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Changes in sooty shearwater (*Puffinus griseus*) abundance and harvesting on the Rakiura Tītī Islands

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Abstract We estimated the change in abundance of sooty shearwater (titi, *Puffinus griseus*) at six Rakiura Titi Islands, New Zealand, by comparing historical and recent surveys of the density of entrances to breeding burrows. We found evidence that entrance density between 1994 and 2006 was lower than it was between 1961 and 1976. Our overall estimate of the annual rate of change in burrow entrance density is -1.0% (95% CI -2.3 to -0.1%). Declines have been slower on four islands where Rakiura Maori maintain a traditional harvest of sooty shearwater chicks ("muttonbirding") compared with three unharvested islands. Density-dependent population processes may explain this difference: rates of decline have been faster in areas of relatively high initial entrance density, and historically the harvested islands have had lower initial density. There was a strong, apparently linear, relationship between entrance density and chick density on breeding colonies, so changes in entrance density probably do indicate a real population decline. The western side of Taukihepa, the largest of the Titi Islands, first became accessible for muttonbirding with the advent of helicopters in the 1970s, but it is unknown whether this has caused an increase in the number of sooty shearwaters harvested by Rakiura Maori.

Keywords density dependence; harvesting; muttonbirding; population declines; *Puffinus griseus*; sooty shearwaters

INTRODUCTION

Rakiura Māori, New Zealand's southernmost indigenous people, maintain a traditional harvest of sooty shearwater (*Puffinus griseus*) chicks (Stevens 2006). Near-fledging chicks (called "tītī" by Māori) are harvested from 35 islands around Rakiura (Stewart Island) between the beginning of April and middle of May each year. In the nanao, the first part of the harvesting season, the chicks are extracted from burrows during daylight. In the rama, the last part of the season, the chicks are caught at night as they

emerge from breeding burrows to strengthen wing muscles and shed down feathers (Lyver 2000a; Kitson 2002).

Sooty shearwaters are wide-ranging and abundant apex predators in Pacific marine ecosystems (Shaffer et al. 2006). Population changes in sooty shearwaters could therefore indicate large scale ecological perturbations and provide information about the impacts of systemic drivers such as: climate change (Veit et al. 1997; Lyver et al. 1999); fisheries (Uhlmann et al. 2005); harvesting (Hunter & Caswell 2005; Moller 2006); and predation of eggs and chicks by recently introduced predators (Bell 1978; Scofield & Christie 2002; Moller et al. 2003a).

Understanding sooty shearwater population dynamics could potentially assist ecological management of several internationally significant nature reserves in southern New Zealand, where the dense burrowing and abundant defecation of shearwaters at breeding colonies affects nutrient fluxes, soil formation and vegetation recruitment (Moller et al. 2000; Hawke & Newman 2005). Interspecific competition may affect the abundance of other nesting seabirds if sooty shearwater numbers change at breeding colonies. A better understanding of the population dynamics of sooty shearwaters is also needed to assess the sustainability of sooty shearwater harvesting, which is a culturally and economically important traditional harvest for Māori (Stevens 2006). Quantification of the potential harvest impacts is also important if sooty shearwater abundance is to be used as a robust bio-indicator of the well-being of oceanic ecosystems, as advocated by Furness & Camphuysen (1997).

Declines in numbers of sooty shearwaters in recent decades have been detected from beach patrol counts of dead birds washed ashore (Scofield & Christie 2002), harvest success rate (Lyver et al. 1999), counts of birds at-sea off the United States coast (Viet et al. 1997), breeding-burrow entrance density on The Snares (Scott et al. 2008) and burrow occupancy on Whenua Hou (Lyver et al. 1999) and Tuhawaiki Island (Jones 2000). Collectively, these studies provide strong evidence for population declines from the 1960s or 1970s until the mid 1990s. However, each of these indices of population change involves problems that potentially preclude their accuracy in assessing rates of decline. Counts from beach patrols may be influenced by mortality rates and prevailing weather, as well as by population size. Breeding burrow occupancy is labile, because it is greatly affected by the proportion of adults breeding and by egg and chick survival

(McKechnie et al. in press a). Changes in at-sea counts partially reflect changes in movement patterns rather than changes in population size alone (Spear & Ainley 1999; Oedekoven et al. 2001). All of these methods are applied to sites away from harvested breeding colonies. Harvest rate is a measure that applies only to the Tītī Islands where harvest takes place. Harvest rate may not be linearly related to population density, at least during the nanao (Lyver 2000a,b; Kitson 2004; Moller et al. 2004; McKechnie in press b.).

Assessing the relative rate of change of sooty shearwater populations at breeding areas harvested at different levels of intensity is one way of evaluating harvest impacts. Measures of the relative rate of population change on harvested and unharvested colonies are also needed, in order to construct and externally validate mathematical models of sooty shearwater demography (Hamilton & Moller 1995; Hunter et al. 2000; Yearsley et al. 2003; Hunter & Caswell 2005). These will be important tools for guiding future sooty shearwater harvest management.

Before the start of our research project, *Kia Mau Te Tītī Mo Ake Tōnu Atu* ("Keep the Tītī Forever") in 1994, there were no systematic or well-replicated counts of sooty shearwater abundance on the Rakiura Tītī Islands (Moller 1996). This paper compared the few available historical observations of sooty shearwater breeding burrow entrance density with an extensive set of recent estimates at the same places. This approach allowed us to (i) assess whether there is evidence of change in sooty shearwater abundance, (ii) estimate the annual rate of change, and (iii) compare the rate of change on harvested and unharvested islands.

Conservation management often relies on fragmentary data, gathered for different purposes. The methods of analysis we describe here for estimating rates of change in breeding population density may be useful for similar seabird conservation management challenges where limited historical data are available for trend assessment. We present data to evaluate the utility of burrow entrance counts as reliable measures of population density in burrowing petrels. In addition, historical notes of harvesting activity from 1961 are reported. They describe the only systematic historical survey of harvesting other than Richdale's (1946) survey account from a single island. Changes in the number of birders actively harvesting is itself potentially useful as an indirect index of changes in sooty shearwater abundance (Lyver 2000b).

Study areas

The historical observations analysed were primarily from eight Titi Islands off the south-west shores of Rakiura (Fig. 1, Table 1). We also report from a historical survey of sooty shearwater harvesting (Bell 1962) centred on Taukihepa (Big South Cape Island). Taukihepa accounts for around half of the sooty shearwater harvest (Bull 2002; Newman et al. 2008b). In addition, some data are incorporated from recent comparisons of burrow entrance density and corresponding chick density (Fig. 2) from 12 Rakiura Titi Islands surrounding Rakiura. Historical counts from Little Mangere (latitude 44°16'47"S; longitude 176°19'31"W), a small island in the Chatham group, are also recorded here.

