

## Assessing the monitoring of sooty shearwater (*Puffinus griseus*) abundance in southern New Zealand

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**Abstract.** Recent declines of many seabird populations have placed increased emphasis on determining the status of potentially threatened species. However, the burrow-nesting habits and inter-annual fluctuation in breeding numbers of some species make trend detection difficult, and so knowledge of their population dynamics often remains coarse. Here we report observed fluctuations, and assess the efficacy of monitoring of sooty shearwaters (*Puffinus griseus*), on three islands in southern New Zealand between the breeding seasons of 1996–97 and 2004–05. Apart from a steady increase in burrow-occupant density at one island, few significant trends in abundance measures were detected. Considerable variation among individual sites within islands led to high uncertainty in island-wide trend estimates. Simulations showed that the measurements of occupant density have a limited ability of detecting all but very pronounced trends, whereas changes in burrow-entrance density are more likely to be detected. Annual fluctuations in the proportion of occupied burrows at individual sampling sites were highly synchronous within islands and reasonably synchronous between two of the islands, suggesting that breeding numbers are at least partly determined by broad-scale factors. The large declines in the abundance of sooty shearwaters reported from the late 1980s to mid-1990s appear not to have continued through our monitoring period. Lack of adequate within- and among-island replication, and short time series of data may severely reduce our ability reliably to detect population trends in many studies of burrowing Procellariiformes.

### Introduction

Sooty shearwaters (Tītī, *Puffinus griseus*) are medium-sized, burrowing petrels that breed on islands around southern New Zealand, Australia and South America. Populations on the Tītī Islands around Stewart Island and Foveaux Straight in southern New Zealand are subject to a large-scale customary harvest of chicks ('muttonbirding') by Rakiura Māori (Wilson 1979). Evidence for a substantial recent decline in abundance (Veit *et al.* 1997; Lyver *et al.* 1999; Scofield 2001; Scofield and Christie 2002) and the susceptibility of long-lived species to anthropogenic threats (Baker *et al.* 2002) have prompted recent concern over the current status of the harvesting system (Moller 2006).

Despite recent research, there remains considerable uncertainty about population trajectories and the mechanisms influencing fluctuations. Factors hypothesised to have influenced historical declines are similar to those threatening other species of Procellariiformes, including fisheries by-catch (Uhlmann *et al.* 2005), climate perturbations (Lyver *et al.* 1999), harvesting (Baker *et al.* 2004; Moller 2006) and predation by introduced predators (Jones 2000; Lyver *et al.* 2000). However, previous estimates of sooty shearwater population trends have been restricted to relative indices of the size of the breeding population such as at-sea densities of

adults (Veit *et al.* 1996, 1997), harvest rate (Lyver *et al.* 1999), beach patrols for dead birds (Scofield and Christie 2002) and burrow-entrance density (Scofield 2001). Replicated, ongoing monitoring of the absolute size or density of the breeding population is essential to estimate current population status, determine harvest sustainability and validate demographic model predictions.

Continuous monitoring at a range of geographically distant sites allows not only relative population growth rates, but also synchrony among sites to be assessed. Synchronous population fluctuations between geographically distant colonies of seabirds are increasingly being detected, and are thought to indicate broad-scale oceanic conditions (Cuthbert *et al.* 2003; Gaston 2003). Quantifying synchrony is important for several reasons. Because of the lack of comparably sized, accessible and unharvested sooty shearwater populations, in close proximity to the main harvested sites, assessing the sustainability of harvesting relies on the use of the geographically distant Snares Islands as a control site. Identification of broad-scale drivers of population fluctuations is important for validating the use of this site as a control. Furthermore, the identification of synchrony, or otherwise, will help test the scale of operation of the factors affecting the breeding population in a given year.

The present study aims to (1) assess recent trends in the size of the breeding population of sooty shearwater at one harvested and two unharvested islands, (2) assess the sampling intensity required to obtain precise estimates of population growth over the monitoring period, given the observed annual variation in abundance, and (3) measure synchrony in population abundance within and among populations on different breeding islands.

## Materials and methods

### Study sites and sampling layout

Breeding populations on two unharvested islands, North-east Island, the Snares (280 ha; 48°01'S, 166°36'E) and Whenua Hou (Codfish Island, 1396 ha; 46°45'S, 167°38'E), and on one harvested island, Putauhinu Island (129 ha; 47°13'S, 167°23'E) (Fig. 1), were monitored across nine breeding seasons between 1996–97 and 2004–05.

The Snares Island group supports the largest non-harvested sooty shearwater population without the presence of introduced predators in southern New Zealand. About 2 million burrow entrances were estimated to be present on the North-east Island

between 1996 and 2000, a decline of 37.3% since 1969–71 (Scofield 2001). North-east Island has a low-diversity vegetation community, dominated by a closed-canopy forest (3–6 m) consisting of *Olearia lyalli* (tūpare) and *Senecio stewartiae*. The understorey is largely unvegetated owing to the activity of sooty shearwater, although there are areas with dense prickly shield fern (*Polystichum vestitum*) and the coastal fringe supports extensive *Poa astonii* and *P. tennantiana* grassland. A detailed description of the habitat is given by Fineran (1969).

Whenua Hou represents the largest non-harvested sooty shearwater population in close proximity (<40 km) to the harvested Titi Islands. The island supports a diverse vegetation community dominated by podocarp forest, a range of coastal shrub species and often dense understorey vegetation (Johnson 1982). Weka (*Gallirallus Australis*), brushtailed possums (*Trichosurus vulpecula*) and kiore (pacific rat, *Rattus exulans*) were eradicated from the island in 1984, 1987 and 1998 respectively. The implications of these removals for the dynamics of sooty shearwater population are largely unknown; however, kiore is unlikely to have been a significant predator of a seabird of this size (Booth *et al.* 1996).

