

## Variation in abundance and harvest of sooty shearwaters (*Puffinus griseus*) by Rakiura Maori on Putauhinu Island, New Zealand

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**Abstract** Sooty shearwater (*Puffinus griseus*, titi) abundance, harvest levels and chick mass were monitored repeatedly on Putauhinu Island, south-west of Rakiura (Stewart Island) between 1997 and 2005. Putauhinu is the second largest of the Titi Islands and has a relatively high density of chicks distributed over most of the island, so it supports what is likely the second-largest population of sooty shearwaters in the Rakiura region (after Taukihepa, Big South Cape Island). Rakiura Maori harvested chicks from five “manu” (family birding areas) that covered 56% of the 128.4 ha of breeding colony of the island. Chick density was lower on the unharvested area in the interior of the island than on harvested areas. Burrow entrance density was higher where there was more ground cover (mainly fern) vegetation, but these areas had lower burrow occupancy, so overall chick density was

similar at different levels of ground cover. Twenty-six harvesters present on Putauhinu in 2005 took 31 280 chicks in total, equivalent to 8.4% (95% CI = 6.6–12%) of the available chicks on the entire island. Seasonal variation in total chicks harvested (CV 15–22%) was not related to chick abundance or mass. Refuges, including impenetrable patches of vegetated ground within manu, the unharvested centre of the island, and even nearby unharvested islands, will ameliorate localised impacts of harvest if density-dependent immigration is operating.

**Keywords** harvest intensity; muttonbirding; sooty shearwater; sustainability

### INTRODUCTION

Rakiura Māori harvest tītī (sooty shearwater chicks; *Puffinus griseus*) on the Tītī Islands around Stewart Island in southern New Zealand, in what is one of the few remaining large-scale cultural harvests permitted in the country (Wilson 1979). This species is an abundant, medium-sized petrel that nests in burrows on islands around southern New Zealand, South America and Tasmania (Warham & Wilson 1982; Reyes-Arriagada et al. 2007). After breeding during the austral summer, most of the population migrate to the North Pacific during winter (Shaffer et al. 2006).

Harvesting of tītī dates back to prehistoric times (Hawke et al. 2003), but may have increased in scale about the time of European settlement of southern New Zealand (Anderson 1997; but see Davis 1999 and Moller 1999). The Rakiura muttonbird harvest remains a culturally defining and economically important activity for many harvesters (Stevens 2006; Kitson & Moller 2008; Moller et al. 2009a this issue) and an important early example of co-management of conservation by Māori in Aotearoa/New Zealand (Moller et al. 2000).

Research investigating the sustainability of the tītī cultural harvest was initiated in 1994 (Moller 1996; Moller et al. 2000, 2009b). The research programme

aimed to predict long-term harvest sustainability by combining population monitoring (McKechnie et al. in press; Clucas et al. 2008) and investigations of population parameters (Scofield et al. 2001; Jones et al. 2003; Clucas et al. 2008; Newman et al. 2009), threats (Hamilton & Moller 1995; Lyver et al. 1999; Jones 2003; Uhlmann et al. 2005) and specific aspects of harvesting practice (Hunter et al. 2000a; Lyver 2000; Kitson 2002; Newman et al. 2008) in mathematical models (Hamilton & Moller 1995; Hunter et al. 2000b; Hunter & Casswell 2005). Estimates of the total number of chicks harvested (hereafter termed harvest) and temporal variation in hunter-prey dynamics will be crucial for these sustainability predictions. To date, the only published estimates of harvest and harvest intensity (the proportion of available chicks that are harvested) are for Poutama Island in the 1994 and 1995 harvesting seasons (Lyver 2000) and Taukihepa (Big South Cape Island) between 1999 and 2005 (Newman et al. 2008). Poutama Island differs from the majority of harvested Tītī Islands in that harvesting is managed under an “open” system, where the harvesting area is treated as common property with all harvesters present on the island able to take chicks from any area (Kitson & Moller 2008; Moller et al. 2009a). Muttonbirders from most other islands operate a “closed” system where families have exclusive use of a “manu” i.e., a subsection of the breeding colony. Common property theory suggests that incentive to maximise harvest is increased in open systems, so replication of Lyver’s (2000) study is certainly necessary. Similarly, the harvest for Taukihepa may not be comparable to other Tītī Islands, if it is affected by factors such as the island’s large size, long history of harvest, vegetation structure and the presence of a large, unharvested, internal colony.