On all islands, sooty shearwater breeding burrows were found primarily beneath a low "muttonbird scrub" canopy dominated by *Olearia* species (Johnson 1982).

Survey methods

Historical surveys

Brian Bell and Don Merton undertook a general survey of sooty shearwater harvesting practices on the southwest Titi Island group in April 1961. Their only formal count of sooty shearwater breeding burrow entrances was in a single 10 × 10 yard plot, probably near Boat Harbour on Taukihepa. Counts of the number of families harvesting and estimates of the number of chicks taken were made after visiting nearly all of the manu (family harvesting territories) on Taukihepa during that season.

Peter Johnson and Douglas Flack visited several south-west Titi Islands in January 1976 to survey vegetation, learn about robin (*Petroica australis*) ecology and to assess the suitability of the Titi Islands for transfers of black robin (*Petroica traversi*). The main purpose of their plot sampling was to measure vegetation structure and cycling, with sooty shearwater burrow entrances counted incidentally. Replication is therefore limited, and the placement of their plots was not formally random. Instead, plots were selected to represent the vegetation and density of breeding sooty shearwaters generally.

Douglas Flack surveyed four 10 × 10 m plots for entrances on Little Mangere Island in the Chatham group in late January 1976, for comparison with the Titi Island plots. These observers were able to distinguish burrow entrances of smaller Procelariiformes (broad-billed prions *Pachyptila vittata*, diving petrels *Pelecanoides urinatrix* and mottled petrels *Pterodroma inexpectata*), so we are confident

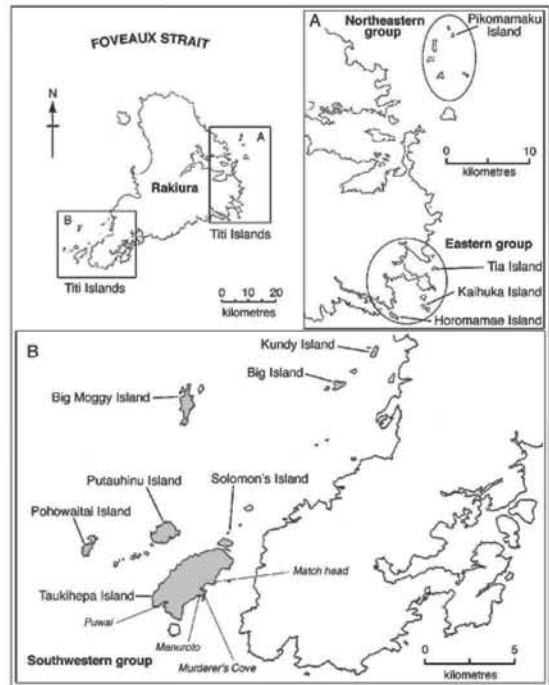


Fig. 1 Location of study areas.

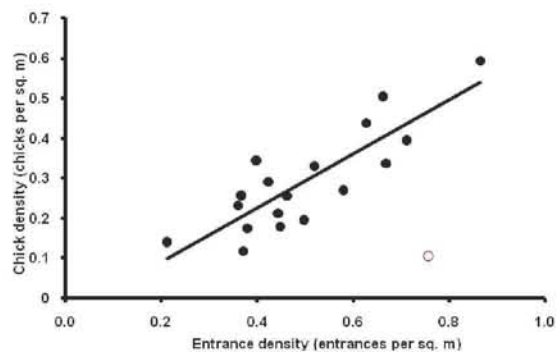


Fig. 2 Relationship between chick density and burrow entrance density at 19 manu on 12 Rakiura Titi Islands, 2000–05. The Paopuka site from Taukihepa (open circle) is not included in the regression model, which is described by $Y = 0.6765x - 0.046$ ($R^2 = 0.7123$).

that the holes counted were entrances to sooty shearwater breeding burrows. In some instances the holes were additionally recorded as "open" or "closed" holes, the latter being those obstructed by an accumulation of branches, twigs and leaves. Parent birds actively drag debris into the burrow entrance when they leave the chicks unattended, presumably

to help keep them warm and/or reduce light (Warham 1996; McKechnie 2006). Burrow-scoping of closed entrances (Lyver et al. 1998) has confirmed that many are occupied, unless the debris is tightly root-bound to the surrounding soil, by which time a formed burrow entrance is difficult to detect. Accordingly, we analysed the combined total of open and closed entrances in this study for both historical and recent surveys.

Recent surveys

A systematic study of sooty shearwater harvest sustainability started on Poutama Island in 1994, shifted to Putauhinu Island in 1996, and broadened to include one-off 5–9 day surveys by 4–6 people on manu through several of the other Tītī Islands

from 1999 until 2006. See Moller et al. (1999), Lyver (2000b), McKechnie et al. (in press a) and Newman et al. (2008a,b, 2009) for more detailed descriptions of the study design and survey methods. Detailed results are presented separately for Timore and Putauhinu Nuggets by Moller et al. (2003b) and Bragg et al. (2003) respectively.

All surveys were conducted between mid March and mid April (before any chicks had been removed by harvesters) using a stratified random design across 4–14, roughly equal-sized areas within each manu. Circular plots had a radius of 3 m on all islands except Poutama, where they were 2 m. Observed burrow occupancy by chicks was “corrected” for detection failures, as described by McKechnie et al. (2007).

Table 1 Historical sooty shearwater burrow entrance counts.

Island	Location	Plot size	Closed entrances	Open entrances	Total entrances
Surveys in April 1961 by Bell (1962)					
Taukihepa (Big South Cape Island) [‡]	“Probably near Boat Harbour”	10 × 10 yards			52 ^α
Surveys in January 1976 by Johnson (1976a,b) and Flack (1976)					
Taukihepa [‡]		No formal count made [‡]			
Poutama (Evening Island) [‡]	West side	10 × 10 m			52
		10 × 10 m	23	20	43
		10 × 10 m	16	12	28
Putauhinu Nugget PN2 [§] Islet [‡]	Western face	10 × 10 m	14	79	93
Un-named Taukihepa islet [‡]	West facing slope	10 × 10 m	21	54	75
Kundy Island [‡]	On headland [¶]	10 × 10 m	7	12	19
Te Poho-o-Taieara (Big Island, Stage Island) [‡]		5 × 5 m	6	0	6
		10 × 10 m	21	11	32
		5 × 5 m	8	2	10
Timore (The Chimney) islet [‡]	Top of south side	5 × 5 m	2	25	27
Pohowaiti [‡]		No formal count made ^Δ			
Little Mangere Island [‡]		10 × 10 m	8	113	121
		10 × 10 m	11	86	97
		10 × 10 m	0	69	69
		10 × 10 m			>121 ^ε

[‡]Regularly harvested.

