locations of the two low-altitude colony sites are shown in Fig. 1. The Valley colony was located at ~110 m altitude on a sharp ridge rising above a stream bed. The vegetation at the site was dominated by old-growth Pohutukawa interspersed with regenerating Kauri and coastal broadleaf communities. This

colony consisted of 46 burrows spread over ~5400 m². The Tirikakawa colony was located at an altitude of 115 m on a ridge dominated by mid-altitude Rata and Tawa forest with occasional large Kauri emergents. Fifty burrows were counted at this site, extending over an area of ~4000 m². The average burrow densities at plots recorded from these sites was very similar to those recorded from sites above 300 m (Table 4).

The low-altitude colony sites differed markedly in vegetation and habitat characteristics from other low-altitude locations sampled during our main habitat survey. Both sites retained mature phase vegetation, in contrast to surrounding low-altitude forests dominated by regenerating pioneer species at various stages of growth. The Valley site was dominated by large Pohutukawa, with several trees greater than 1500 cm in dbh. At the Tirikakawa site, large Tawa and mature Kauri were present, with individual Kauri in stands measuring 60-70 cm in dbh and one specimen of 110 cm dbh. Despite potential variable interactions and a small sample size for the lowaltitude colony dataset, there were significant differences between data collected from plots at the low-altitude colonies (averaged across 42 plots in total) and other low-altitude sites (Table 4). The low-altitude colonies had habitat characteristics more similar to high-altitude habitats where the bulk of Cook's Petrel burrows were found (Table 4). At the low-altitude colonies, burrows were positioned closer to the ridge top, on steeper slopes and the canopy and understorey cover and

Table 2. Best-fit autologistic and logistic regression habitat models of island-wide stratum membership, islandwide presence or absence of Cook's Petrel burrows and above-300 m presence or absence of Cook's Petrel burrows Dependent variable for the island-wide stratum model – strata above and below 300 m. Dependent variable for the island-wide presence/absence and above-300 m presence/absence models – presence or absence of Cook's Petrel burrows. Predictor variables: PC1, PC2 and PC7 are principal components selected as significant in respective model. Auto1000 is an autocovariate variable incorporating a neighbourhood size of 1000 m. Model discrimination assessed using receiver operating curve (ROC): Island-wide strata model = 0.99 (>0.9 indicates very good discrimination), Island wide presence/absence model = 0.93, Above-300 m presence/absence model = 0.75 (0.7–0.9 indicates reasonable discrimination)

Predictors	β	S.E. β	Walds χ^2	d.f.	Р	
Island-wide strata model						
Intercept	2.25	0.72	9.71	1	0.0018	
PC1	-2.35	0.58	16.64	1	< 0.0001	
Auto1000	-10.16	2.59	15.43	1	< 0.0001	
PC2	1.47	0.49	9.12	1	0.0025	
Island-wide presence/absence model						
Intercept	3.45	0.71	23.88	1	< 0.0001	
PC1	-1.48	0.33	19.77	1	< 0.0001	
Auto1000	-3.43	1.16	8.73	1	0.0031	
PC2	0.32	0.15	4.37	1	0.0366	
Above-300 m presence/absence model						
Intercept	-0.26	0.22	1.42	1	0.2331	
PC1	0.53	0.15	13.54	1	< 0.001	
PC7	-0.44	0.21	4.50	1	0.0339	
Whole model tests			χ^2	d.f.	Р	R^2
Island-wide strata model						
Likelihood ratio test			216.72	3	< 0.00001	0.81
Island-wide presence/absence model						
Likelihood ratio test			118.28	3	< 0.0001	0.50
Above-300 m presence/absence model						
Likelihood ratio test			21.02	2	< 0.0001	0.15

Table 3. Correlations between model-selected principal components (see Table 1) and the original data

'Both strata' represents principal components from the island-wide dataset selected as significant in both the island-wide stratum and presence/absence models. 'Above-300 m stratum' represents the principal components selected as significant in the above-300 m presence/absence model. Values shown are Pearson product-moment correlation coefficients. Correlations discussed in text shown in bold