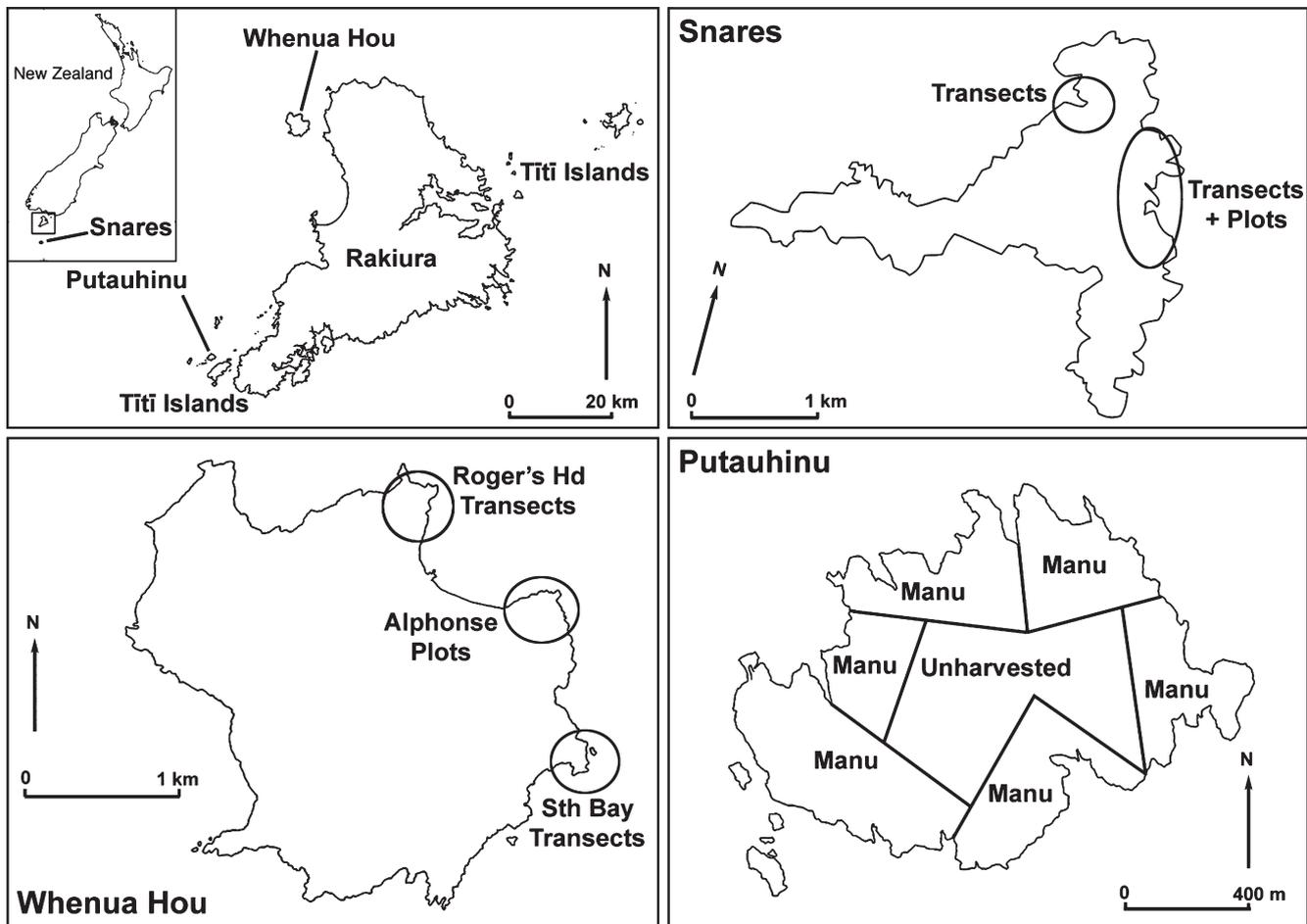


Fig. 1. Location of sampling sites on the three breeding islands of sooty shearwater in southern New Zealand monitored between the breeding seasons of 1996–97 and 2005–06.

Putauhinu Island is the only harvested site where consistent, multi-year monitoring has occurred. The coastal region of the island consists of six roughly equal-sized sections (termed manu, a harvesting ground), of which five are subjected to harvesting by individual whānau (families). The sixth manu has not been harvested for at least 30 years (Moller *et al.* 1999). The individual manu have not been labelled in Fig. 1 to prevent data from being linked to individual harvesters. Habitat in the coastal region is dominated by tūpare (*O. lyalli*) and tētēaweke (*O. oporina*) forest, with both open (bare soil) and closed (dominated by several fern species and pūnui – *Stilbocarpa lyalli*) understorey. The interior of Putauhinu consists of a large, contiguous area of dense mixed vegetation and a lower-density colony that is currently unharvested. Harvesting of sooty shearwater chicks occurs on Putauhinu Island between 1 April and 31 May each year.

### Sampling layout

We used a mixture of plots (quadrats) and transects to monitor the size of the breeding population. Within the plots, we also banded juvenile and adult birds for estimation of recruitment and survival, and monitored the success of nesting attempts through inspection hatches. We established three plots of differing size on both the Snares (392–628 m<sup>2</sup>) and Whenua Hou (513–2226 m<sup>2</sup>). Plot size was dependent on population density, with the target being ~100 breeding attempts per plot per year. We established transects to increase spatial replication. We extended them from their random starting point on a random bearing, until 20 burrow entrances were detected within a strip 1 m (2 m on Whenua Hou because of the low burrow-entrance density) either side of the centre line. Entrances were included only if their centre point was on, or within, the transect boundary.

We randomly established the plots on the Snares within the Tūpare habitat type and in reasonable proximity to the research base. Transects were randomly established over a wider geographical area and were stratified according to the habitat. Eighteen transects were located in areas of open (<30% vegetation cover below chest height) and 15 in areas of closed (>30% vegetation) habitat beneath the Tūpare canopy.

We established the plots on Whenua Hou on the north-eastern coast (Alphonse area), roughly 500 m apart. Fifteen transects were randomly established in two discrete groups at Roger's Head (northern coast,  $n=3$ ) and South Bay (south-eastern coast,  $n=12$ ). All transects were located in closed areas because no consistent open understorey exists on this island.

Detection of population trends on Putauhinu relied solely on monitoring of transects. We established 12 transects on each of four of the five harvested manu and 10 transects on the non-harvested Manu III. We established half of the transects on each manu in open, and half in closed habitat.

We occasionally could not refind transects in some years when they became obscured in thick vegetation, or when marker stakes had become buried. Therefore, the actual sample sizes in several years are slightly lower than the number of original transects stated above. For the purposes of trend detection, we will refer to individual plots and transects as sites, and islands will refer to the three long-term monitoring islands.

### Sampling periodicity

We initiated monitoring on all three islands in 1996–97 (Table 1). We surveyed plots on the Snares and Whenua Hou for population abundance annually, until the cessation of monitoring in 2004–05. We measured burrow-entrance density at the Whenua Hou plots until the breeding season of 2005–06. Sampling on transects was less intensive and consisted of two discrete periods, between 1996–97 and 1998–99, and between 2002–03 and 2004–05.

We generally measured population abundance at each island during one, or more, of the three distinct stages of the breeding season. The egg stage was measured after laying (between 30 November and 25 December), the hatching/early chick period was generally measured as soon after egg hatching as possible (between 15 January and 24 February), and the fledging monitoring period occurred between 15 March and 20 April, before any chicks had left burrows, thus allowing an estimate of the number chicks fledging to be made. Because of logistical constraints, the number of stages sampled on the Snares and Whenua Hou each season varied between one and three.

Access to harvested Tīi Islands is prohibited outside the muttonbirding season; consequently, the timing of sampling on Putauhinu was restricted. The season begins on 15 March when birders travel to the islands and undertake preparations for the onset of harvesting, which begins on 1 April. All harvested sites on Putauhinu were therefore sampled between 15 March and 1 April, before the removal of any chicks by the harvesters.