^αOpen and closed entrances were not distinguished.

[‡]Flack (1976) states: “Burrow density is roughly half that on Little Mangere Island”.

[§]This islet was designated as PN2 by Bragg et al. (2003).

[‡]Seldom if ever harvested. Infrequent visits by fishers for “lunchtime” birds possible.

[¶]Burrow density noted as greater elsewhere on Kundy.

^ΔLetter from D. Flack to P. N. Johnson states that this plot had even greater density than the others but the vegetation prevented complete measurement. We set this “greater than 121” observation to equal to 121 in all our statistical analyses.

^εFlack (1976) states: “The soils and burrow density are very similar to Poutama Island.”

[‡]Flack (1976) notes that this island was “seldom and ineffectively muttonbirded in 40–50 years. Burrow density probably high in 1937. Amount of use last century?”. Plots noted to be under mature forest with a lower storey of *Senecio* and lower tangle of dead branches and *Muehlenbeckia*.

Statistical methods

Estimating the change in entrance density

Our aim to estimate the ratio of the recent mean burrow density to the historical mean burrow density for each site raised several issues:

- (1) There was no replication in the historical surveys;
- (2) Variation in plot-sizes used in the historical surveys. Patchy distribution of burrow entrance density counts means the natural variation in counts from different-sized plots differ even after conversion of the counts to burrows per m^2 ;
- (3) For some sites, the data from the recent surveys were not normally or log-normally distributed.

We took the following steps to overcome these problems.

Determining effective sample size

It was first necessary to specify the historical equivalents of the plot-size used in the recent surveys. At one extreme, if burrow density is randomly distributed in space, a plot with an area of $100 m^2$ would, for example, be equivalent to two plots of $50 m^2$ each. At the other extreme, if burrow density is patchily distributed, a plot with an area of $100 m^2$ might be virtually equivalent to a single plot with an area of $50 m^2$, depending on the scale of patchiness.

At Poutama, for example, the survey in 1976 used three $10 \times 10 m$ plots, while those in 1994 and 1995 used circular plots with a radius of 2 m, i.e., an area of approximately $12.6 m^2$. At one extreme, we might therefore consider each of the $10 \times 10 m$ plots to be equivalent to $100/12.6 \approx 8$ of the 2 m circular plots, suggesting that the 1976 survey is best viewed as if it had used 24 recent plots. This will tend to overestimate the “true” effective sample size, as we are assuming that burrow density is randomly distributed. At the other extreme, we might consider each of the $10 \times 10 m$ plots to be equivalent to just one of the 2 m circular plots, making the 1976 survey therefore equivalent to just three recent plots. This would tend to underestimate the true effective sample size, as each $10 \times 10 m$ plot clearly covers a greater area than a 2 m circular plot. We expected the true “effective sample size” to be somewhere between these two extremes, and it was clearly difficult to judge exactly where. Our aim was to see how different the analyses would be for these two extremes: if they led to essentially the same conclusions, there would be no need to specify an exact effective sample size.

The effective sample sizes for the historical surveys at each site also required consideration. At Taukihepa, the survey in 1961 used one 10×10 yard plot, covering c. $83.6 m^2$. At one extreme, this would be equivalent to $83.6/28.3 \approx 3$ of the recent plots, or, at the other extreme, just one recent plot. By the same logic, at Putauhinu Nuggets, the survey in 1976 used one $10 \times 10 m$ plot, equivalent to recent plots ranging from $100/28.3 \approx 4$ to just one. At Te Poho-o-Taiea, the survey in 1976 used one $10 \times 10 m$ plot and two $5 \times 5 m$ plots, equivalent to recent plots ranging from $(100+25+25)/28.3 \approx 6$ to three. At Timore, the survey in 1976 used one $5 \times 5 m$ plot, equivalent to 1 recent plot.

At Pohowaitai and Taukihepa, no surveys were carried out in 1976. At Pohowaitai, the density was reported to be the “same as at Poutama”. We therefore treated Pohowaitai as if exactly the same data had been collected there as at Poutama, and this 1976 “survey” was equivalent to between three and 12 of the recent plots. Likewise, the burrow density at Taukihepa in 1976 was reported to be about “half that of Little Mangere”. We therefore treated Taukihepa as having observations in 1976 which were exactly half of those from Little Mangere (four $10 \times 10 m$ plots), equivalent to between four and 16 of the recent plots.

For the 1976 survey at Te Poho-o-Taiea, involving different sized plots, we estimated the mean density using the total number of burrows observed divided by the total area of the plots.

Defining duration between surveys

The recent surveys on Taukihepa, Putauhinu Nuggets and Poutama spanned more than one season (Table 2). We calculated the annual rate of change at these sites by taking the period between the historical and recent surveys to be the average number of years between the historical survey and each of the counts made in the recent surveys. Although this involves an approximation, the effect on the analysis is likely to be minor, and it simplifies the procedure used to calculate confidence limits (see below).

Estimating population change

Suppose the recent survey used n_2 circular plots, and the historical survey is considered equivalent to a survey with n_1 recent plots. Let the mean densities observed in the historical and recent surveys be $\bar{y}_1$ and $\bar{y}_2$ respectively, with the corresponding population means being μ_1 and μ_2 . We estimate the ratio $\rho = \mu_2/\mu_1$ by calculating $\hat{\rho} = \bar{y}_2/\bar{y}_1$.

In order to calculate a confidence interval for ρ , we proceeded as follows. Initial examination of the data suggested that assuming a normal or lognormal distribution for the counts would not be reliable: the distributions were generally non-normal and were sometimes skewed to the left. We therefore used a studentised bootstrap procedure (Davison & Hinkley 1997), the details of which are given in Appendix 1. This entailed the assumption that the population distribution of the effectively circular plot counts that were taken at the time of the historical survey was the same shape as the population distribution for these counts in the recent survey. In addition, we estimated this population distribution using the observed distribution of counts in the recent survey, i.e., without specifying a parametric form for the population distribution. The sample sizes for the recent surveys were large enough (minimum = 34) for us to be confident that the observed distribution would provide a reasonable estimate of the population distribution.

Estimating annual and aggregated rates of change

Suppose the lower and upper 95% confidence limits for ρ are ρ_L and ρ_U respectively. Assuming a constant decline during the period of T years between the two surveys, the estimate of annual change is given by $\hat{\alpha} = \hat{\rho}^{1/T} - 1$, with 95% confidence limits given by $\alpha_L = \rho_L^{1/T} - 1$ and $\alpha_U = \rho_U^{1/T} - 1$.