In this study we quantify temporal fluctuations in the number of tītī available to harvesters, the number of tītī harvested, and thus harvest intensity, on Putauhinu Island, a medium-sized island managed under a closed harvesting system. We also investigate the effect of understorey vegetation on chick density. The traditional ecological knowledge (TEK) of several harvesters suggested that chick density may be related to the coverage of understorey vegetation in the surrounding area (Moller et al. 2009c this issue). Testing this relationship has important implications for investigating the role of spatial refuges when determining harvest impacts. Dense vegetation is known to prevent harvesting in certain areas (Lyver 2000; Moller et al. unpubl. data), so the relative densities of chicks and the connectivity

between vegetated and open areas may determine the proportion of the population vulnerable to harvest on a certain manu, or island, and sustained recruitment in vegetation refuges may partially compensate for harvesting impacts.

Putauhinu Island is the only harvested island where temporal variation in population abundance, mass of chicks and harvest intensity has been repeatedly monitored at fixed sites. An understanding of temporal variation in harvest intensity and population abundance is required to reliably predict long-term harvest impacts, as fluctuations in a wildlife resource makes achieving sustainable harvesting difficult (Lande et al. 1995; Engen et al. 1997). This may particularly be the case for tītī, as large natural fluctuations in their abundance and chick size are well known and are thought to play an important role in determining the success of the harvesting season (Lyver et al. 1999; Clucas et al. 2008).

## METHODS

### Study site

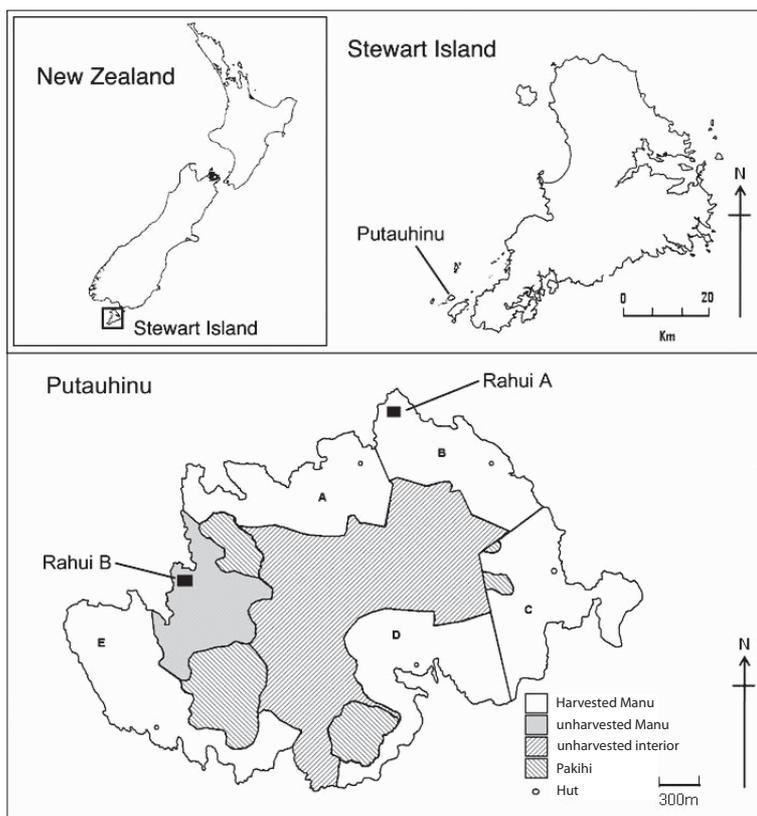
Consistent, multi-year monitoring of the tītī harvesting system has been undertaken on Putauhinu Island, New Zealand (46°45’S, 167°38’E; Fig. 1). The coastal region of the island consists of six manu, of which five are subjected to harvesting by individual whānau (families) (Fig. 1). The sixth manu has not been harvested for at least 30 years (Moller et al. 1999), so it was designated as non-harvested for the purposes of this study.