We measured trends in abundance by using data from the individual monitoring period (egg, hatching, or fledging)

**Table 1. Description of timing and periodicity of sampling at the three monitored sooty shearwater breeding islands**

E, the egg stage; H, hatching stage; F, the fledging stage

Season	Whenua Hou		Snares		Putauhinu transects
	Plots	Transects	Plots	Transects	
1996–97	H <sup>A</sup>	E	H <sup>B</sup>	E	F
1997–98	H	E	H <sup>C</sup>	E	F
1998–99	F	F	H <sup>D</sup>	E	F
1999–2000	H	–	F	–	–
2000–01	H	–	H	–	–
2001–02	H	–	H	–	–
2002–03	E	E	H	H	F
2003–04	H <sup>E</sup>	E	H	E	F
2004–05	H	E	H	E	F

<sup>A</sup>In several years there appeared to be inconsistencies in the boundaries of Plot C on Whenua Hou, preventing estimates of burrow-entrance density (and thus chick density) from being made at this site; however, boundaries in the first and last seasons of monitoring were correct, making counts in these years comparable, and allowed an overall change to be investigated.

<sup>B</sup>Plot B on the Snares was sampled only during the fledging stage in 1996–97.

<sup>C</sup>Plot D on the Snares was established in 1997–98; thus, no measures were available in the first year of the study.

<sup>D</sup>The three plots on the Snares were halved in the 1998–99 breeding season, with monitoring restricted to one randomly selected half. This change in sampling practice had little or no effect on measures of population abundance (McKechnie *et al.* 2008).

<sup>E</sup>Plot C on Whenua Hou was sampled only during the egg stage in 2003–04.

during which the most consistent monitoring occurred at each site (Table 1). On several occasions, data for a particular season did not exist for this most consistently monitored stage (Table 1). We developed simple correction factors by calculating the mean difference in abundance between stages from years when sampling occurred during more than one period; where possible, the correction factors were developed by using data only from plots (because of the more reliable sample sizes of occupants than in transects) for the specific islands. No correction was undertaken when the 95% confidence interval of the correction factor included the value of 1. We assessed the consequences of these corrections by repeating our analyses, with these corrected years omitted from the dataset. In all cases, the absolute magnitude of the difference in the mean estimate of population growth rate between the corrected data and the data with corrected data removed was  $<0.009$  and did not affect the ecological inferences being made.

#### *Methods of assessing population abundance*

Once established, all burrow entrances in the monitoring plots were counted and prospected with an infrared burrowscope to determine burrow occupancy (following Lyver *et al.* 1998). If there were fewer than 20 burrow entrances encountered when a previously established transect was resurveyed, we extended the transect on its original orientation until 20 entrances were encountered. We then prospected 20 entrances with the burrowscope. If we encountered 20 or more entrances, then the transect length remained the same and all entrances were prospected.

#### *Measures of population abundance*

We considered a burrow entrance to be viable if at least one tunnel extended  $>20$  cm from the entrance, the shortest previously found to be occupied (Lyver *et al.* 1998). Burrow-entrance density was calculated by dividing the count of viable burrow entrances by the surface area of the transect.

A recent calibration study revealed that estimates of burrow occupancy determined with a burrowscope consistently underestimated the true occupancy by up to an average of 16.7% on some islands, because of the difficulties of detecting chicks in long and convoluted burrows (McKechnie *et al.* 2007). We therefore used two measures of occupancy to estimate trends in population abundance. We calculated simple occupancy as  $SO = C/E$ , where  $C$  is the total number of chicks detected and  $E$  is the total number of entrances prospected on the site. Although  $SO$  fails to account for biases in abundance estimates when an infrared burrowscope is used, it has displayed a very strong linear relationship with the actual abundance (McKechnie *et al.* 2007). It is, therefore, adequate for trend estimation, provided detection probabilities remain constant throughout the monitoring period.

On Putauhinu, we corrected occupancy measures by using the methodology of McKechnie *et al.* (2007). The distance of burrow occupants from the burrow entrance is a very strong predictor of their detection with the burrowscope, and corrections incorporating a detection function based on this burrow characteristic have been shown to improve occupancy estimates (McKechnie *et al.* 2007). We calculated corrected

occupancy (CO) by incorporating a detection rate  $g(x)$ , defined as the probability that a chick is detected  $x$  metres from the burrow entrance, given that it is present at that distance. This rate was calculated as a linear-logistic function based on the intercept and slope terms from the average detection model of McKechnie *et al.* (2007). The total number of chicks ( $N$ ) at a site is then given by

$$\hat{N} = \sum_x \frac{n_x}{\hat{g}(x)}, \quad (1)$$

where  $n_x$  is the count of chicks at each distance increment (10-cm intervals).

This method of correcting raw occupancy estimates was developed by using detection functions estimated during the mid-late chick stages of the fledging period. Uncertainty about the form of detection functions during the hatching and egg stages precluded the use of this correction on the data from the Snares and Whenua Hou.

We calculated egg and chick densities (hereafter occupant density) at each site by multiplying burrow occupancy by burrow-entrance density.

#### *Detection and comparison of trends*

We calculated trends in the various abundance measures on the three islands by using multilevel (hierarchical) linear regression (Gelman and Hill 2007). We log-transformed all abundance measures (after adding a constant of 0.01 to chick-density data to allow for the few occasions when zero densities were observed) before analysis. We excluded from the analyses any sites where abundance was measured fewer than four times over the complete monitoring period.

Because of the differences in the magnitude of variances among the islands, we modelled the abundance data for each island separately. The most simple model we considered allowed the intercept and slope regression parameters at each site to vary randomly, with the resulting data-level model structure being as follows:

$$Y = \beta_{1j} + \beta_{2j}X_{ij} + \varepsilon_{ij}, \quad (2)$$

where  $Y_{ij}$  is the abundance estimate in year  $i$  at site  $j$ ,  $\beta_{1j}$  is the intercept parameter that varies among sites,  $\beta_{2j}$  is the slope parameter that varies among sites and  $\varepsilon_{ij}$  is the residual error, assumed to follow a normal distribution with a mean of 0 and standard deviation of  $\sigma_\varepsilon$ . The  $\beta_{1j}$  and  $\beta_{2j}$  parameters are further modelled by assuming they come from a bivariate normal distribution, as follows:

$$\begin{pmatrix} \beta_{1j} \\ \beta_{2j} \end{pmatrix} = \text{Normal} \begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} \begin{pmatrix} \sigma_1^2 & \rho\sigma_1\sigma_2 \\ \rho\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix}, \quad (3)$$

where  $\mu_1$  and  $\mu_2$ , and  $\sigma_1$  and  $\sigma_2$  are the group-level means and standard deviations (hyperparameters) of the data-level intercepts and slopes, respectively, and  $\rho$  is the correlation between the parameters.