In order to obtain an overall estimate of change for a group of islands, we proceeded as follows. We supposed the true annual rate for island i was α_i , and

wished to estimate the mean of α_i across a population of islands, which we denoted as $\bar{\alpha}$. Let $\hat{\alpha}_i$ be our estimate of α_i . If we assume that we have a random sample from the population of islands, we can estimate $\bar{\alpha}$ by the mean of the $\hat{\alpha}_i$, which we denote as $\bar{\hat{\alpha}}$. In order to calculate confidence limits around this estimate, we used a studentised bootstrap procedure, the details of which are given in Appendix 2.

Comparing initial densities

In order to obtain an overall estimate of the burrow density on a group of islands, we proceeded as follows. We let the true burrow density on island i be β_i . We estimated the mean density across a population of islands ($\bar{\beta}$) by the mean estimate over our sample of islands ($\bar{\hat{\beta}}$), and calculated confidence limits around this estimate using a studentised bootstrap procedure described in Appendix 3.

RESULTS

Historical harvest intensity

Brian Bell and Don Merton investigated muttonbirding in the south-west Tītī Islands groups between 5 April and 4 May 1961. Most of that time was spent encamped on Taukihepa to visit 27 of 28 families or “parties” as they harvested, but they were also able to record the number of parties on other nearby islands (Table 4). They considered a “party” as the occupants of a “residence” on the island, as each

Table 2 Changes in sooty shearwater breeding burrow entrance density on Rakiura Tītī Islands from historical to recent surveys. The number of plots surveyed is given in brackets; the effective replication levels for historical surveys are given in the text.

Island	Year of historical survey	Year(s) and sample size for recent survey	% change in entrance density	% annual rate of change in entrance density (with 95% CI) assuming historical survey has minimal or maximal effective replication	
				Minimal effective replication	Maximal effective replication
Taukihepa	1961	2000–05 ^a ($n = 872$)	33.9	–1.0 (–4.4 to +0.4)	–1.0 (–2.4 to –0.1)
Taukihepa	1976	2000–05 ^a ($n = 872$)	19.4 [†]	–0.8 (–2.6 to +0.4)	–0.8 (–1.6 to –0.1)
Poutama	1976	1994–95 ^a ($n = 160$)	+7.8	–0.4 (–2.1 to +2.3)	+0.4 (–0.4 to +1.2)
Putauhinu	1976	2002–05 ^a ($n = 54$)	41.0	–1.9 (–6.6 to +0.3)	–1.9 (–3.7 to –0.7)
Nuggets PN2					
Te Poho-o-Tairea	1976	2006 ($n = 51$)	2.9	–0.1 (–4.3 to +2.4)	–0.1 (–2.7 to +1.8)
Timore	1976	2002 ($n = 34$)	47.7	–2.5 (–7.1 to –0.2)	–2.5 (–7.1 to –0.2)
Pohowaiti	1976	2001 ($n = 165$)	23.2 [‡]	–1.1 (–3.5 to +0.7)	–1.1 (–2.2 to –0.1)

^aThe mean year was used when calculating annual decline.

[†]Using data from Little Mangere (see text for details).

[‡]Using data from Poutama (see text for details).

of these had their own manu. The parties varied in size but most were two persons, usually husband and wife, occasionally accompanied by a child. The variation in number of chicks harvested reflected the number in each party rather than any difference in their harvesting efficiency. Also, some parties spent a longer time on the island, while some were present only for the rama period.

The two most densely populated and worked areas were Puwai Beach and Murderers Cove. Twenty-seven boats operated on Big South Cape, including the “government steamer” (Stewart Island ferry). About half the parties depended for fuel on burning tūpare (*Olearia colensoi*) in an open fire. The rest of the parties used coal ranges, primus or rock gas stoves. At least some of the chicks were within arm’s length of the entrance, but others in longer burrows were either snared with a hooked wire or stick, or a “puru” (hole) was dug above the nesting chamber to extract the chick. The birders reported that burrows were deeper on Taukihepa than on outer islands, which they attributed to the muttonbirds’ response to predation by the introduced weka (*Galirallus australis*) on Taukihepa. Two-thirds of the chicks were captured by “torching” (once emerged at night), and a third extracted from burrows by day during the nanao. Some birders were developing the use of wax to remove pin feathers at the time of the survey. Two instances were noted of netting fences used to catch the fledglings before they left the island by directing them into catching pens as they moved towards take-off points.

The 1961 season was poor, with comparatively small chicks. In an average year the birders could fit 40 processed chicks into a 4 gallon tin and the annual tally varied from 1500 to 8000 amongst the 16 parties queried. In 1961 this overall take was reduced by one quarter. The average number of birds taken was approximately 4000 per party, so the 61 parties on all the south-west islands harvested approximately 240 000 chicks in 1961.

The birders cleared some vegetation in the expectation that it would increase bird numbers, facilitate harvesting, or both. The researchers believed that the density of burrow entrances was about the same in cleared and in uncleared areas. Fifteen parties questioned were in favour of clearing and six against; the birders considered that the recent advent of the chainsaw was likely to increase the amount of clearing in future. There was evidence of extensive former fires in the “pākihi” (swampy scrub) areas, but 14 of 18 parties opposed the use of fire away from dwellings.

Weka were harvested for food, which Brian Bell considered would assist conservation by reducing their abundance. Many birders were in favour of liberating more weka on more islands as an additional food supply, but some realised that weka on small islands would eliminate ground-nesting birds, small petrels and, in time, possibly reduce the population of muttonbirds.

Generally, the birders were in favour of research on harvest sustainability, although some were a little cautious and would not commit themselves. None were happy about having to fund such studies. The report recommended that the government appoint a biologist to investigate sooty shearwater harvesting (Bell 1962).

Relationship between entrance density and chick density

There was a strong, apparently linear, relationship between entrance density and the actual number of chicks per m² at the breeding colonies in the recent surveys (Fig. 2). The Paopuka site is a largely unharvested steep slope in the middle of Taukihepa, characterised by (i) unusually tall vegetation, (ii) a canopy dominated by southern rātā (*Metrosideros umbellata*) and other broadleaved species, especially broadleaf (*Griselinia*), punga (mainly *Dicksonia squarrosa*) and kāmahi (*Weinmannia racemosa*), rather than *Olearia*, (iii) the presence of several mottled petrels (Scott et al. 2006; Newman et al. 2008b), and (iv) exceptionally wet soil. When this outlier with unusually low occupancy of burrows was excluded, entrance density explained 71% of the variation in late season chick density (before harvest).

Changes in burrow entrance density and occupancy

Assuming low effective replication, mean burrow entrance density on harvested islands in 1976 was 0.40 burrows per m² (95% CI: 0.22–0.56), while that on unharvested islands was 0.99 burrows per m² (95% CI: 0.59–2.35), a difference of 0.59 burrows per m² (95% CI: 0.17–1.78). The corresponding estimates obtained from assuming high effective replication, were 0.41 burrows per m² on harvested islands (95% CI: 0.32–0.49), 0.95 burrows per m² on unharvested islands (95% CI: 0.30–1.50), corresponding to a difference of 0.54 burrows per m² (95% CI: –0.09–1.07). A higher proportion of the entrances in unharvested plots were open (81%) compared with harvested plots (41%).