Both	strata	Above-300 m stratum		
PC1	PC2	PC1	PC7	
0.53	0.20	0.10	0.35	
0.35	0.28	0.33	0.18	
0.03	-0.26	-0.10	0.15	
0.30	0.65	0.60	0.00	
0.19	-0.37	-0.10	0.10	
0.32	0.20	0.20	0.66	
0.10	0.22	0.02	0.31	
0.28	0.10	0.10	0.24	
0.10	0.04	0.00	0.38	
0.14	0.23	0.05	0.25	
0.66	0.01	-0.03	0.01	
0.79	-0.45	-0.90	0.11	
0.09	0.59	0.52	0.27	
-0.83	-0.10	0.03	0.12	
0.10	0.10	0.00	0.00	
0.17	0.20	0.26	0.33	
0.17	0.49	0.65	0.07	
0.39	-0.28	-0.32	0.33	
0.30	-0.57	-0.69	0.06	
	Both PC1 0.53 0.35 0.03 0.30 0.19 0.32 0.10 0.28 0.10 0.14 0.66 0.79 0.09 -0.83 0.10 0.17 0.17 0.39 0.30	Both strata PC1 PC2 0.53 0.20 0.35 0.28 0.03 -0.26 0.30 0.65 0.19 -0.37 0.32 0.20 0.10 0.22 0.28 0.10 0.10 0.44 0.14 0.23 0.66 0.01 0.79 -0.45 0.09 0.59 -0.83 -0.10 0.17 0.20 0.17 0.49 0.39 -0.28 0.30 -0.57	Both strata PC1 Above-300 n PC2 0.53 0.20 0.10 0.35 0.28 0.33 0.03 -0.26 -0.10 0.30 0.65 0.60 0.19 -0.37 -0.10 0.32 0.20 0.20 0.10 0.22 0.02 0.10 0.23 0.20 0.10 0.22 0.02 0.10 0.22 0.02 0.10 0.23 0.05 0.66 0.01 -0.03 0.10 0.04 0.00 0.14 0.23 0.05 0.66 0.01 -0.03 0.79 -0.45 -0.90 0.09 0.59 0.52 -0.83 -0.10 0.03 0.10 0.10 0.00 0.17 0.20 0.26 0.17 0.49 0.65 0.39 -0.28 -0.32 0.30 -0.57 -0.69	

^AOriginal variable log-transformed.

^BOriginal variable arcsinh-transformed.

canopy heights were greater than other low-altitude sites (Table 4). These sites differed from high-altitude sites in having fewer small stems <20 cm in dbh and being closer to the ridge top.

Discussion

Methodological and logistical constraints in investigating the distribution of burrow-nesting seabirds are well recognised and common to most locations where these species breed (Hunter *et al.* 1982; Brooke 2004). In this study of Cook's Petrel the issues we faced included a very large area of potential nesting habitat, rugged terrain, and the selection of appropriate habitat descriptors. As with other studies of the distribution of breeding seabirds at their colonies (Lawton *et al.* 2006), ecologically relevant stratification allowed the analysis of distributional patterns across a large area of challenging terrain. The habitat variables we measured were selected on the basis of studies of other burrow-nesting seabirds (Catry *et al.* 2003; Schulz *et al.* 2005) or deemed appropriate to characterise the structure of the Cook's Petrels forest habitat. Our analyses revealed three key results:

- (1) The breeding distribution of Cook's Petrels is predominantly above 300 m asl on Little Barrier Island.
- (2) Within this distribution, burrows are more likely to be at high altitude, in habitats associated with steeper slopes, shorter distance to the ridgeline, lower canopy heights, less canopy cover, and more large stems.
- (3) Human-mediated effects appear to have played a significant role in the current distribution of Cook's Petrels.

Distribution of Cook's Petrel on Little Barrier Island

Our study confirms that the distribution of Cook's Petrel on Little Barrier Island is predominantly restricted to the island's upper slopes. Although burrows also occur below 300 m, the densities present were below a level that could be captured by our sampling regime. This suggests that the number of birds occupying these habitats is very low compared to that above 300 m. The burrow densities revealed by our study (0.04 burrows m⁻²) are low compared with known densities of other gadfly petrels: Barau's Petrel (*Pterodroma baraui*) on Reunion Island has burrow densities of 0.11 burrows m⁻² (Probst *et al.*

Table 4. Comparison of habitat characteristics of low-altitude colonies (table centre) with data	a						
from plots below 200 m and from plots above 300 m where burrows were present							
Data from the two low-altitude colonies were averaged across 42 plots in total. All values presented with							

 \pm 95% confidence intervals; *significant difference at $\alpha = 0.05$. Please see Table 1 for explanation of cover classes

Variable	<200 m	Low-altitude	>300 m	
	(n = 90)	colonies $(n = 2)$	(n = 56)	
Density of burrows (number per plot)	0.00	1.61 (± 0.47)	1.89 (± 0.22)	
Canopy cover class	2.15 (± 0.23)	2.69 (± 0.26)	2.71 (± 0.29)	
Understory cover class	2.13 (± 0.21)	2.78 (± 0.26)	$2.40 (\pm 0.29)$	
Ground cover class	1.85 (± 0.21)	1.71 (± 0.21)	1.89 (± 0.25)	
Canopy height ^A (m)	2.16 (± 0.12)	2.44 (± 0.11)	2.32 (± 0.12)	
Number of stems 1–20 cm dbh	3.25 (± 2.36)	19.26 (± 2.42)	26.78 (± 3.72	
Number of stems >20 cm dbh	$0.67 (\pm 0.20)$	$0.87 (\pm 0.20)$	$1.07 (\pm 0.27)$	
Slope (°)	21.78 (± 2.48)	38.00 (± 2.18)	36.26 (± 3.07)	
Altitude (m)	96.85 (± 13.66)	112.00 (± 32.00)	509.56 (± 24.67)	
Distance to ridge ^B (m)	4.33 (± 0.31)	$2.65 (\pm 0.36)$	4.17 (± 0.35)	
Aspect (°)	224.72° (± 41.35°)	263.52° (± 18.51°)	48.15 (± 155.47°)	

^AOriginal data log-transformed.