We considered two alternative models to determine the influence of vegetation on shearwater abundance on the Snares and Putauhinu (all sites on Whenua Hou consisted of the closed vegetation class). Initially, we constructed a model that allowed site-specific intercept and slope parameters to differ between the

vegetation classes (open and closed). This model had a data-level model structure identical to that presented above; however, the group-level structure was modified such that

$$\begin{pmatrix} \beta_{1j} \\ \beta_{2j} \end{pmatrix} = \text{Normal} \left( \begin{pmatrix} \mu_1 + \beta_3 X_{2j} \\ \mu_2 + \beta_4 X_{2j} \end{pmatrix}, \begin{pmatrix} \sigma_1^2 & \rho\sigma_1\sigma_2 \\ \rho\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix} \right), \quad (4)$$

where  $X_{2j}$  is an indicator variable for whether site  $j$  has open or closed vegetation,  $\beta_3$  and  $\beta_4$  are the coefficients of the effect of vegetation on the intercept and slope of the regression respectively. The second alternative model constrained vegetation effects to influence the intercept parameters only; thus, the data-level model was identical to that above except that the  $\beta_4$  coefficient is removed and the mean of the  $\beta_{2j}$  is simply reduced to  $\mu_2$ .

An additional complication arises on Putauhinu where sites are structured within the five manu. Consequently, we can modify the basic model to accommodate this by adding the structure

$$\begin{pmatrix} \beta_{1jk} \\ \beta_{2jk} \end{pmatrix} = \text{Normal} \left( \begin{pmatrix} \mu_{1k} \\ \mu_{2k} \end{pmatrix}, \begin{pmatrix} \sigma_1^2 & \rho\sigma_1\sigma_2 \\ \rho\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix} \right), \quad (5)$$

where  $\mu_{1k}$  and  $\mu_{2k}$  are the group-level means of the data-level intercepts and slopes for each of the  $k$  manu. These parameters are further modelled as coming from higher-level normal distributions, e.g.  $\mu_{1k} = \text{Normal}(\lambda_1, \sigma_{\mu 1})$  and  $\mu_{2k} = \text{Normal}(\lambda_2, \sigma_{\mu 2})$ . This model can easily be extended to include the vegetation effects.

We fitted models in a Bayesian framework using MCMC algorithms in the software package OpenBUGS 3.0.2 (Spiegelhalter *et al.* 2007), which we implemented via the statistical software package R.2.6.1 (R Development Core Team 2004). Convergence of the sampler was determined by running three chains and examining the Brooks–Gelman–Rubin diagnostic (Brooks and Gelman 1998), with the first 10 000 samples discarded as a burn-in. A further 10 000 samples beyond this point were stored for each chain, from which we estimated the parameters of the model. We estimated 95% credible interval limits as the 2.5 and 97.5 percentiles of the posterior distributions.

#### Measuring synchrony among sites

To quantify synchrony in population abundance among islands we calculated cross-correlation functions (Pearson moment correlations) of time series between all pairwise combinations of sites. Burrow occupancy was chosen as the measurement of interest because changes in this measure determine fluctuations in occupant density (burrow-entrance density remained relatively stable among years). Cross-correlations were undertaken on both detrended datasets (to remove the chance of cross-correlations partly reflecting common trends in abundance among sites) and raw values. Occupancy data were log-transformed after adding a constant of 0.01.

Bootstrap confidence intervals were generated to circumvent the problem of non-independence in the cross-correlation coefficients (e.g. Bjørnstad *et al.* 1999). Bootstrap samples of sites (each with a sample size equal to that for the original data) were drawn with replacement. Individual cross-correlation coefficients were calculated, and were summarised by their

mean. A confidence interval for this mean was found by performing the resampling 10 000 times, with the standard deviation of the mean cross-correlation across all 10 000 bootstrap samples providing an estimate of the standard error of this mean (Efron and Tibshirani 1993).

#### Assessing alternative monitoring schemes

We developed a simulation approach for assessing the influence that alternative monitoring approaches may have in detecting trends in population abundance. We obtained estimates of the overall mean intercept and slope (population growth rate) on each island, and their respective standard deviations and the correlation between them, from our analyses above. With these estimates of the hyperparameters and assuming a bivariate normal distribution, we were able to simulate intercept and slope values for the individual sites. We then projected the trends deterministically (Gibbs and Melvin 1997), with variation added as a normally distributed deviate with a mean of 0 and the appropriate residual standard deviation as estimated in the analyses. This simulation step was conducted in R.2.6.1 and the resulting data can be considered a single generated dataset that can then be analysed by calling OpenBUGS, using the model developed for the original data. Details of the model fitting are the same as in the original analyses. In total, we generated 500 datasets each of which was analysed in this manner. A common approach to carrying out these simulations involves changing the trend projected and calculating the statistical power of the test by observing the proportion of the time that the null hypothesis of no trend is rejected. Our approach differed in that we projected just one trend (1% increase annually, although the focal results are invariant to this choice) and calculated more informative measures of the ability of the model to detect trends, such as the width of the 95% credible interval of the overall mean trend (hyperparameter). We simulated monitoring on the basis of the actual study design used in the present study, i.e. sampling transects in the first and last 3 years, and plots in all years. We randomly deleted data from individual years to ensure that sample sizes at individual sites closely matched those in the observed data. We compared monitoring strategies that adopted between 7 and 100 individual sites on an island. We selected seven as a pragmatic lower limit owing to the difficulties of estimating hyperparameters reliably when replication is low; 100 was selected as an approximate upper bound to the number of sites that could be sampled, given the logistical capacity within our study.

## Results

### Changes in abundance

Burrow-entrance density was relatively stable at all three monitoring sites (Fig. 2, Table 2). Average entrance densities were considerably higher on the Snares and Putauhinu than on Whenua Hou (Fig. 2). On the Snares and Putauhinu, where sites were established in both open and closed habitats, differences in entrance density existed. On the Snares, higher entrance densities were observed at open than at closed sites, whereas the opposite was observed on Putauhinu. This is reflected in the models that allowed the regression intercept to vary between open and closed sites. On the Snares, the density at closed sites is predicted to be

0.780 (0.691–0.922) of the density at open sites, whereas on Putauhinu, the density at closed sites is predicted to be 1.156 (1.028–1.299) times higher than that at open sites. Models that allowed the slope (population growth rate) to vary between habitats had less support. On the Snares, the population growth rate at open sites was predicted to be 0.994 times the rate at closed sites (95% CI=0.984–1.005), with similar results observed on Putauhinu (mean=1.006, 95% CI=0.989–1.025). Inferences of the changes in density were therefore made from models where only the intercept varied between habitats. There was substantial variation in regression slopes among individual sites within islands and thus confidence intervals of population growth rate were generally moderately wide and included the value of 1 (i.e. stable population growth), in most cases. The exception was a slight decline at the Snares (mean=0.993, CI=0.988–0.998).