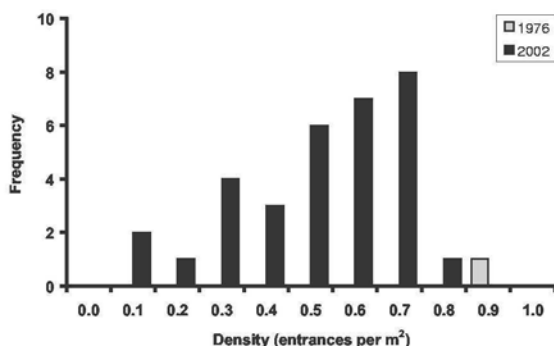


Fig. 3 Distribution of density of sooty shearwater burrow entrance densities on thirty-four 28 m² circular plots (2002) and one 100 m² (1976) on Putauhinu Nugget B.

Individual estimates of annualised rate of change of sooty shearwater burrow entrances per island have very wide confidence intervals (Table 2). When using the minimum assumed “effective” replication (column 5 of Table 2), only Timore has a confidence interval that does not encompass zero. However, when the maximum replication is assumed (column 6 of Table 2), only the intervals for Poutama and Te Poho-o-Taiera do include zero. For all islands except Poutama, the estimate of the annual change is negative and most of the span of the confidence interval is also negative, irrespective of the degree of replication assumed. The same is true of the pooled estimates, so we can be reasonably confident that there have been broad-scale declines in numbers of burrows (Table 3).

Table 3 Overall percentage annual rates of change (with 95% CI) in sooty shearwater breeding burrow entrance density on Rakiura Tītī Islands, from historical to recent surveys, assuming historical survey has minimal or maximal effective replication.

	Using Taukihepa 1961		Using Taukihepa 1976	
	Minimal effective replication	Maximal effective replication	Minimal effective replication	Maximal effective replication
All harvested islands [†]	-0.5(-1.9 to +0.5)	-0.4(-2.0 to +0.9)	-0.5(-1.8 to +0.4)	-0.4(-1.8 to +0.8)
All unharvested islands [‡]	-2.2(-5.0 to -0.4)	-2.0(-3.8 to -0.6)	-2.2(-5.0 to -0.4)	-2.0(-3.8 to -0.6)
Unharvested versus harvested islands	-1.6(-4.4 to +0.7)	-1.6(-3.6 to +0.3)	-1.6(-4.4 to +0.6)	-1.6(-3.6 to +0.1)
All islands	-0.9(-2.3 to +0.2)	-0.8(-2.1 to +0.5)	-0.9(-2.1 to +0.3)	-0.8(-2.1 to +0.3)
The Snares versus all islands	-0.8(-2.0 to +0.6)	-0.9(-2.2 to +0.4)	-0.9(-2.0 to +0.5)	-0.9(-2.2 to +0.4)

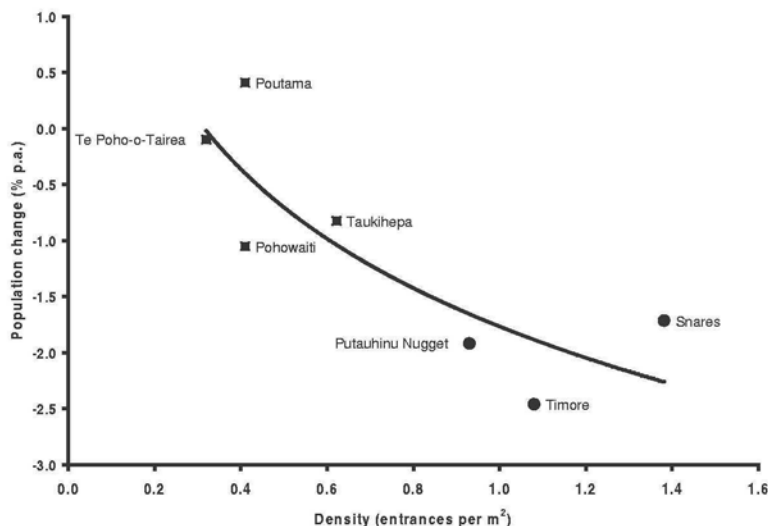
[†]Taukihepa, Poutama, Te Poho-o-Taiera, Pohowaiti.

[‡]Putauhinu Nugget, Timore.

Table 4 Number of families or parties harvesting sooty shearwater chicks on the south-west Tītī Islands in the 1961 and recent harvesting seasons.

Group	Island	No. of families/parties 1961	No. of families/parties 1994–2005
Moggy Islands	Mokinui	3	7
	Mokiti	0	1
Wedge	Pohowaiti	5	6
	Tamaitemioka	1	1
Boat Group	Kundy	2	2
	Betsy	0	1
	Te Poho-o-Taiera (Big)	4	4
South Cape Islands	Kaimohu	1	1
	Rerewhakaupoko (Solomon)	6	7
	Pukaweka	1	1
	Taukihepa	28	65
	Poutama	6	7
All south-west islands combined	Putauhinu	4	5
		61	108

Fig. 4 Rate of population decline versus initial burrow entrance density on six Tītī Islands and The Snares. Harvested islands are shown in squares, unharvested as circles. Data for Tītī Islands are presented in Tables 1 and 2. Rate of population change is assessed from 1961 (Taukihepa), 1969–1971 (The Snares) and 1976 (all other islands) until 1994–2005. The datum for The Snares is from Scott et al. (2008). The equation for the line is $y = -0.015 \ln(x) - 0.0179$. The regression equation explained 71% of the variation.



The overall annual decline on regularly harvested islands is 1.6 percentage points less than that on unharvested islands, although all the confidence intervals include zero (Table 3).

The annual decline on The Snares (1969–71 to 1996–2001; Scott et al. 2008) is 1.7% (95% CI: 2.1–1.3%), which is greater than the overall decline on the Tītī Islands (1976 to 1999–2005), although the confidence intervals again include zero (Table 3).

Despite the wide confidence intervals on rates of change on individual islands, there is a clear pattern suggesting that the rate of decline has been faster on islands with relatively high initial burrow entrance density (Fig. 4): a linear regression of rate of decline against the logarithm of initial burrow entrance density explains 71% of the variance.