Vegetation in the island’s coastal region is dominated by tūpare (*Olearia lyalli*) and tētēaweka (*O. oporina*) forest, with the understorey either open or closed (dominated by several fern species and pūnui—*Stilbocarpa lyalli*). The interior of Putauhinu consists of a large, contiguous area of dense mixed vegetation and supports a lower-density tītī colony, which is not harvested. Several large areas of the cushion bog “pakihi” vegetation community (Johnson 1982) are present on the island and are not used by tītī for breeding. The vegetation communities on Putauhinu are described in detail by Johnson (1982).

### The harvesting system

The harvesting (“muttonbirding”) season begins on 15 March, when harvesters travel to the islands by boat or helicopter. Preparations are then made for

**Fig. 1** Map showing the location of Putauhinu, the layout of harvested and unharvested areas within the island, and the position of rahui (non-harvested) areas used to measure chick mass.



**Table 1** The size of sections on Putauhinu with details of the timing and intensity of tiff abundance sampling. For each section, plots are the total number of circular plots (3 m radius) used to estimate burrow entrance density, and transects are the total number of strip transects (2 m width, each containing 20 burrow entrances) prospected with a burrowscope to determine burrow occupancy.

Section	Year	Size (m <sup>2</sup> )	Plots ( <i>n</i> )	Transects ( <i>n</i> )
Manu A	2003	139 007	242	12
Manu B	2003	120 560	252	12
Manu C	2004	145 078	238	12
Manu D	2005	156 156	259	11
Manu E	2004	165 187	269	12
Unharvested manu	2003	99 155	159	10
Unharvested island interior	2005	459 183	239	–
Pākihi	–	71 746	–	–
Total	–	1 356 071	–	–

the harvest itself, which begins on 1 April. Between 1 April and c. 20 April (the “nanao” period) chicks are extracted from breeding burrows during the day using a flexible wire that is fed into the burrow. From c. 21 April until 31 May (the “rama” period) fledgling chicks are targeted at night when they emerge from burrows to exercise their wings, lose

down and fledge. Harvesters patrol track systems that cover the manu using torches to detect chicks. Procuring chicks is much more difficult during the nanao period than the rama and requires a high level of skill, so harvest during this period is generally lower. Whānau were present on each manu on Putauhinu during both harvest periods in each year

of our monitoring. Research authority to survey birded manu within the project was conditional on results remaining anonymous, so we refrain from linking the values for individual manu to their identities on maps or to link results to particular whānau. Accordingly the map key and Table 1 identifies the study sites as A–E, whereas Fig. 2–5 and Tables 4 and 5 designate areas I–V. The association between the alphabetical and numerical codes has been randomised.

### Monitoring chick abundance

We established transects in randomly-selected locations on three harvested and one unharvested manu in 1997, with an additional harvested manu added to the monitoring programme in 1999. There was no regular monitoring on the final harvested manu, but a survey of total population size and harvest was completed there in 2005. Each transect was defined as a 2 m wide strip containing 20 tītī burrow entrances; hence, the length of the transect depended on the entrance density. Aluminium stakes were placed at either end of each transect as permanent markers. Once established, all burrow entrances within the transect boundaries were counted and prospected with an infra-red burrowscope to determine burrow occupancy (Lyver et al. 1998). We defined a burrow entrance as any tunnel that extended for >20 cm in length.

We revisited each transect annually between 1996–99, and 2003–05, to measure burrow entrance density, burrow occupancy and chick density. If fewer than 20 burrow entrances were encountered on a transect when it was resurveyed, we extended the transect on its original orientation until it included 20 entrances. If more than 20 entrances were encountered, the transect remained the same length and all entrances were prospected.