Occupant density was variable among years on all islands. A pronounced decrease in density was observed between the onset of monitoring in the breeding season 1996–97 and the one in 1997–98 on Whenua Hou and the Snares (Fig. 3A, B). No consistent decline in density occurred between these years on Putauhinu (Fig. 3C). Consistent increases were then observed on transects on all islands in 1998–99, although this change was less pronounced on the Snares transects than on Whenua Hou and Putauhinu, and a continued slight decrease in density was observed on the Snares plots in this season. Density then increased relatively consistently on the Snares, before reaching a peak in the 2001–02 season and then declining until the cessation of monitoring. In contrast, density on Whenua Hou fluctuated more, with perhaps a slight increasing trend evident. The absence of monitoring on Putauhinu between 1999–2000 and 2001–02 precludes robust comparisons with the other two islands; however, density over the final 3 years of monitoring appeared to be relatively stable, with little concordance in trends among the individual manu.

Growth rates of occupant density varied substantially both within and among islands (Table 2). Confidence intervals were consequently very wide and made inferences about the presence of any trends in population growth rate at the island level difficult. On the Snares, a model allowing the intercept to vary between habitat types again had support, with occupant density at open sites predicted to be 0.466 (95% CI=0.291–0.744) of the density at closed sites. In contrast, density showed no consistent differences between habitats on Putauhinu, with density at open sites 0.964 (95% CI=0.815–1.140) of the density at closed sites. Growth rate was similar between habitat types, with the rates at open sites predicted to be 0.977 (95% CI=0.913–1.049) and 1.023 (95% CI=0.990–1.056) of the rates at closed sites on the Snares and Putauhinu respectively. Inferences on the Snares were again made only from the models allowing the intercept to vary between habitats, whereas on Putauhinu no allowance was made for differences between habitats. The overall estimated growth rate in occupant density was <1 at the Snares (mean=0.989, 95% CI=0.956–1.023) and slightly >1 at Putauhinu (mean=1.010, 95% CI=0.984–1.034), although confidence intervals were wide

and included the value of 1 (Table 2). Consistent increases in occupant density were detected on Whenua Hou, with an overall growth rate of 1.053 (95% CI=1.017–1.091).

### *Synchrony in abundance*

Strong synchrony in fluctuations of burrow occupancy was observed among sites within each island ( $r > 0.18$ , Table 3). The overall mean cross-correlation coefficient among all individual sites on the three islands reached 0.10 (CI=0.02–0.18). Synchrony was less pronounced among islands, and the relationship between Whenua Hou and Putauhinu was the only between-island comparison with any strength at 0.17 (CI=0.02–0.31). Comparison between the Snares and Whenua Hou was weakly positive and between the Snares and Putauhinu it was weakly negative. In the majority of cases, the correlation coefficients were reasonably similar when raw data were analysed (Table 3). This is presumably due to a lack of similar or highly dissimilar trends among sites.

### *Assessing monitoring intensity*

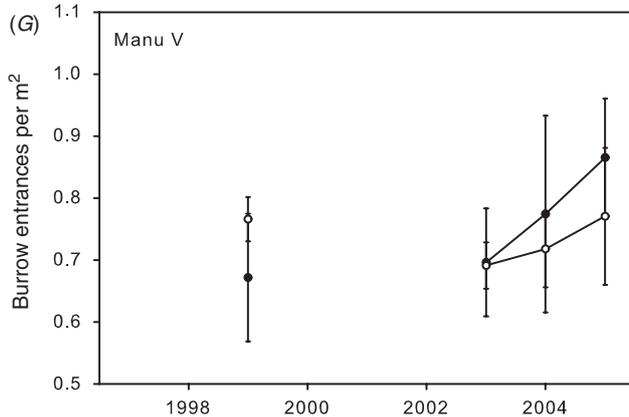
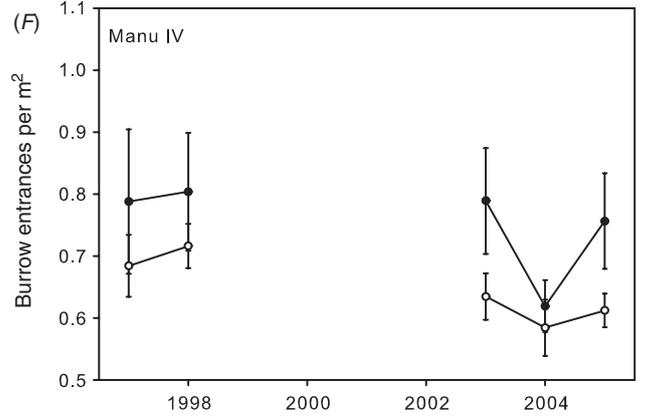
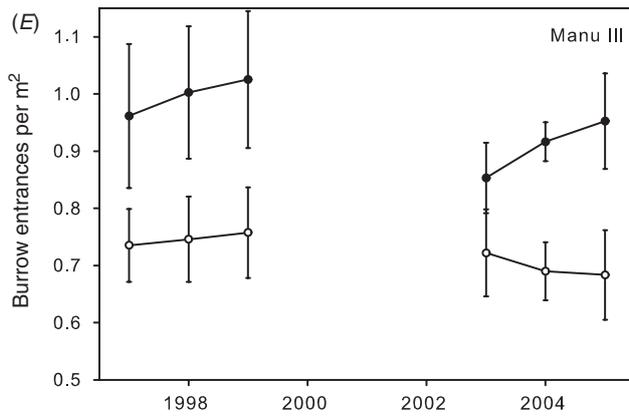
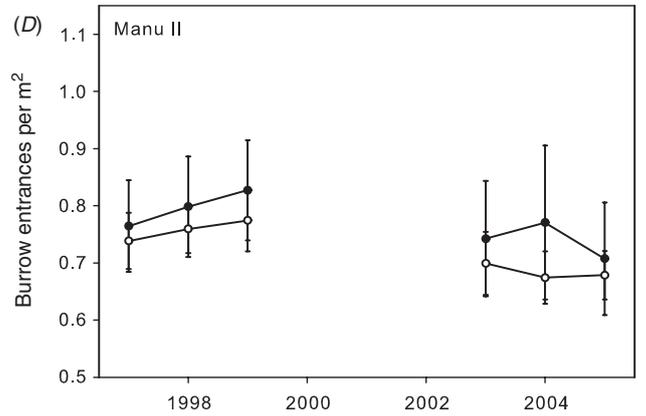
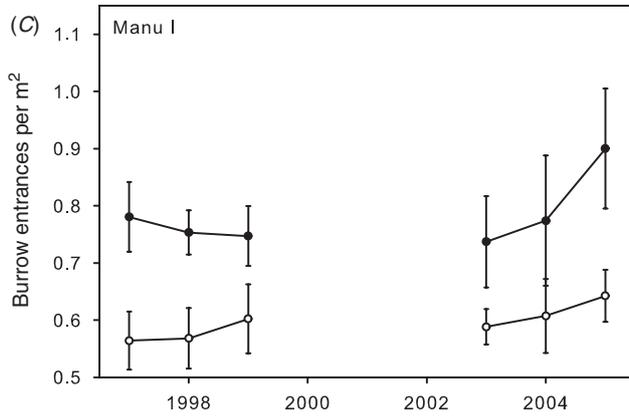
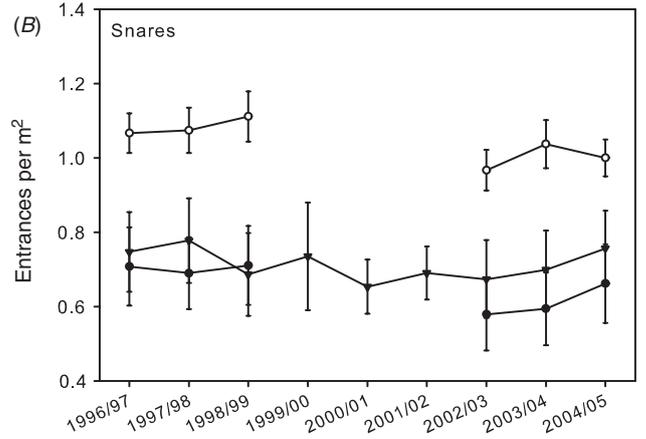
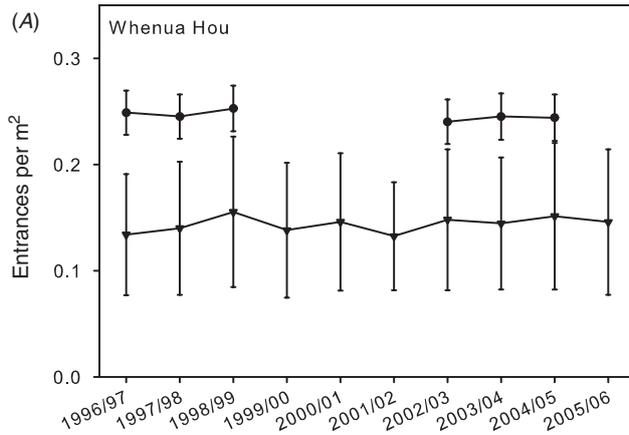
Simulations revealed that high variability in the data can have an impact on our ability reliably to detect trends in some measures of shearwater abundance. Credible intervals for the growth rate of burrow-entrance density were estimated with reasonable precision for all but the smallest sample sizes (Fig. 4A). In fact, gains in precision were relatively minor when sample size increased beyond ~30 sites. Interval widths of ~0.01 were achievable with realistic sample sizes, giving confidence that even relatively moderate departures from stability in the growth rate would be detected with this measure. In contrast, precision of credible intervals around the growth rate of occupant density was poor (Fig. 4B). Gains in precision were again limited beyond ~30 sites; however, interval widths for this measure never dropped below ~0.05, suggesting that even growth rates considerably >1 or <1 might be difficult to detect.