DISCUSSION

Trends in harvest intensity

The estimated annual harvest of 240 000 chicks from the south-west Tītī Islands in 1961 is the earliest reasonably formal investigation of harvest off-take that we have been able to locate. An unpublished report on Lands & Survey files from the Commissioner of Crown Lands at the time states:

“It has never been required of muttonbirders that they supply details of birds taken and there is no reliable information about the total birds taken in any year. As far back as 1908 it was estimated that the number of birds taken annually would amount

to 200 000. I have no way of determining what the total annual catch would be now but a reference on the department’s file to the numbers taken in 1921 from a particular manu is comparable with the number recently taken from the same area and this could suggest that the number taken annually could still be about the same” (Brant 1975).

Although rapid and only semi-formal, Brian Bell’s 1961 investigation provides valuable baseline information for assessing change. Our observations and discussion with all muttonbirding families indicate that similar numbers of families/parties have been harvesting on the islands in the past decade, except on Taukihepa and Mokinui (Table 4). Bull (2002) counted 65 houses on Taukihepa in the 2002 season. Most parties have a single house, so this represents around a 2.3-fold increase in the number of parties over 4 decades. Families have become smaller in recent times, the number of people per party and their length of stay on the islands may well have changed and be distributed differently amongst the available workhouses and houses, so there may have been fewer people per dwelling in recent years. Several of the dwellings on the Tītī Islands are old and are constantly being repaired. Younger members of the family tend to inherit the use of their grandparents’, uncles’ and aunts’ or parents’ set up.

There has been a decline in the number of harvesters on Poutama by two-thirds over that period (Lyver 2000a), even though the number of workhouses is similar. John Wixon, an experienced harvester on Poutama, recently stated (in litt. 25 April 2007):

"In many seasons on Poutama between 1950 and 1965, there would be in excess of 30 people nanaoing. Everyone got good catches. Then most people would spend the full season on the island. Now the island barely supports 3–4 people during the nanao. In my opinion, this is because of the amount of ground you have to cover and the difficulty in catching the chicks at an economical rate. Those years you were governed by the number of chicks you were able to process, now you are governed by the number you are able to catch. In recent years on Poutama, most of the birders arrive for the rama when the chicks are easier to catch. The numbers of birds caught during the rama has also dropped significantly to what was caught prior to the late 1980s."

However, on other islands there have been apparent increases in the numbers of people participating in the harvest over the past 2–4 decades (Newman et al. 2008a).

Our comparison (Table 4) emphasises that much more ground on the western flank of Taukihepa is now occupied by birders since the advent of helicopters in the 1970s to lift equipment, provisions and harvested birds on and off the islands. In the past, steep cliffs on that side of Taukihepa precluded landing and loading, so that western manu were unused, except for Potted Head (Fig. 1). The number of "people-days of harvesting" per manu is by far the most important determinant of annual tally and harvest intensity (McKechnie in press b), as also observed by Bell (1962). At a broad population level, there must have been some reduction in harvest refuge areas over the past 40 years since the initiation of harvest on the western side of Taukihepa, but we do not yet know if this is a quantitatively significant contribution to the decline in overall population size of sooty shearwaters over that period. The view that burrows on Taukihepa are apparently deeper than elsewhere has not yet been tested.

Fewer birders have attended the nanao phase of harvest in recent years. The advent of helicopters has enabled individual parties to travel independently to the islands and leave earlier than was possible when a government steamer carried all the parties together (Kitson 2002; Kitson & Moller 2008; Moller et al. 2009 this issue). It is therefore possible that the total number of people participating in the harvest has increased, even though the overall number of people-days of harvesting has declined. The number of permits issued for the ex-Crown Titi Islands has approximately doubled between 1960 and 2006 (Newman et al. 2008a). On the other hand, Lyver (2000b) hypothesised that harvest intensity has been

self-regulated on Poutama as the population has declined. In summary, despite obvious fluctuations in numbers of birders between islands and years, there is no conclusive evidence for any trend to increasing or decreasing harvest pressure over the past 4 decades.

In recent years, where a harvester participates in both nanao and rama phases of the harvest on manu, 20.5% of the harvest has come from the nanao (McKechnie et al. in press b), compared with around "a third" in 1961. In general, fewer birders have been participating in the nanao in recent years (Kitson 2002; H. Moller unpubl. data; J. Wixon in litt.), so for the entire community it is clear that a much higher proportion of the birds have come from the rama in recent years than in 1961.

The use of net fences to divert fledglings has been vigorously opposed by most members of the Rakiura Māori community and recent draft bylaws propose that they be outlawed. All birders now use gas and wax for cleaning birds, and most have electric generators and operate motorised plucking machines. Whereas these innovations are generally considered to make the laborious work of muttonbirding easier, they have only a marginal impact on the efficiency of processing and capturing birds, and therefore on the total catch per person (Lyver & Moller 1999; Kitson 2002). However, in the past decade, it has been exceptionally rare for a chick to be retrieved within an arm's length of the burrow entrance (H. Moller unpubl. data) in the way described by Brian Bell in 1961. Until 1980, it was possible for birders on Poutama Island often to catch at least two chicks per burrow entrance (J. Wixon pers. comm. 1995), but this was rare in 1994 and 1995 (P. Lyver unpubl. data). This may indicate that the birds now nest deeper in the ground and so more are missed, as indicated by burrow-scoping (McKechnie et al. 2007). Sooty shearwaters prefer to nest further away from the entrances than would be expected by random choice (McKechnie 2004). Alternatively, this reduction in the number of accessible chicks may indicate a genuine reduction in abundance. The lower confidence limit on the annual rate of change on Poutama since 1976 has been -2.1% (Table 2), but our historical comparisons suggest the rate of any decline has been slower there than on other islands (Fig. 4).

Burrow entrance density as an index of population abundance

The strong predictive relationship between entrance density and chick density in recent times (Fig. 2) is partly an artefact of the lack of formal independence

between the predictor and the response variable (since the latter is partly calculated from entrance density). However, the high annual variation in breeding success (Newman et al. 2009), includes a lot of unexplained variation in this relationship, so entrance density may actually have an even tighter relationship with adult population size and its long-term average breeding success than is evident in Fig. 2. Entrance density varies relatively little between years and breeding burrows are rapidly reformed after disturbance (McKechnie et al. 2008, in press). Burrow entrance density, with or without shifts in average burrow occupancy, therefore provides a buffered and relatively robust, linear index of sooty shearwater population size for longer term monitoring of population change. The declines observed in this study and those reported by Scott et al. (2008) on The Snares are therefore likely to reflect real changes in population size. John Wixon states:

"I believe the density of the birds in the burrows has also decreased dramatically, as well as there being fewer holes. Years ago my wife and I could nanao over ground that had been previously worked by other people early in the nanao and still caught adequate tallies. We found it better working over good manu that had been worked, rather than rougher unworked areas on the island. I think that there has been a gradual decline in tītī numbers from when my father was a young man birding, but a drastic downturn in numbers from the late 1980s". (In litt. 25 April 2007).

