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Spatial variation in burrow entrance density of the sooty shearwater (*Puffinus griseus*)

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Abstract The effects of a range of habitat variables on spatial variation of breeding burrow density of sooty shearwaters, *Puffinus griseus,* were measured on 5 islands near Rakiura (Stewart Is) and 1 island in The Snares Is group, during the 2000-01 breeding season. Density estimates for 4 islands where Rakiura Maori harvest chicks ranged from 0.30 to 0.47 burrows per m^2. Density on 2 non-harvested islands occurred at opposite ends of the burrow density spectrum (Whenua Hou, 0.09 entrances per m^2; The Snares, 0.90 per m^2). Burrow density was consistently lower in areas with shallow soil, in inland areas, and where there was more plant debris on the forest floor. The latter may reflect cause or effect because the birds drag woody and leafy debris into their burrows to form nests and to block the burrow entrance. Large amounts of variation in burrow density were not explained by habitat predictors. Detection of harvest impacts on sooty shearwater density on harvested and non-harvested islands will be more powerful if models account for soil depth and island edge-effects, but disregard vegetation variation.

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Keywords burrow density; habitat selection; harvest; *Puffinus griseus*; sooty shearwater; spatial variation

INTRODUCTION

Sooty shearwaters (*Puffinus griseus)* are burrow-nesting petrels that breed on New Zealand's coastal mainland and offshore islands (Warham *et al.* 1982, Marchant & Higgins 1990). During Apr and May of each breeding season, Rakiura (Stewart Is) Māori harvest sooty shearwater chicks (known as tītī) from several of these islands. The harvest of chicks continues to be economically important for Rakiura Māori (Waitangi Tribunal 1991), and holds a special cultural significance as one of the few remaining large-scale harvests of native wildlife within indigenous control (Moller *et al.* 1999, Stevens 2006, Kitson & Moller 2008).

In recent decades there has been a large-scale decline in the number of sooty shearwaters counted at sea in the North Pacific (Veit *et al.* 1996, 1997). It is possible that harvesting of the shearwaters contributed to this decline but climate perturbations, introduced predators and/or fisheries by-catch are probable causes (Lyver *et al.* 1999, Uhlmann 2001, Scott *et al.* 2008).

Rakiura Māori, in conjunction with Otago University, initiated the *Kia Mau Te Tītī Mo Ake Tōnu Atu* (Keep the Tītī Forever) project in 1994.

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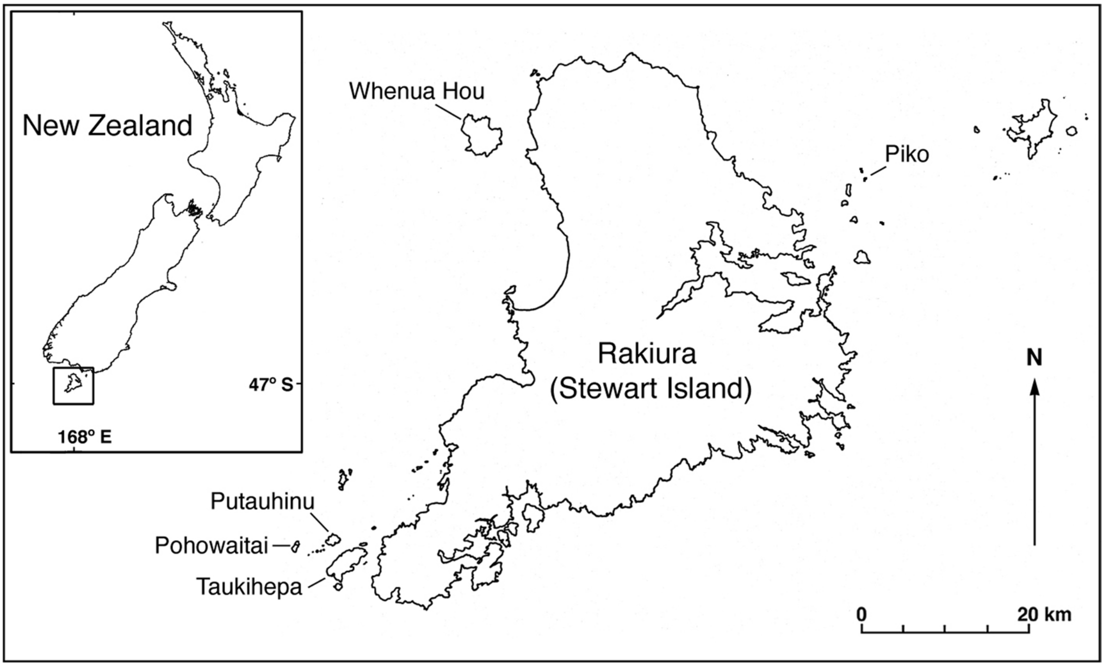