## **Discussion**

### *Synchronous fluctuations in abundance*

Changes in burrow occupancy were highly synchronous among sites within all three islands. Burrow occupancy is determined by the following three factors: the proportion of the breeding population participating in breeding in that season, the time between egg laying and monitoring, and the mortality rate of breeding attempts. The conclusions possible from observing strong synchrony therefore depend on the breeding stage in which synchrony is detected. The majority of the sites were sampled during the egg stage (transects). The strong within-island synchrony at these sites indicates that the proportion of adults participating in breeding is probably determined by factors acting at the whole-island scale. Conversely, all sites on Putauhinu were, by necessity, sampled in the late chick stage. The synchrony observed there indicates that breeding participation and mortality rate of breeding attempts are

**Fig. 2.** Sooty shearwater burrow-entrance density on Whenua Hou between the breeding seasons of 1996–97 and 2005–06, and the Snares and five manu on Putauhinu between the breeding seasons of 1996–97 and 2004–05. Open circles represent open transects, closed circles represent closed transects and closed triangles represent plots.



**Table 2.** Summary of estimates of growth rates in burrow-entrance density and occupant density at the three monitored sooty shearwater breeding islands between 1996–97 and 2004–05

Models on the Snares and Putauhinu allowed for the intercept to vary between open and closed sites on all occasions except for occupant density on Putauhinu where the data did not support this additional complexity. All sites on Whenua Hou consisted of closed habitat and thus the model did not include this complexity

Island	<i>n</i>	Burrow-entrance density				Occupant density			
		Mean	s.d.	2.5%	97.5%	Mean	s.d.	2.5%	97.5%
The Snares	32	0.993	0.003	0.988	0.998	0.989	0.017	0.956	1.023
Whenua Hou	18	0.998	0.003	0.992	1.005	1.053	0.018	1.017	1.091
Putauhinu									
Manu I	11	1.001	0.008	0.987	1.018	1.012	0.012	0.988	1.038
Manu II	12	0.990	0.007	0.975	1.003	1.017	0.013	0.994	1.045
Manu III	11	0.995	0.008	0.980	1.010	1.005	0.013	0.977	1.029
Manu IV	10	0.989	0.007	0.974	1.003	1.009	0.012	0.985	1.033
Manu V	9	1.003	0.009	0.987	1.023	1.006	0.015	0.971	1.034
Total	53	0.995	0.011	0.978	1.014	1.010	0.013	0.984	1.034

correlated island-wide, or at least that within-island differences in one were not strong enough to nullify the effects of the other. The later stage of sampling on Putauhinu and the associated variation introduced by breeding failure may partly explain why synchrony was slightly lower on this island than elsewhere.

Synchrony among islands was considerably more variable. A reasonably strong relationship was observed between Whenua Hou and Putauhinu; however, fluctuations at the Snares showed no synchrony with either of these sites. Between-island synchrony is the result of factors influencing burrow occupancy acting at large spatial scales. In seabirds, these factors are generally thought to be at-sea conditions, and synchrony between geographically distant colonies is increasingly being detected (Dunlop *et al.* 2002; Cuthbert *et al.* 2003; Gaston 2003). Certainly, the synchrony between Whenua Hou and Putauhinu suggests that at least some of the regulation of breeding numbers is occurring at a broad scale. Furthermore, if these sites had been sampled during the same breeding stage, synchrony may have been more pronounced. A decrease in synchrony between these two islands and the Snares supports the common pattern of decreasing synchrony with increasing distance between populations (Ranta *et al.* 1997, 1998; Bjørnstad *et al.* 1999; Bellamy *et al.* 2003). However, the distance between the Snares and the other islands (<200 km) would appear to be small in relation to the scale of the foraging movements of sooty shearwater, which can have a radius of >1500 km (Weimerskirch *et al.* 1997; Shaffer *et al.* 2006).

#### *Consequences of variability for monitoring programs*

Simulations revealed differences in our ability precisely to measure the growth rate of the abundance measures. Lack of precision is related to high variation in the growth rate among individual sites within islands, and was especially pronounced for burrow-entrance density. This could be an artefact of the apparent stability of the population during the monitoring period, with the population at sites increasing or decreasing depending on local dynamics. During periods of more pronounced growth or decline of the population, the trajectories of individual sites may

be more aligned, in which case precision of our estimators may improve.