Monitoring tītī abundance using a burrowscope is known to underestimate the true number of occupants present (Hamilton et al. 1998; Lyver et al. 1998). The distance of burrow occupants from the burrow entrance is a strong predictor of their detection using the burrowscope, and corrections incorporating a detection function based on this covariate have been shown to improve occupancy estimates (McKechnie et al. 2007). We calculated a manu-wide correction factor for burrowscope bias,  $\hat{K}$ , as

$$\hat{K} = \frac{n_T}{\sum_x \frac{n_x}{\hat{g}(x)}}$$

where  $n_T$  is the total number of chicks detected,  $n_x$  is the count of chicks at each distance increment (10 cm intervals), both pooled over all transects on the manu, and  $\hat{g}(x)$  is the detection probability at that distance, estimated using the linear-logistic detection function of McKechnie et al. (2007). The mean distance of chicks from the burrow entrance was similar between vegetation types (average difference of 1.8 cm over all manu in the year of establishment). We therefore pooled data across vegetation types when formulating correction factors.

The number of chicks on transect  $i$ , corrected for burrowscope bias, was calculated as  $N_{c,i} = N_{u,i}/K$  where  $N_{u,i}$  is the uncorrected count of chicks on transect  $i$ . Burrow occupancy (chicks per burrow entrance) was subsequently calculated as  $d_i = N_{c,i}/E_i$  where  $E_i$  is the number of burrow entrances prospected with the burrowscope on transect  $i$ . We calculated the density of burrow entrances (entrances per m<sup>2</sup>) on each transect  $i$  as  $e_i = E_i/A_i$  where  $A_i$  is the area of transect  $i$ . We calculated chick density on each transect by multiplying burrow occupancy and burrow entrance density  $c_i = d_i e_i$ .

### Estimation of the population available for harvesting

A full survey of each manu, involving more extensive sampling of burrow entrance density, was also undertaken, in a single season. Boundaries between manu are generally stable over time and often relate to landscape features (e.g., streams) which were shown to us by the manu owners. Boundaries between manu and the unharvested central region of the island (Fig. 1) were placed (at a distance of about 5 m) around the outside of all tracks that harvesters use to procure chicks on that manu. During surveys we subdivided the manu into between seven and 11 arbitrarily assigned strata; we attempted to keep the strata about equal in area within each manu, but they varied between manu owing to differences in the overall areas of the manu. Circular plots with a 3 m radius (28.27 m<sup>2</sup>) were randomly placed within each stratum, and were used to sample burrow entrance density. The number of plots sampled varied according to the size of the stratum and ranged between 8 and 48. The total number of plots on each manu is listed in Table 1.

Burrow occupancy estimates for the full manu surveys were obtained by pooling the long-term monitoring transects from the given manu in the appropriate year. Burrow occupancy estimates for the unharvested centre of the island were obtained by applying the mean occupancy over all surveyed

manu. The mean used for this extrapolation was calculated by weighting mean occupancy on each separate manu by manu area. The methods used to estimate population size were as follows.

We calculated population size on each individual manu in the season when the extensive sampling of burrow entrance density occurred. We initially calculated a mean density of burrow entrances in stratum  $j$  as

$$\bar{e}_j = \frac{1}{n_j} \sum_{k=1}^{n_j} e_{j,k}$$

where the  $e_{j,k}$  is the number of entrances per  $m^2$  observed on plot  $k$  in stratum  $j$  ( $k = 1, \dots, n_j$ ). We then calculated an estimate of the mean density of burrow entrances across the whole manu as

$$\hat{e} = \sum_{j=1}^m W_j \bar{e}_j$$

where  $W_j$  is the area of stratum  $j$  as a proportion of the total area of the manu ( $j = 1, \dots, m$ ). We estimated the mean number of chicks per burrow entrance as

$$\hat{d} = \frac{1}{p} \sum_{i=1}^p d_i$$

where  $d_i$  is the observed number of chicks per burrow entrance on transect  $i$  ( $i = 1, \dots, p$ ). We could then calculate the overall estimate of chick density (number per  $m^2$ ) on the manu, corrected for bias incurred from using a burrowscope for estimating population size, as