Fig. 1. Study area including Piko, Pohowaitai, Putauhinu, Taukihepa and Whenua Hou. The Snares are situated 105 km south-southwest of Rakiura.

The project aimed to assess the sustainability of the harvest through monitoring trends in population abundance, measuring harvest off-take and formulating demographic models (Moller 1996, Moller *et al.* 1999). Population models used for assessing the effects of harvesting require information on the density of populations and environmental factors that may affect them. Demographic models have been developed to estimate the impact of harvest on shearwater populations (Newman *et al.* 2008a). One way of externally checking these demographic models is to compare their predictions to the observed abundance of sooty shearwaters on harvested and non-harvested islands. If we assume that burrow densities on all islands were similar before any harvesting whatsoever occurred and that subsequent harvesting had a negative impact on the size of the breeding population, then it is predicted that harvested islands would support fewer sooty shearwaters than unharvested islands (Moller *et al.* 1999). This measurement of harvest impacts may, however, be confounded by ecological factors that may influence nest-site selection. This is especially likely if those factors that affect burrow abundance are not equal in the harvested and non-harvested areas.

This study investigated ecological correlates of burrow density so that such predictors can be factored out of comparisons between harvested and non-harvested sites. Burrowing seabirds do not select their burrow location at random (Furness 1991) and specific habitat characteristics may determine the distribution and abundance of sooty shearwater burrows within the breeding colony (Warham 1996). Factors thought to affect the use of the nesting environment by shearwaters include the amount of habitat disturbed by ground debris (Hill & Barnes 1989, Reyes-Arriagada *et al.* 2006), slope (Warham *et al.* 1982, Lawton *et al.* 2006), and soil depth (Warham 1960). Two other species of burrowing petrel, Manx shearwater (*Puffinus puffinus)* and Westland petrels (*Procellaria westlandica)* have been reported to colonise areas preferentially where the vegetation is disrupted by erosion or is devoid of ground vegetation (Storey & Lien 1985).

In this study, we sought to determine which factors contribute to variation in burrow density on several harvested and non-harvested shearwater breeding islands. We investigated whether breeding burrow entrance density could be predicted by habitat type, slope, aspect, soil depth, ground cover, canopy cover, canopy height, and/or distance from coast. Our overall aim was to determine which habitat variables should be taken into account when comparing sooty shearwater abundance on harvested and non-harvested islands.

METHODS

Study area

The study was conducted from Jan to May 2001 on 6 islands in the south of New Zealand: Whenua Hou, Putauhinu, Pohowaitai, Taukihepa, Piko and the North East Is of The Snares group (referred to hereafter as 'The Snares'). With the exception of The Snares all sample islands were located off the coast of Rakiura and are known locally as the Tītī Is (Fig. 1). No harvesting occurs on Whenua Hou or The Snares, but is practiced on the other 4 islands. The islands varied in several geographical and ecological dimensions: proximity to Rakiura, size, introduced predator history, and the presence of other burrowing seabirds (Table 1).