^BOriginal data arc-sinh transformed.

2000), Great-winged Petrel (*Pterodroma macroptera*) on Moutohora Island, New Zealand, 0.11 burrows m⁻² (Imber *et al.* 2003*c*) and a mixed colony of Juan Fernadez (*Pterodroma externa*) and Stejneger's (*Pterodroma longirostris*) Petrels on Isla Alejandro Selkirk has densities of 0.63 burrows m⁻² (Brooke 1987). The low densities for Cook's Petrel may be characteristic of this forest-nesting species, or the result of population decline following predation by introduced mammals (Imber *et al.* 2003*a*).

The Cook's Petrel, and the much larger Black Petrel, are the only burrow-nesting species breeding in the forests of Little Barrier Island and, given our burrow-selection methods, we are confident that our counts of burrows are species specific. However, several biases could have affected our density estimates. Burrow-occupancy data were not collected at each survey site and it is possible that some burrows counted were temporarily unoccupied or possessed double chambers containing multiple breeding pairs. The construction of a burrow represents a large investment in time and energy for petrels (Brooke 2004). On Little Barrier Island, most new burrows found at long-term study sites are occupied by breeding pairs in the following season (M. J. Rayner, unpublished data). This suggests that newly constructed burrows most likely represent valid additions to the breeding population. Further, in the course of examining many hundreds of burrows on Little Barrier Island, we found no evidence for more than one pair of Cook's Petrel using multiple breeding chambers within single burrows and consider the effects of these biases to be negligible.

Adaptive significance of habitat use

On Little Barrier Island, Cook's Petrels predominantly occupied unmodified high-altitude and summit forest habitats associated with steeper slopes, and shorter distances to ridge tops. Within such habitats burrows also occurred in higher densities at sites with low, open canopies and increased numbers of stems >20 cm in dbh. Although our analyses suggest that altitude plays a major role in habitat selection by Cook's Petrel, data collected from two low-altitude colonies, and observations from the species' other breeding site on Codfish Island (Fig. 1, Imber et al. 2003a, M. J. Rayner, personal observation), suggest caution. The two low-altitude colonies surveyed in this study confirm the importance of steeper slopes, shorter distances to ridge tops and the maturity of forest habitats in the presence of Cook's Petrel. They also suggest that altitude and the low, open canopies correlated with altitude may not be vital to Petrel breeding success but are circumstantial associations linked to altitudinal temperature gradients and wind exposure. This hypothesis is supported by the finding that on Codfish Island, Cook's Petrels breed successfully from sea level to ~350 m asl in a broad range of habitats (Stead 1936; West 1990).

The adaptive significance of the habitats used by Cook's Petrel is likely to be related to several factors. As with other gadfly petrels, Cook's Petrel is an adept climber (Warham 1990). However, access to breeding sites remains important because collision or entanglement with trees can be a cause of mortalities (M. J. Rayner, personal observations). Ridge-top habitats with steep slopes and mature trees provide airspace and take-off points for birds. Individual Cook's Petrels have been

observed walking up to 100 m from burrows to locations with these favoured characteristics (M. J. Rayner, personal observations). In studies of other small petrels, similar habitat characteristics are important. Slender-billed Prions (Pachyptila belcheri) select sites with steeper slopes (Catry et al. 2003), whereas Chatham Petrels (Pterodroma axillaris) prefer mature forest habitats with leaning trees for climbing (Sullivan and Wilson 2001). Suitable soil is also important in the distribution of burrow-nesting seabirds (Storey and Lien 1985; Warham 1996). On Little Barrier Island, the steep terrain has a high rate of erosion, resulting in shallow soils on slopes and rocky substrates in the valley bottoms where the force of runoff prevents soil accumulation. Thick stable soils are concentrated near ridge tops and are ideal for burrowing petrels (Hamilton 1961). By selecting burrowing sites close to ridge tops Cook's Petrels gain the advantages of safe take-off spots, ease of burrow construction, reduced burrow collapse through erosion, and free-draining soil preventing burrow flooding.