$$\hat{c} = \frac{\hat{e} \hat{d}}{\hat{K}}$$

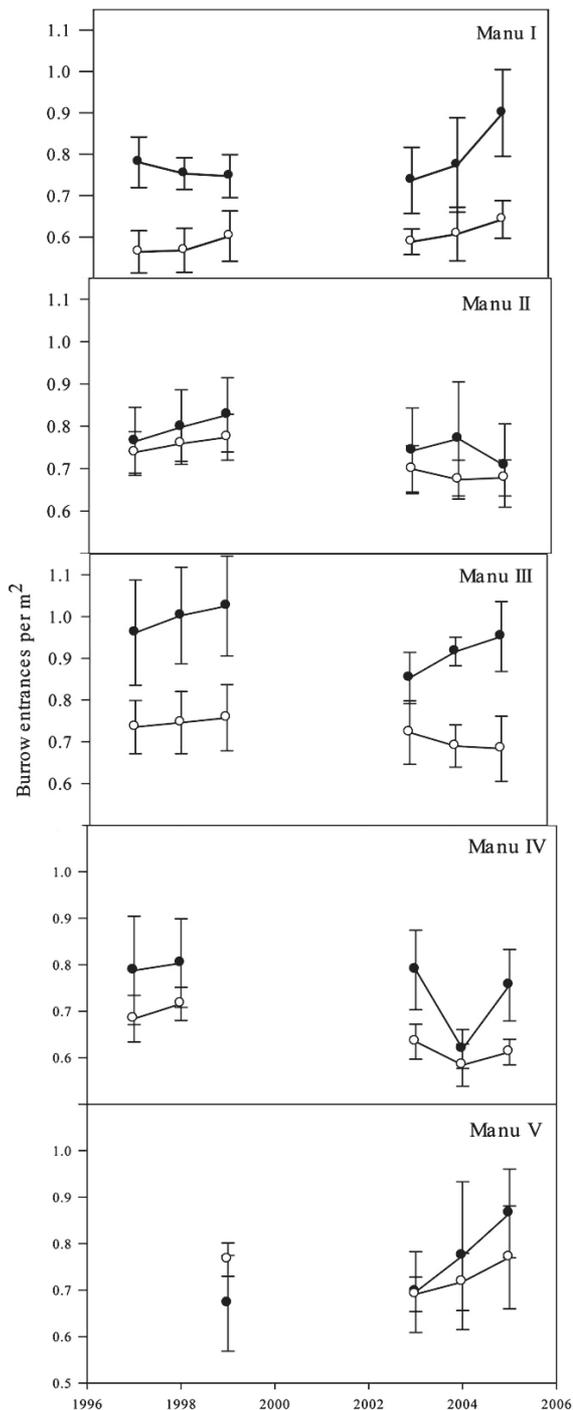
where  $\hat{K}$  is the manu-specific estimate of burrowscope bias described above. We estimated the total number of chicks on the manu as

$$\hat{N} = A \hat{c},$$

where  $A$  is the overall two-dimensional area of the manu.

As chick density could also be calculated for each year in which transects were monitored (1997–99 and 2003–05, on most manu) it was also possible to estimate the population size of chicks on the manu in these years. If we refer to the year when we carried out the survey of the entire manu as year 1, and year 2 refers to another year for which we had monitoring data for the transects, then we could estimate the relative change in chick density (uncorrected for burrowscope bias) at transect  $i$  between year 1 and year 2 as

$$r_i = \frac{e_{i2} d_{i2}}{e_{i1} d_{i1}}$$



**Fig. 2** Temporal changes in mean tītī burrow entrance density on transects with closed (closed circles) and open (open circles) understorey on five manu on Putauhinu, New Zealand. Error bars are standard errors.

where  $e_{i1}$  and  $e_{i2}$  are the densities of burrow entrances on transect  $i$  in years 1 and 2, respectively, and  $d_{i1}$  and  $d_{i2}$  are the chicks per burrow entrance on transect  $i$  in years 1 and 2, respectively. We could then calculate a “corrected” estimate of relative change in chick density as

$$\hat{R} = \frac{\hat{K}_1}{\hat{K}_2} \bar{r},$$

where  $\hat{K}_1$  and  $\hat{K}_2$  are the burrowscope correction factors for years 1 and 2 respectively, and  $\bar{r}$  is the mean of the estimates of relative change in uncorrected chick density over all transects on the manū. Chick density in year 2 ( $c_2$ ) could then be estimated from chick density in year 1 ( $c_1$ ) using

$$\hat{c}_2 = \hat{R} \hat{c}_1,$$

and we could estimate the total number of chicks in year 2 as  $\hat{N}_2 = A \hat{c}_2$ .