Of the 4 main habitat types found on the Tītī Is, forest is the most prevalent. Most of the smaller islands are completely covered by a forest of tūpare *Olearia colensoi* and tētēaweka *O. angustifolia* trees. Despite this general similarity, aspects of the vegetation and habitat composition were specific to each island. On Taukihepa and Putauhinu, pakahi (a scrub habitat) occupies the inland regions beyond the steeper coastal slopes (Fineran 1973, Johnson 1982, Newman *et al.* 2008b, Bragg *et al., in press*). Pakahi is marsh with an iron pan that prevents complete drainage, and its vegetation is composed of moss interspersed with patches of sapling species including inaka *Dracophyllum longifolium*, *Pseudopanax simplex, Senecio reinoldii, Griselina littoralis* and flax *Phormium cookianum*. The vegetation between the forest and pakahi is characterised by a 'fringe' habitat containing species from both pakahi and forest habitats. Pohowaitai is the farthest west and most exposed of the south-western Tītī Islands (Fig. 1). The vegetation is dominated by the bush *Hebe elliptica* and tētēaweka, with some open areas of maritime tussock habitat *Poa astonii* (Fineran 1973). The canopy cover of Piko Is is dominated by *Myrsine chathamica* and *Muehlenbeckia australis* with occurrences of tētēaweka on the southwest-coast. The ground cover on Piko is made up of open areas found below tētēaweka, and closed areas (large fern cover) beneath *Myrsine chathamica* and *Muehlenbeckia australis* (Johnson 1976). The eastern side of Whenua Hou is covered mostly with mixed forest and scrub. The coastal forest is diverse and includes 10 or more mid-canopy species ranging from 3 - 8 m in height (Fineran 1966, Meurk & Wilson 1989). Further inland there is a gradual change to larger tree species including rimu *Dacrydium cupressinum*, miro *Podocarpus ferrugineus* and kamahi *Weinmannia racemosa* with a canopy height of 8 to 15 m. The canopy vegetation on The Snares is dominated by *Olearia* spp. and *Brachyglottis stewartiae* with some *Hebe elliptica* (Hay *et al.* 2004). The forests are surrounded by meadows of tussock consisting of *Poa astonia* and *Poa tennantiana,* which extend outwards towards the coastal cliffs. The majority of the ground under the *Olearia* canopy is bare except in places where trees have blown down and plants have taken advantage of new light conditions.

Sample design

The number of transects completed per island was based on the size of the island, the time available, and the required minimum number predicted by a power analysis based on burrow density data collected from The Snares. This analysis suggested that a minimum of 6 transects per stratum were required to achieve a reasonable level of precision. Māori harvesters have previously described a difference in abundance of sooty shearwater burrows on the east and west coasts of the Titi Is (Charleton 2002, Moller *et al., in press*) Therefore, where possible we placed more than 6 transects with equal numbers on the east and west side of each island.

The coastal area of each island was first divided into equal blocks for the number of transects required. Each transect was randomly placed within each block to run perpendicular to the coast. Circular habitat plots of 3 m radius (28.3 m^2) were measured at intervals of 3, 15, 27, 45, 63, 93, 123, 174, 225 and 324 m from the coast along each transect. Sampling along the transect was terminated when either (a) 2 habitat plots had been sampled and no burrows had been found, (b) the centre of the island was reached and continued sampling would decrease the distance to the opposite coast, or (c) all 10 habitat plots had been completed. Due to time constraints, habitat plots on Piko Is did not follow the complete sampling regime outlined above. Instead, plots were sampled at 10 m intervals along each transect.

Each plot was broadly categorised into 1 of 4 habitat types: 'forest', '*Poa*', 'pakahi' or 'fringe'. A plot was classified as '*Poa*' if more than 50% of ground cover was *Poa astonii* or *Poa tennantiana* and there was no canopy cover present (open sky = 100%), 'pakahi' if ground cover was predominantly moss and/or saplings (height < 2 m), and 'fringe' if vegetation consisted of species found in both forest and pakahi areas (listed under Study Area). All other plots were classified as 'forest'.