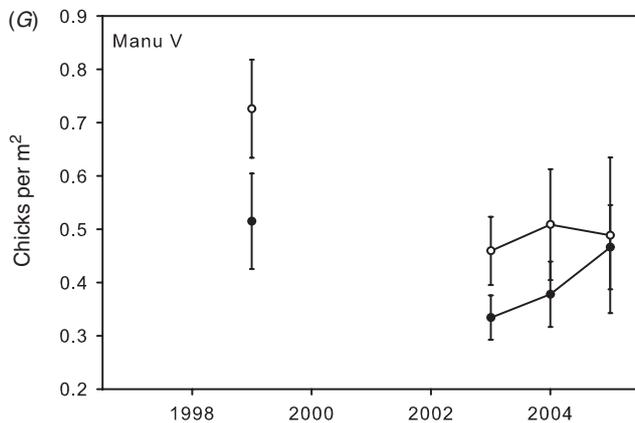
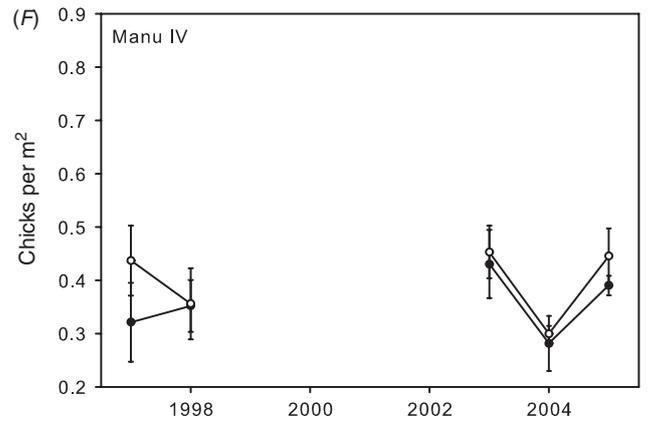
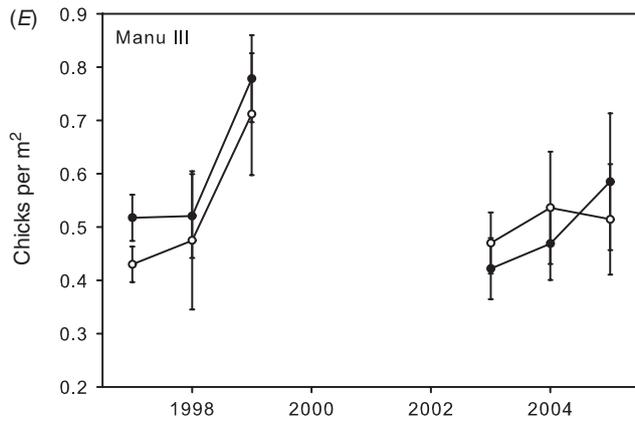
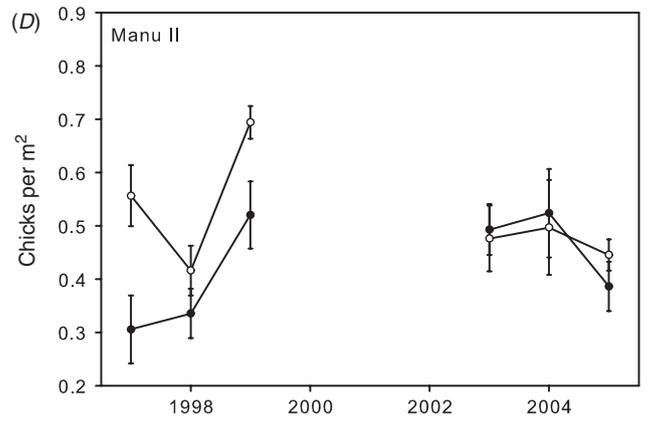
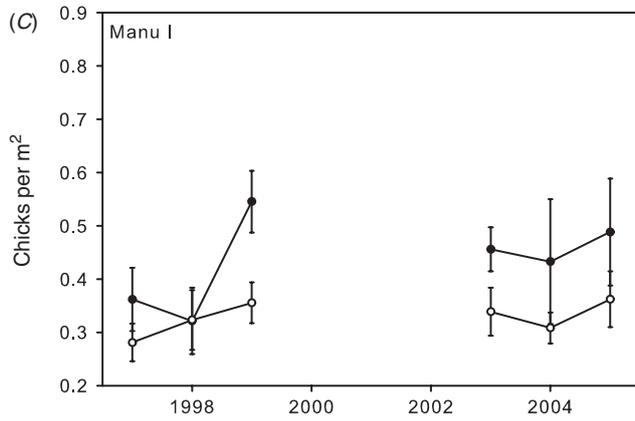
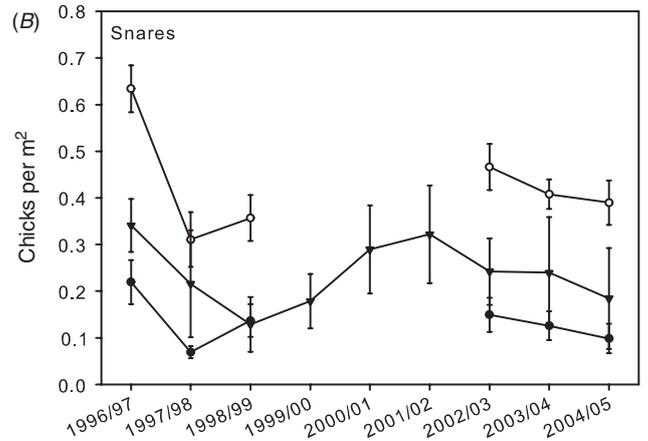
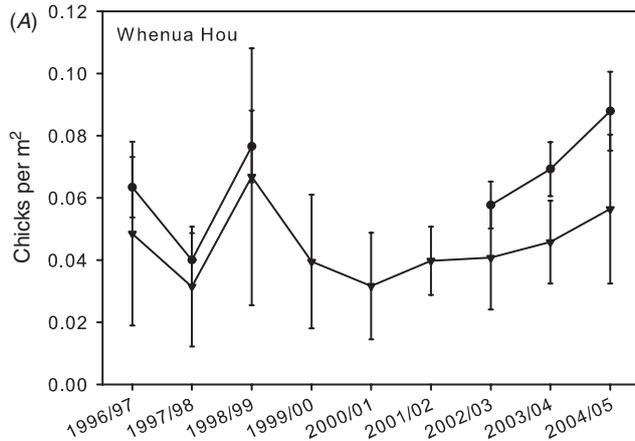
Previous monitoring of burrow-nesting petrels has often been characterised by an overall lack of within- and among-island replication, owing to the difficulties of monitoring these species. The disparate trends among sites within islands in our study send a strong warning that such practices will be inadequate at describing overall island- or species-wide population trajectories if similar variation is observed in other species. Furthermore, simulations suggest that even under very intense monitoring programs lack of precision of our estimates may prevent all but the most profound changes in abundance from being detected. Our inability to reliably detect trends on individual islands suggests that distinguishing differences in the rate of change at harvested and unharvested sites will be futile unless this difference is profound.