Anthropogenic impacts on the distribution of Cook's Petrel

Many external factors are likely to have affected the distribution of Cook's Petrel on Little Barrier Island. Burrows would have been destroyed by the clearance of forest at lower altitudes both through the felling of trees and the use of bullocks to haul the logs to the sea. Within the existing distribution of Cook's Petrel this effect may be reflected in the lower numbers of burrows in Kauri and mid-altitude forests, in comparison with the island's uncut upper slopes. Mature trees present at the low-altitude colony sites suggest that these locations escaped the major period of logging, with stands of Kauri of between 60 cm and 110 cm dbh representing age-classes of between 150 and 500 years old (Moinuddin and Ogden 1987). Loss of forest cover may also have affected the continuity of colonies, with birds abandoning sites without adequate cover and pre-breeders preferring to prospect in unmodified habitats with higher levels of aerial activity of Petrels. Boscawen (1895) noted the widespread damage to the island's vegetation by livestock, and grazing on the lower slopes would have completed the loss of vegetation. The impacts of introduced predators would also have been enhanced in warm low-altitude habitats where predator densities were found to be greater than at higher altitudes during most of the year (Veitch 2001). Feral Pigs eat petrel eggs and chicks (Collar et al. 1992) and were observed to have severe affects upon petrel burrows on Little Barrier Island (Reischek 1886, 1887). Feral Cats are one of the mammals most damaging to petrel populations (Imber 1975; Moors and Atkinson 1984) and, before their eradication in 1980, were estimated to have killed over 5000 Cook's Petrels annually (Imber et al. 2003a). Pacific Rats also appear to have been significant predators of Cook's Petrel eggs and chicks (Pierce 2002; Imber et al. 2003a). Predation, however, fails to explain the presence (and survival during pre-Pacific Rat and pre-Cat eradications) of the low-altitude colonies of Cook's Petrel present in our study. Alternative explanations may be that the colonies were established during the 26 years since eradication of Cats, or that localised Cat control conducted by resident rangers (Veitch 2001) may have helped to protect these sites.

Conservation implications

It appears likely that Cook's Petrels formerly occupied both the upper and lower slopes of Little Barrier Island. The current distribution of this population is a function of habitat selection and the impacts of human settlement operating across an altitudinal gradient. With the continued protection of Little Barrier Island as a nature reserve, the regrowth of modified habitat and the removal of introduced predators, negative impacts on this population are now limited to at-sea factors, such as the availability of food and marine pollution across the migratory range of the species. Because this population is likely to be a fraction of its historical size, and the species forages mainly on noncommercial cephalopods and crustaceans (Imber 1996), it should not be limited by foraging resources. Consequently, providing marine pollution does not have a negative impact on this species, a population expansion is expected. The distribution and densities of burrows revealed in this study suggest that the population of Cook's Petrels on Little Barrier Island may be significantly larger than previously thought (Taylor 2000). Management objectives should focus upon obtaining data on burrow occupancy in a range of habitats to clarify the results of this study, and on monitoring of the population to detect any expansion after the removal of Pacific Rats. As with other gadfly petrels, Cook's Petrel is long lived (Warham 1990). This factor and the low fecundity of the species (Imber et al. 2003a) will make the identification of population change difficult to detect and future long-term monitoring work should be conducted.

Our study suggests that Cook's Petrel exhibits a high degree of habitat flexibility consistent with a wide former distribution the length of the New Zealand archipelago (Worthy and Holdaway 2002). Conservation efforts aimed at restoring the Great Barrier Island Cook's Petrel population, or re-establishing colonies at other island locations or on the New Zealand mainland, should focus on sites with mature forest habitats with adequate soils for burrowing, positioned on steep slopes on or near ridge tops allowing safe access to nesting sites. Further, these actions should be conducted in conjunction with comprehensive predator control programs.

Acknowledgements

The Ecology, Evolution, and Behaviour Group at the University Of Auckland, School of Biological Sciences, funded this research, whereas Matt Rayner was supported by a New Zealand Tertiary Education Commission Bright Futures Scholarship. Many thanks go to the Department of Conservation for granting access to Little Barrier Island and for transport on the departmental boat Hauturu. This project would not have been possible without the logistical support and field experience of Department of Conservation staff Rosalie Stamp, Richard Griffiths, Pete and Helen Barrow and Hugh Gardiner. We are equally grateful to volunteers Mike Anderson, James Andrews, Mark Green, Darryl Jeffries, Troy Makan, Wendy Rayner, Cleo Rothschild and Jono Walter whose sweat and blood were exuded in equal amounts across challenging terrain. Thanks go to Allen Rodrigo and Steven Miller for statistical help and to Brendan Dunphy, Emma Marks, Rose Thorogood, Mike Imber, and three anonymous referees whose comments vastly improved this manuscript. Work was conducted under a Department of Conservation Research Permit and with ethics approval from the University of Auckland Animal Ethics Committee.

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Manuscript received 15 August 2006, accepted 18 January 2007