The following variables were recorded within each plot: number of burrows, aspect, slope, soil depth, ground cover, canopy cover and canopy height. Burrows were included in the count if they had at least half of the burrow entrance within the plot boundary and the tunnel was more than 20 cm long. Aspect was measured to the nearest 1^0 at the central point of each plot using a Silva™ sighting

Table 1. Summary of physical and ecological characteristics of each of the study sites. Modified from Moller *et al.* (1999).

Status	Island Group	Māori Name(s)	Non-Māori Name(s)	NZMS260 Map Reference	Distance from Rakiura (Stewart) Is (km)	Size (ha)	Predators
Harvested	Northern	Piko	Womens	$46^0$49′S 168^{0}13′E	8.6	8	Absent
	Southwestern	Taukihepa	Big South Cape	$47^0$13′S 167^{0}23′E	2.8	930	*Rattus rattus** *Gallirallus australis*
	Southwestern	Pohowaitai	Wedge	$47^0$13′S 167^{0}18′E	7.3	30	Absent
	Southwestern	Putauhinu	Hidden	$47^0$12′S 167^{0}21′E	4.3	140	Absent**
Unharvested	Northwestern	Whenua Hou	Codfish	$46^0$45′S 167^{0}38′E	3.0	1396	Absent***
	Snares	–	North East	$48^0$01′S 166^{0}36′E	100.0	280	Absent

R. rattus eradicated in 2006
**R. exulans* eradicated in 1990s
***Eradications: *Gallirallus australis* 1984, *Trichosurus vulpecula* 1983-1987, *R. exulans* 1998

compass. Slope was measured using a clinometer to the nearest 1^0 from the highest point of the habitat plot to the opposite side of the plot in the direction of aspect. Soil depth was measured in the centre of the plot with a 50 cm metal rod. The rod was driven into the ground until either bedrock was reached, or the full 50 cm was buried. The ground categories used were bare ground, debris (sticks, leaves, fallen stems), dead wood, trees (estimated amount of ground displaced by trunk), rock, moss, and vegetation. Canopy cover measurements summed to 100% and included the proportion of tree species and the proportion of open sky visible.

Limited habitat measurements were recorded on Piko Is with only ground and canopy cover being estimated. The categories for ground cover included open (bare or debris) and closed (vegetation). Canopy cover measurements followed the procedure outlined above.

Statistical methods

Effect of habitat type within islands

A one-way ANOVA was conducted for each island, testing for an effect of habitat type on burrow density.

Differences in burrow density

To test for differences in burrow density in forested habitat between islands, the average burrow density was calculated by dividing the average number of burrows per habitat plot for each island by the area of the habitat plot (28.3 m^2). A one-way ANOVA was used to test for differences in the average number of burrows per square metre in forest habitat for all islands sampled. Fisher's Least Significant Difference (LSD) test was used to assess differences between islands.

Principal Components Analysis of forest variables

As the forest areas of some islands contained high numbers of different species in the ground cover and canopy composition, we categorised the data into fewer, biologically meaningful categories. Forest species that were present in <5% of plots sampled were excluded. To further reduce the number of variables, Principal Components Analysis (PCA) was used to identify a predictive subset of structural variables that explained the majority of variation present in all variables measured.

Multiple regression modelling

A model was constructed using variables that were common to the forested areas of each island: distance from coast, aspect, slope, soil depth, canopy height, percentage of bare ground, percentage of debris ground cover, and percentage of *Olearia* canopy cover. In addition each plot was categorised as being located on the east or west of each island. This model was run for each of