In the absence of three-dimensional estimates of the surface area of each manū, we used measurements of slope at each transect to correct for the negative bias incurred when relying on planar estimates. This assumes that slope measurements taken on transects provide a random representation of the actual slope of the manū. A corrected estimate of the population size in year 1, for example, would be

$$\frac{\hat{N}'_1 = \hat{N}_1}{\bar{b}}$$

where  $\bar{b}$  is the mean over all transects of  $b_i = 1/\cos(\theta_i)$ , and where  $\theta_i$  is the slope measured on transect  $i$  using an inclinometer. Planar areas were calculated from an aerial image of the island rasterised into a data layer in GIS software (Mapinfo) using reference GPS positions collected while surveying the island.

### Estimating harvest intensity

The total number of chicks taken from each manū every year was recorded by the muttonbirders. In the majority of cases, harvest tallies for every day of the birding season and the time spent hunting were recorded on prepared harvest record forms, but sometimes the information was restricted to a simple total number of chicks harvested for the season. Harvest intensity was defined as the proportion of the available number of chicks on the manū, prior to the onset of harvesting, that were taken by the harvester on that manū.

### Assessing differences in tītī density between vegetation types

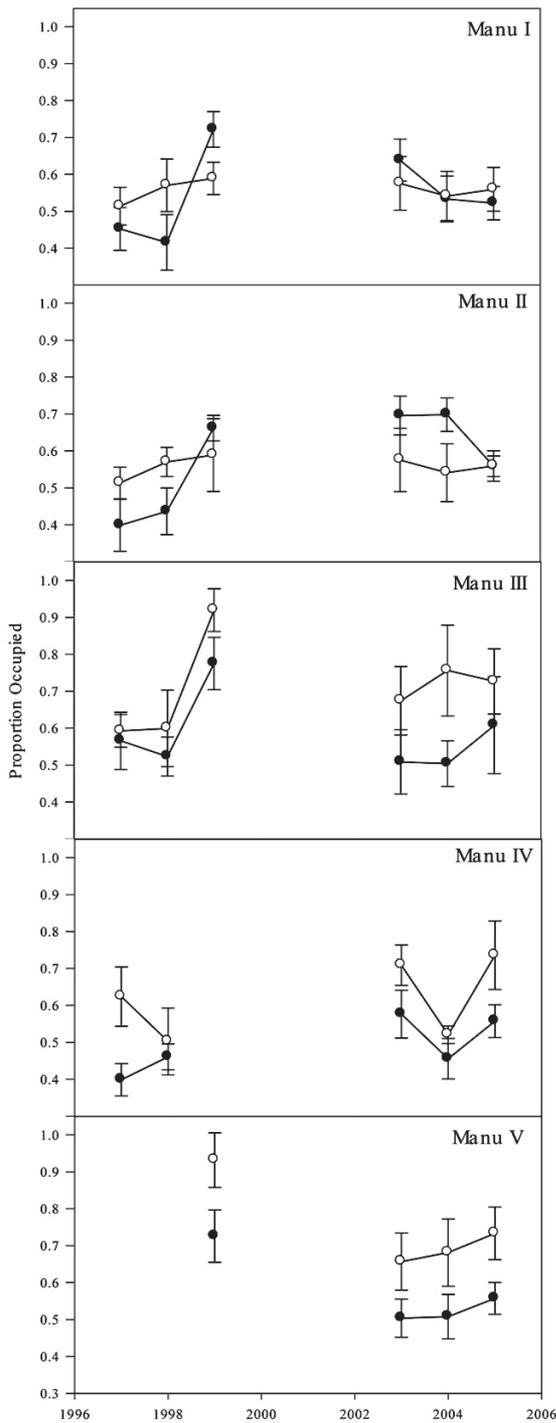
We tested the hypothesis that tītī density varies between two understorey vegetation types on