Bootstrapping to estimate uncertainty

We used bootstrapping to calculate confidence intervals for population change in order to avoid assuming a specific parametric distribution for burrow entrance density. In particular, burrow entrance density in the recent surveys was clearly skewed to the left, suggesting that neither the normal, Poisson, nor the negative binomial distribution would be an appropriate model for the variation (Fig. 3). If there had been greater replication in the historical surveys, we could have made use of the Central Limit Theorem, because mean burrow density would have been approximately normally distributed for both surveys. If we had then assumed that variance in density was the same for the historical and recent surveys, we could have adopted a simpler analysis.

Sources of uncertainty

It is unsurprising that the island-specific confidence intervals we calculated were wide. The historical surveys were not designed to provide baselines to

measure future population trends. Once estimates were pooled across islands, the confidence intervals were less than 5 percentage points wide (Table 3), but this is still a considerable level of uncertainty for a long-lived and slowly-reproducing species like the sooty shearwater that has a maximum rate of intrinsic increase of c. 7.2% (Fletcher et al. "Age at first return to the breeding colony, juvenile survival rate and transience of sooty shearwater (*Puffinus griseus*)" (in prep.)).

Placement of historical plots in "representative" areas, rather than by random selection, probably expanded our calculated confidence intervals, because the historical plots are more likely to have fallen around the median than at the tails of the distribution. Accordingly, the bootstrap estimates of uncertainty may have been considerably overestimated, reducing our chances of detecting real differences between harvested and unharvested islands, or between historical and recent densities. There is clear patchiness in the entrance density within different parts of the breeding colony (Lyver 2000a; Charleton 2002; Scott et al. 2009 this issue), but the mean size of patches has not been measured and we do not know whether the minimal or maximum effective replication is appropriate.

The high concentration of "open" entrances in unharvested plots compared to harvested plots possibly indicates higher occupancy of breeding burrows in areas where the population is not harvested. If so, the difference in rate of decline observed in unharvested compared to harvested populations over the past 2 or 3 decades may have been even greater than suggested by Fig. 4. However, it remains possible that mean burrow occupancy has remained higher in unharvested ground in recent years (we will test this assumption elsewhere), in which case we will have incurred no bias in inferring relative population change from differential changes in entrance density. Indeed, the close linear relationship seen between entrance density and chick density (Fig. 2) suggests that any such bias will have been small.

Further uncertainty is introduced by the unquantified nature of the "relative" assessment of entrance density on Taukihepa and Pohowaiti in 1976 and the non-independent estimates for individual islands. However, the observers were experienced ornithologists who had wandered widely over many of the islands to establish their comparison. Furthermore, the annual rate of decline since 1961 (when a plot was measured) was very similar to that observed since 1976 (when no formal count was made). Therefore,

we believe that the extra uncertainty introduced by the unquantified comparison in 1976 is probably minor.

Despite the many assumptions and methodological challenges in comparing the historical and recent data, the overall pattern of decline in burrow density they show is consistent with all the other evidence that has been reported from beach patrol counts, at-sea counts, burrow-occupancy changes, and harvest rates (Veit et al. 1997; Lyver et al. 1999; Scofield & Christie 2002; Jones et al. 2003; Scott et al. 2008). A strong, apparently density-dependent, relationship emerged from only seven islands (Fig. 4). The bootstrapping methods and assumptions used for six of these islands is consistent with the rate of decline observed on The Snares over a similar time period using a much firmer historical dataset provided by Warham & Wilson (1982). It is difficult to conceive of an alternative *post-hoc* explanation for the observed relationship between initial density and subsequent rate of decline. We are therefore confident that our analysis overestimates the degree of uncertainty surrounding our conclusions, as is appropriate from an environmental precautionary principle to guide conservation and harvest management.

Evidence for harvest impacts and density dependent compensation of harvest offtake?

We conclude that the rate of decline has been lower on harvested areas and also lower on areas with initially high burrow densities. The historical surveys were done on relatively few islands, and included one, Little Mangere, distant from the Tītī Islands group, so we cannot be sure that the lower historical density on the harvested islands indicates a harvest impact per se. However, the most likely explanation for the observed pattern is a combination of density-dependent effects on sooty shearwater population changes, plus the higher density observed on unharvested than on harvested ground in historical times (Table 2; Fig. 4). Several other possible interacting mechanisms for these two findings will be considered elsewhere, some of which will be tested by simulation modelling. They include: (i) the population inputs at all high density colonies (especially breeding success and immigration) may be clamped down by localised density dependence; (ii) between 1976 and recent times, overharvesting and some extrinsic factor (e.g., climate change, Veit et al. 1997; Lyver et al. 1999) have perturbed vital rates (e.g., adult survival), adding to the reductions in all populations but at different rates on unharvested

versus harvested islands; (iii) in recent years only, alleviation of harvest pressure has equalised productivity on harvested and unharvested ground, in part or wholly; (iv) the birders themselves have altered the habitat in breeding areas (Bell 1962; Kitson & Moller 2008), slowing the decline on harvested ground.

Demonstrations of strong density dependence in Procellariiformes are rare in the literature (Birkhead & Furness 1985; Croxall & Rothery 1991); the observation that albatrosses commenced breeding earlier when fisheries bycatch had reduced their populations (Croxall et al. 1990; Tuck et al. 2001) is one of few published examples. The results depicted in Fig. 4 are thus both surprising and important. A density dependent increase in productivity is a potentially important compensation for harvest mortality (Moller 2006). Mathematical models assessing harvest sustainability will need to account for the pattern we describe before they can reliably predict future populations. It is clear that a simple additive model of harvest impact on breeding success is inadequate, particularly in explaining past trends in population abundance. Under such a model, the observed rate of decline would be higher on harvested islands than on unharvested ones. This is the opposite of the pattern reported here. This does not necessarily imply that future harvests will be secured indefinitely by density dependence. Contemporary and future populations may be regulated by different ecological factors than those that operated between 1961 and 1976 and now. If oceanic conditions are changing in ways that reduce "carrying capacity", the relationship between density and reproductive and migration rates operating over the past 30 years may no longer apply. Nevertheless, the available evidence suggests that density dependence should be built into future model projections attempting to predict sustainable harvests. Rakiura Māori can have confidence only in a model that has been externally validated by predicting the differences in declines in the abundance of sooty shearwater described here. Such a model should provide a reliable tool for ensuring the continuation of their culturally defining customary harvest tradition under a variety of conditions, including alternative future harvest management scenarios, fisheries-bycatch risks and climate change. Sooty shearwaters are important ecosystem engineers, so mathematical models constructed to guide sustainable harvest management will also help predict changes in health of their breeding island ecosystems.

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Appendices over page

Appendix 1 Bootstrap procedure for each island.