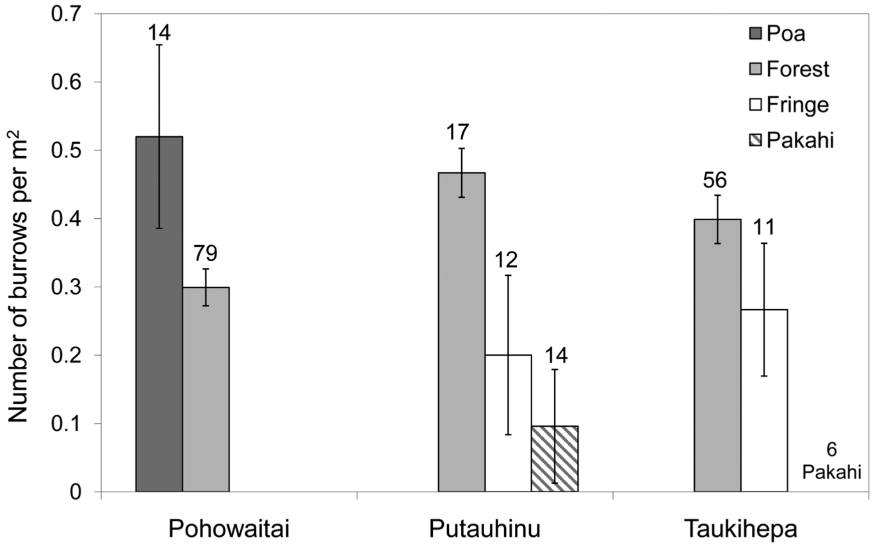

Fig. 2. Burrow density in different habitats on the three islands where multiple habitat types were sampled. Error bars show 95% confidence intervals and the number of plots in each habitat type is given above each bar.

the 5 islands, and the 'Best Subsets' procedure in Minitab (1991) was used to include only the subset of habitat variables that accounted for the majority of explainable variation in burrow entrance density for each island.

RESULTS

Burrow density between habitat types

On the 3 islands where we sampled multiple habitat types, burrow density varied significantly between forest, pakahi, fringe and *Poa* (F-value 13.2, df 5, $p < 0.01$) (Fig. 2). *Poa* contained the highest density of burrows; followed by forest, pakahi and fringe areas contained the lowest burrow density. Across islands there were too few plots in all but the forest type to characterize variation in burrow density adequately. Therefore, all remaining data analysis was conducted only on data from forested areas of islands.

Between-islands comparison of burrow density

Burrow density varied significantly between forested areas of the islands (F-value = 14.1, df = 5, $p < 0.01$) (Fig. 3). Fisher's pair-wise comparisons exposed significant differences in burrow density for all between-island forested area comparisons except between Taukihepa and Piko, Taukihepa and Putauhinu, and Piko and Pohowaitai. Density estimates for harvested islands ranged from 0.33 burrows per m^2 (Pohowaitai) to 0.43 burrows per m^2 (Putauhinu). The non-harvested islands had a much larger range: burrow density on Whenua Hou was one tenth of that on The Snares (0.09 burrows per m^2 compared to 0.90 burrows per m^2).

Principal Components Analysis

The first 2 principal components (PCs) accounted for less than 15% of the variation in the original variables. This was judged to be an inadequate characterization of the variation to justify simplification of several predictor variables into a few predictor PCs. The PCA was therefore abandoned from further analysis.

Correlation between predictor variables

Many of the ground and canopy cover variables exhibited multicollinearity, a problem that was due in part to plot measurements summing to 100%. The R^2 value often changed by less than 1% with the presence of these correlated variables. Therefore it was sometimes unclear whether the variable chosen in the 'best subsets' analysis was the most important predictor for burrow density. The variable chosen may code for ecological effects driven by its correlate.

Habitat variables that were highly correlated to debris, distance from coast and soil depth may be important indicators of burrow density but were not included in the model due to multicollinearity. Bare ground was highly correlated with burrow density for The Snares and Putauhinu Is ($r \geq 0.322$), but due to high multicollinearity, the variation was explained by other predictors such as debris (correlation between bare ground and debris; $r \geq -0.253$). Likewise, open sky was highly correlated with burrow density for Whenua Hou and Pohowaitai ($r \geq 0.344$), but was explained by multiple predictors including distance from coast, debris and soil depth. On Piko Is, more sooty shearwater burrows occurred under vegetation compared to open areas consisting of a mixture of bare ground and debris.