Putauhinu, using the transects established for long-term monitoring. Vegetation type was initially measured on each transect on four manū in 1998 (a fifth in 1999) and again in 2005 to assess any changes over the monitoring period. Sampling involved estimating the proportion of ground coverage of plant species within  $50 \times 20$  cm quadrats placed perpendicular to the transect centre line at each metre point. The side of the centre line on which the quadrat was placed alternated every metre, after being assigned randomly at the first sampling point. Vegetation cover was estimated as the proportion of the horizontal area between the ground surface and the quadrat held at chest height that was obscured by living vegetation. Transects were classified into the categories “closed” if the proportion of vegetation coverage (all plant species pooled) below chest height covered  $\geq 30\%$  of the transect area. Transects with less understorey vegetation cover than this threshold were classified as “open”. Differences in burrow entrance density (log transformed), burrow occupancy and chick density between the vegetation cover types were tested within each of the years 1996–99 and 2003–05, using two-way ANOVA with variables representing manū, and vegetation effects. Linear regression models were then fitted to the respective measurements for each individual transect over the monitoring period. Differences in slope of the regression lines were then tested using two-way ANOVA.

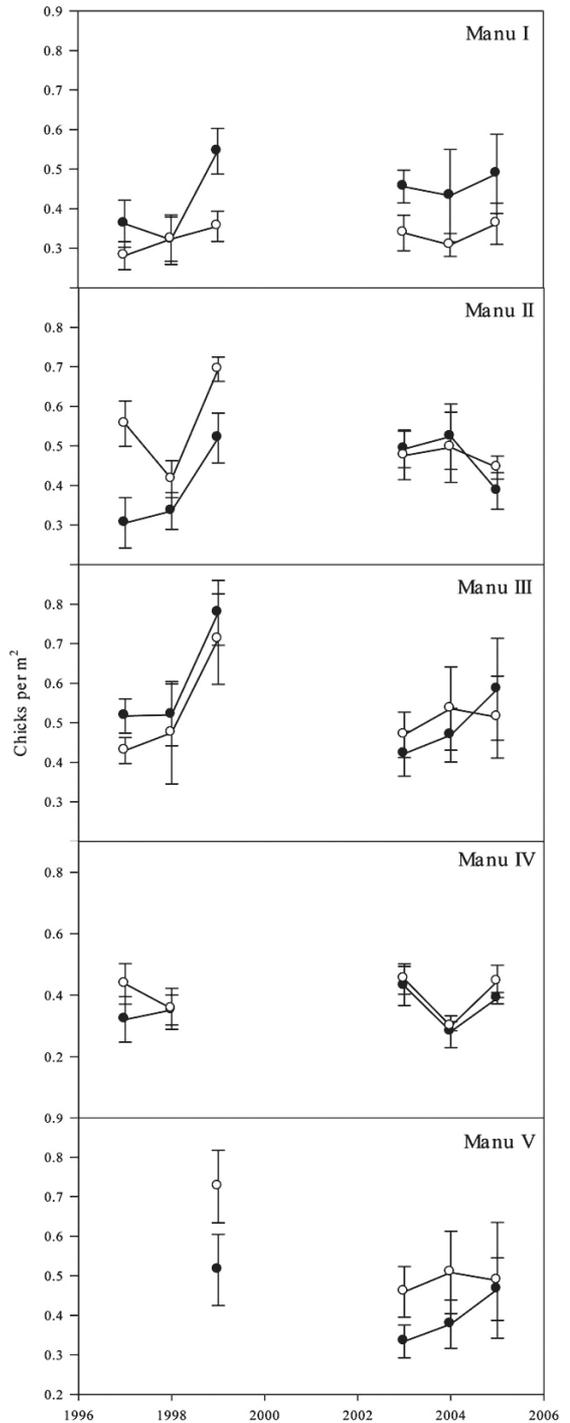
Changes in the understorey vegetation cover on Putauhinu were estimated in two ways. Firstly understorey vegetation cover on the transects was compared between the initial survey in 1998 and the resurvey in 2005. Broad changes in vegetation cover at the manū scale were also tested using data from the wider survey. The proportion of an individual manū that was covered by “open” or “closed” understorey vegetation (using the same  $\geq 30\%$  threshold) was estimated on four manū in 1998 using the proportion of circular plots (3 m radius) falling into each category. These estimates were then compared with the proportion of circular plots in each category during the wider surveys of burrow entrance density undertaken on individual manū between 2003 and 2005.