- (1) Generate a bootstrap sample for the recent survey by selecting a random sample (with replacement) of size n_2 from the observations for the recent survey. The mean of this bootstrap sample is denoted $\bar{y}_2^*$.
- (2) Generate a bootstrap sample for the historical survey by selecting a random sample (with replacement) of size n_1 from the observations for the recent survey and then dividing each of the selected observations by $\hat{\rho}$. This implies that we are assuming that $\Pr(Y_1 = y_1) = \Pr(Y_2 = \rho y_1)$, where Y_1 and Y_2 are random variables representing circular-plot counts in the historical and recent surveys respectively. The mean of this bootstrap sample is denoted $\bar{y}_1^*$, and the ratio of the two means is $\hat{\rho}^* = \bar{y}_2^* / \bar{y}_1^*$.
- (3) Calculate the studentised value of the logarithm of $\hat{\rho}^*$ as

$$t^* = \frac{\ln(\hat{\rho}^*) - \ln(\hat{\rho})}{SE[\ln(\hat{\rho}^*)]}$$

where $SE[\ln(\hat{\rho}^*)]$ is the estimated standard error of $\ln(\hat{\rho}^*)$, calculated using

$$SE[\ln \hat{\rho}^*] \approx \sqrt{CV(\bar{y}_1^*)^2 + CV(\bar{y}_2^*)^2}$$

where $CV(\bar{y}_2^*) = \frac{s_2^*}{n_2 \bar{y}_2^*}$ and we set $CV(\bar{y}_1^*) = \frac{n_2}{n_1} CV(\bar{y}_2^*)$,

with s_2^* being the standard deviation of the bootstrap sample for the recent survey.

- (4) Repeat Steps 1–3 to obtain 10 000 values of t^*
- (5) Calculate lower and upper 95% confidence limits for $\ln(\rho)$ as follows (Davison & Hinkley 1997):

$$\text{Lower limit: } L = \ln(\hat{\rho}) - t_{\alpha}^* SE[\ln(\hat{\rho})]$$

$$\text{Upper limit: } U = \ln(\hat{\rho}) + t_{\alpha}^* SE[\ln(\hat{\rho})]$$

where t_{α}^* and $t_{1-\alpha}^*$ are the 2.5th and 97.5th percentiles of the 10 000 values of t^* ,

and $SE[\ln(\hat{\rho})] = \sqrt{CV(\bar{y}_1)^2 + CV(\bar{y}_2)^2}$, with $CV(\bar{y}_2) = \frac{s_2}{n_2 \bar{y}_2}$

and $CV(\bar{y}_1) = \frac{n_2}{n_1} CV(\bar{y}_2)$ (cf. Step 3), where s_2 is the standard deviation of the data from the recent survey.

- (6) Lower and upper 95% confidence limits for $\rho = \mu_2 / \mu_1$ are given by back-transformation, i.e., by $\rho_L = \exp(L)$ and $\rho_U = \exp(U)$ respectively.

Appendix 2 Bootstrap procedure for mean rate of change.

1. Select a random sample of size m (with replacement) from the m islands. These are referred to as “bootstrapped islands”.
2. Generate a bootstrap sample for each bootstrapped island using Steps 1 and 2 of the bootstrap procedure in Appendix 1. Let ρ_i^* denote the value of $\bar{y}_2^*/\bar{y}_1^*$ for bootstrapped island i ($i = 1, 2, \dots, m$).
3. Convert ρ_i^* to an annual rate of change by calculating $\hat{\alpha}_i^* = (\rho_i^*)^{1/T_i} - 1$, where T_i is the number of years between the historical and recent surveys on island i ($i = 1, 2, \dots, m$). The mean of the $\hat{\alpha}_i^*$ is denoted as $\hat{\alpha}^*$.
4. Calculate the studentised value of $\hat{\alpha}^*$, as

$$t^* = \frac{\hat{\alpha}^* - \hat{\alpha}}{SE(\hat{\alpha}^*)}$$

where $SE(\hat{\alpha}^*)$ is the estimated standard error of $\hat{\alpha}^*$, calculated using

$$SE(\hat{\alpha}^*) = \frac{s^*}{\sqrt{m}}$$

where s^* is the standard deviation of the $\hat{\alpha}_i^*$ ($i = 1, 2, \dots, m$).

5. Repeat Steps 1–3 to obtain 10 000 values of t^* .
6. Calculate lower and upper 95% confidence limits for $\hat{\alpha}$ as follows:

$$\text{Lower limit: } L = \hat{\alpha} - t_{U}^* SE(\hat{\alpha}^*)$$

$$\text{Upper limit: } U = \hat{\alpha} - t_{L}^* SE(\hat{\alpha}^*)$$

where t_{L}^* and t_{U}^* are the 2.5th and 97.5th percentiles of the 10 000 values of t^* , and $SE(\hat{\alpha}^*) = \frac{s}{\sqrt{m}}$, where s is the standard deviation of the $\hat{\alpha}_i$ ($i = 1, 2, \dots, m$).

Appendix 3 Bootstrap procedure for mean burrow density in the historical survey.

1. Select a random sample of size m (with replacement) from the m islands. These are referred to as “bootstrapped islands”.
2. Generate a bootstrap sample for each bootstrapped island using Step 2 of the bootstrap procedure in Appendix 1. Let $\hat{\beta}_i^*$ denote the value of $\bar{y}_1^*$ for bootstrapped island i ($i = 1, 2, \dots, m$). The mean of the $\hat{\beta}_i^*$ is denoted as $\hat{\beta}^*$.
3. Calculate the studentised value of $\hat{\beta}^*$ as

$$t^* = \frac{\hat{\beta}^* - \hat{\beta}}{SE(\hat{\beta}^*)}$$

where $SE(\hat{\beta}^*)$ is the estimated standard error of $\hat{\beta}^*$, calculated using

$$SE(\hat{\beta}^*) = \frac{s^*}{\sqrt{m}}$$

where s^* is the standard deviation of the $\hat{\beta}_i^*$ ($i = 1, 2, \dots, m$).

4. Repeat Steps 1 to 3 to obtain 10 000 values of t^* .
5. Calculate lower and upper 95% confidence limits for $\hat{\beta}$ as follows:

$$\text{Lower limit: } L = \hat{\beta} - t_{U}^* SE(\hat{\beta}^*)$$

$$\text{Upper limit: } U = \hat{\beta} - t_{L}^* SE(\hat{\beta}^*)$$

where t_{L}^* and t_{U}^* are the 2.5th and 97.5th percentiles of the 10 000 values of t^* , and $SE(\hat{\beta}^*) = \frac{s}{\sqrt{m}}$, where s is the standard deviation of the $\hat{\beta}_i$ ($i = 1, 2, \dots, m$).