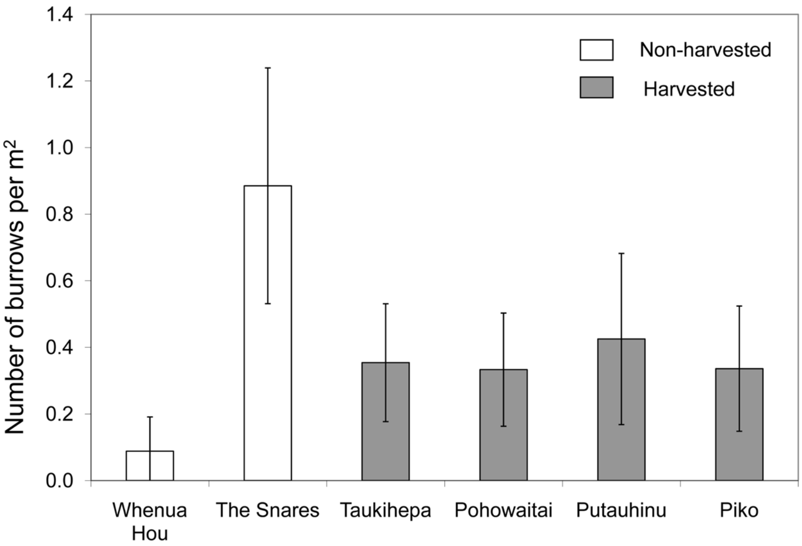

Fig. 3. Burrow density in forested areas of each island. Error bars show 95% confidence intervals.

Multiple regression modelling

Inspection of residuals suggested that a linear model to predict the square root of burrow density was most appropriate on Whenua Hou (Table 2). A simple linear model was best for all other islands and none of the predictor variables needed transformation to meet assumptions of normality and linearity. For 5 of the islands the models were broadly similar. The model from Piko Is was different from the others because most of the predictor variables had not been measured. For all islands R^2 ranged from 26-37 % (Table 2). The models revealed that across islands there were 3 consistent key predictor variables: soil depth, amount of debris on the ground, and distance from the coast. Areas with deeper soil were consistently associated with higher burrow density. This was true for all 5 islands where soil depth was measured. Burrow density was significantly lower in areas where there was more debris covering the ground (Table 2). Using the multiple regression model for each island, we examined the effects of simulating a 20% increase in debris coverage while keeping all other predictors at the inter-island average. This simulation produced 25% fewer burrows per plot on The Snares and Whenua Hou and 12% less on Pohowaitai and Putauhinu.

Burrow density was lower in inland areas on most islands, significantly decreasing with increasing distance inland for Putauhinu, The Snares and Whenua Hou. Whenua Hou exhibited the strongest decrease in number of burrows inland, with a complete absence of burrows in plots located 100 m inland. The effect occurred to a lesser extent on Putauhinu and The Snares with a decrease of 25% and 10%, respectively, when comparing number of burrows in coastal plots with plots 100 m inland. The direction of the effects was consistent between islands (Table 2); the highest burrow density was found on The Snares and the lowest on Whenua Hou.

DISCUSSION

Influence of habitat variables on burrow density

Burrow density varied markedly with vegetation type. The highest density was found in the grassland (*Poa*) areas, and the lowest in fringe and pakahi, with forested areas showing intermediate densities. Burrowing in grassy areas may be easier than in forested areas because roots do not impede digging (Warham & Wilson 1982). The marsh-like vegetation in pakahi areas prevents complete drainage resulting in densely compacted and often waterlogged soils, so it is not surprising that few burrows occur there.

Burrows were present in moderate to high densities in most forest sites, provided the soil was deep enough and debris was not concentrated. Shearwaters are constrained to breed in areas where the substrate provides crevices and opportunities to excavate (Jones 1986). Our results are consistent with those of other shearwater studies. Warham (1958, 1960) found that both flesh-footed shearwaters *Puffinus carneipes* and short-tailed shearwaters *Puffinus tenuirostris* used 99% of all areas in which soil depth was adequate.