Our analyses clearly demonstrate the differences in variability between the abundance measures. Both temporal variation at the individual monitoring sites and variation among sites were considerably more pronounced for occupant density than burrow-entrance density. This would appear to make the latter measure more applicable for monitoring programs, especially given the relative ease of its estimation in comparison to occupant density; for this reason, determining the status of several species has involved estimation of this measure in isolation (Scofield 2001; Nel *et al.* 2002). However, until the relationship between burrow-entrance density and absolute abundance has been investigated over a wide range of abundances, we do not recommend relying on this measure alone.

#### *Population fluctuations*

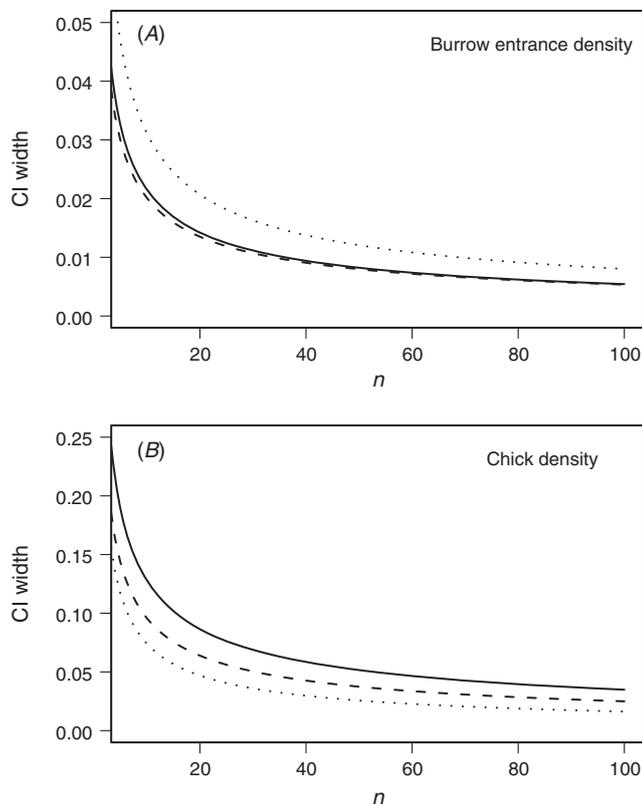
There was evidence for a longer-term oscillation in occupant density at the plots on the Snares (Figs 2B, 3B). However, we failed to detect this phenomenon on Whenua Hou and the lack of continuous monitoring on Putauhinu allowed for few insights into patterns of abundance. Previous monitoring of the abundance of Procellariiformes has detected evidence of systematic fluctuations related to indices of climatic variation

**Fig. 3.** Sooty shearwater chick density on (A) Whenua Hou, (B) the Snares and (C) five manu on Putauhinu between the breeding seasons of 1996–97 and 2004–05. Open circles represent open transects, closed circles represent closed transects and closed triangles represent plots.



**Table 3. Mean cross-correlation coefficients measuring synchrony in raw and detrended fluctuations in simple burrow occupancy, within and among the three sooty shearwater breeding islands**  
95% confidence intervals are given in parentheses

	Island	Whenua Hou	Snares	Putauhinu	Total
Raw values	Whenua Hou	0.33 (0.14)			
	Snares	0.01 (0.17)	0.28 (0.15)		
	Putauhinu	0.20 (0.10)	-0.11 (0.09)	0.18 (0.09)	
	Total				0.09 (0.06)
Residuals	Whenua Hou	0.33 (0.20)			
	Snares	0.07 (0.20)	0.36 (0.14)		
	Putauhinu	0.17 (0.15)	-0.10 (0.14)	0.19 (0.11)	
	Total				0.10 (0.08)



**Fig. 4.** Estimates of the width of the 95% credible intervals of population growth rate, given different sample sizes of sites ( $n$ ) used in simulations for burrow-entrance density and occupant density. The solid, dashed and dotted lines relate to the Snares, Whenua Hou and Putauhinu respectively.

(Lyver *et al.* 1999; Thompson and Ollason 2001; Dunlop *et al.* 2002). Unfortunately, the length of our time-series (less than one apparent cycle) prevents us from drawing firm conclusions about the persistence, strength and mechanisms influencing potentially regular fluctuations in density. However, if oscillations are a real phenomenon, then linear-regression techniques will be inadequate for modelling the dynamics of sooty shearwater populations. Restriction of observed oscillations to the plots on the Snares suggest that our analyses are currently suitable, although a longer monitoring period is necessary to confirm

this. No regular fluctuations in burrow-entrance density were observed, perhaps because of the lagged deterioration of these structures after they become unoccupied (Bancroft *et al.* 2005).

#### *No evidence of continued declines*

Our estimates of population trajectory are characterised by variation both within and among sites, and high levels of uncertainty. Despite the lack of precision in our estimates, there appears to be no strong evidence for the continuation of the large putative decline in the population during the late 1980s and early 1990s (Veit *et al.* 1997; Lyver *et al.* 1999; Scofield and Christie 2002). The annual decline between late 1980s and mid-1990s from these studies was between ~3 and 10%. Most of this interval is within the range where our sampling would have almost certainly detected the decline. In fact, the largest change we observed in our study period was a strong increase in occupant density on Whenua Hou. Aside from this result, there was very little evidence for substantial differences in any of the abundance measures at the island level. It is possible that part of the increase on Whenua Hou relates to the few data points available at most sites, with abundance in the second period of monitoring (2002–03 to 2004–05) being higher because of random fluctuations over that period. Continued monitoring is necessary to confirm that this is indeed not a spurious increase.

Unfortunately, strategic monitoring of the breeding colonies of sooty shearwater was not carried out during the time period reported by Veit *et al.* (1997), Lyver *et al.* (1999) and Scofield and Christie (2002); thus, there remains uncertainty about whether the postulated declines were overestimated and/or the decline has failed to continue beyond the mid-1990s, or a combination of the two. There is certainly reason to be cautious of these previous studies because they all constituted relative indices of population size, which have an unknown relationship with the actual abundance. The 90% decline in the abundance of sooty shearwater in the Californian current system during migration in the Austral winter between 1987 and 1994 (Veit *et al.* 1997) includes an unknown effect of changing at-sea distributional patterns, whereas Lyver *et al.* (1999) provided evidence for a strong decline in the harvest rate of only one muttonbird on Poutama Island between 1979 and 1998. Scofield and Christie (2002) reported substantial declines in the number of adult (2.6% per year) and juvenile (3.8% per year) sooty shearwaters that were

recovered dead on New Zealand beaches over the period 1961–99. However, these figures, in conjunction with the decline in sooty shearwater burrow-entrance density between a survey carried out over the period 1969–71 and a second survey over 1996–2000 (Scofield 2001) and decreases in the harvest rate of several other muttonbirders (H. Moller, unpubl. data), suggest that a substantial decline occurred during that time period, although not at the absolute rate suggested by some of the independent indices.

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