The association between high levels of ground debris and low burrow density may reflect either cause or effect. Sooty shearwaters were observed clogging the mouth of the burrow with leaves, grasses and herbage. Daytime checks revealed that those with their entrances blocked in this way were

Table 2. Multiple regression models testing relationship between burrow density and habitat variables for each island.

Island	R^2 (%)		Constant	Coast (east/ west)	Distance from coast	Aspect	Slope	Soil Depth	Bare Ground	Debris	*Olearia* Sp.	Open Ground*
Piko	36.6	Coefficient	13.282	—	NM	NM	NM	NM	NM	NM	—	-0.080
		P-Value	0.000									0.000
Pohowaitai	33.0	Coefficient	4.017	—	-0.010	—	0.056	0.117	—	-0.049	—	NM
		P-Value	0.105		0.188		0.163	0.008		0.001		
Putauhinu	33.6	Coefficient	6.182	-3.052	-0.030	—	—	0.265	—	-0.081	—	NM
		P-Value	0.051	0.000	0.000			0.000		0.000		
North East Snares	26.5	Coefficient	0.266	—	-0.026	—	—	0.123	—	-0.301	0.399	NM
		P-Value	0.753		0.064			0.008		0.000	0.015	
Taukihepa	36.1	Coefficient	-4.763	NM	—	—	—	0.305	0.039	—	—	NM
		P-Value	0.125					0.000	0.000			
Whenua Hou**	34.4	Coefficient	-0.454	NM	-0.010	-0.002	—	0.057	—	-0.012	—	NM
		P-Value	0.669		0.000	0.014		0.008		0.003		

Table 2. continued.
NM = not measured
— = Variable not included by Best Subsets procedure.
* Piko had ground cover categorized as either open (non-vegetative cover) or closed. This coefficient represents a combination of debris and bare ground cover.
** Response variable transformed to square root of burrow density.

almost always occupied; conversely, unblocked burrows were generally empty. Muttonbirders on Pohowaitai believe that the good 'mother birds' cover the entrance with debris, whereas the poor mothers leave the entrance open (K. Charleton, *pers. comm.*). In addition, shearwaters have been reported to drag large quantities of vegetation into burrows for nesting material (Warham *et al.* 1982, Maesako 1985, Warham 1996), with eggs often found on a pile of *O. lyalli* leaves and sticks (Hamilton 1997, McKechnie 2006). Thus, even if burrows are concentrated in an area because of other microhabitat variables, this may lead to the area being relatively free of debris. Alternatively, heavy layers of debris may indirectly index other ecological variables, such as the amount of vegetative ground cover, open sky and/or distance from the coast, which themselves may directly influence breeding burrow density.

Although the decrease in burrow density as distance from the coast increased was statistically significant, its ecological significance may be weak because the change was slight in most instances. On Whenua Hou there was a transitional change in forest species composition and an increase in canopy height 100 m inland (from 7 m to 8-15 m) which coincided with the disappearance of burrows. This canopy height difference may make it dangerous for shearwaters to land (they fold their wings and fall once among the vegetation), but the thickness of the vegetation may also prevent them getting through. Many were observed to crash into the trees and then drop to the ground.

We predicted that burrow density would vary with the presence of particular vegetation species that offered preferential substrate. Although this may have been reflected to some degree, with *Brachyglottis* canopy cover on The Snares being related to low burrow density, we found that general models using broad vegetation categories explained a similar amount of variation in burrow density as species-specific models. This is in accord with Gillham (1961), who found that burrowing birds are less sensitive to vegetation type than to soil type. Similarly, a more extensive survey on Taukihepa showed relatively little relationship between vegetation and burrow density (Newman *et al.* 2008b).

Variation in burrow density between islands

Of the main predictors, Whenua Hou consistently had low burrow density and The Snares had high burrow density, whereas the 3 harvested islands were similar to one another between these extremes. The models show that the differences we observed in overall burrow density (Fig. 3) were not driven by large-scale differences in the habitats present on separate islands, or by the presence or absence of harvesting. This suggests that something other than habitat and harvest caused the major differences in burrow density between islands. Our finding that aspect has a significant effect on burrow density suggests that prevailing winds and weather direction might contribute to differences between islands. Other potential influences include island size, and presence or absence of rodents (Table 1). Testing these hypotheses is beyond the scope of the present study, which aimed specifically to investigate habitat variation as an explanation for burrow density differences.

The large difference in abundance found between The Snares and Whenua Hou suggests that it may be necessary to include a larger number of islands to give sufficient statistical power to detect harvest effects. There are several possible explanations for this population difference. The canopy cover species composition of Whenua Hou was markedly different from that exhibited on all other islands in this study, which may have impacted on burrow density there. *Olearia* species were present in only 5% of vegetation plots on Whenua Hou, in comparison to a frequency range of 40-98% on the other islands. The biology of this tree species may be related to the biology of the sooty shearwater, and indicates that the colony we studied on Whenua Hou is relatively new. *Olearia* provide a dense canopy cover, allowing the birds to first land on vegetation and then drop to the ground below. Other possible reasons for the difference in burrow density exhibited on Whenua Hou include the historical presence of possum, *Trichosurus vulpecula*, cattle, *Bos taurus,* kiore, *Rattus exulans*, and weka, *Gallirallus australis*, which may have shaped the present landscape and ecological composition (Harper 2006, 2007).

Density dependence

Burrow density may be a poor indicator of habitat quality (Maurer 1986) since large spatial variation in density exists within islands even after controlling for habitat type. Thus variation in burrow density may be due to intrinsic differences in local quality indicating additive or real aggregation. Many colonial birds exhibit crowding in patches even when other equally favourable sites are under-exploited and there is no genuine limitation in favourable nesting sites (Danchin & Wagner 1997).

An indirect way of ascertaining the influence of density dependence would be to measure differential recruitment or productivity in areas of colonies with high versus low density. Our study demonstrated considerable variation in density between islands, which allows such a comparison. A 10-fold difference in burrow density occurred between Whenua Hou and The Snares, and approximately 70% of that variation was independent of discernable habitat predictors. Provided that habitat characteristics are matched closely (for soil depth, amount of debris, distance from coast, amount of bare ground), there may be considerable scope to use the spatial comparison approach to indirectly measure the effect of density. Had a large amount of the variation been explained by habitat, it would not be possible to use the inter-island comparison method to determine density effects. Our study suggests that the current approach of the *Kia Mau Te Tītī Mo Ake Tōnu Atu* project of comparing recruitment and productivity on The Snares, Taiaroa Head and Whenua Hou to infer density dependence (Newman *et al.*, *in press*, Newman *et al.* 2008a) is defensible. However, this study also signals a warning about sample size. A stronger paired comparison of high- and low-density sites (matched for habitat and location) within each island may be needed to gain sufficient power to characterise density dependence.

Implications of comparing harvested and non-harvested sites for sustainability of harvest

Many of the harvested islands range in size from 8 ha to 150 ha, other than Taukihepa, the largest, at 930 ha (Moller *et al.* 1999). In contrast, most of the non-harvested islands are stacks or islets that are too small to support a whānau (extended family) birding. Because burrow density is highest around the coast, a disproportionate 'edge effect' may influence burrow density estimates on very small islands. Because the non-harvested islands used in the present comparisons were considerably larger than the harvested islands, the estimated burrow density on the non-harvested islands may have been artificially deflated. This is likely to increase the likelihood of inferring a harvest impact, by leading to a higher observed density on non-harvested (but smaller) islands compared to harvested (but bigger) islands. Externally checking harvest predictions from demographic models may be problematic until the magnitude of edge effects is determined.

Our present finding that several habitat variables significantly influence burrow density suggests that harvested and non-harvested islands must be matched closely for these factors if harvest impacts are to be determined from spatial comparisons of sooty shearwater abundance. Nevertheless, 70% of variation in burrow density was not explained by the predictor variables we tested, suggesting that further work is required to investigate other factors that influence sooty shearwater nesting behaviour.

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