### Measuring temporal changes in chick mass

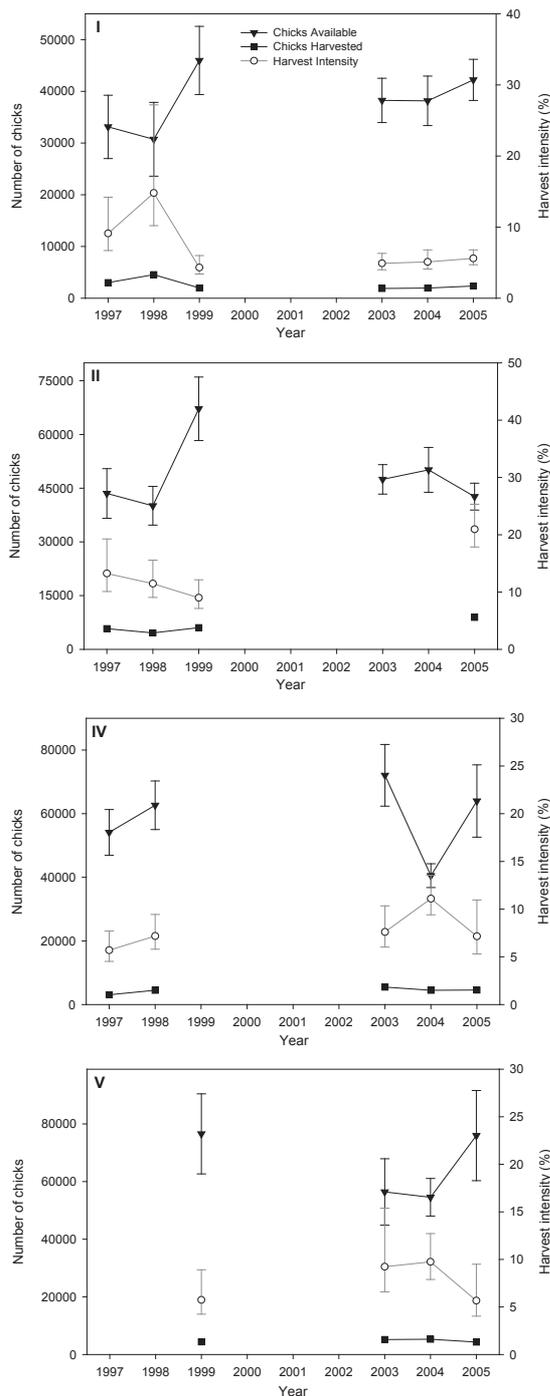
We measured chick mass annually between 1998 and 2005 at two sites designated as “rahui” (harvest prohibited areas). Sixty plywood or ceramic tile inspection hatches were placed over sooty shearwater nesting chambers at both Rahui A (c.  $45 \times 25$  m)



**Fig. 3** Temporal changes in mean tītī burrow occupancy on transects with closed (closed circles) and open (open circles) understorey on five manua on Putauhinu, New Zealand. Error bars are standard errors.



**Fig. 4** Temporal changes in mean tītī chick density on transects with closed (closed circles) and open (open circles) understorey on five manua on Putauhinu, New Zealand. Error bars are standard errors.



**Fig. 5** Temporal changes in the mean number of tūī chicks available, number harvested and harvest intensity (proportion of available chicks harvested) on four manu on Putauhinu between 1997 and 2005. Error bars are standard errors.

and Rahui B (c.  $60 \times 40$  m; Fig. 1), to allow easy access to chicks for measuring. The sites were visited between 15 and 20 April each year, except 2003, in which logistical constraints required measurements to be undertaken slightly later, on 26 and 27 April for Rahui A and B respectively. The visits were timed to determine the quality of chicks in the harvest season, before any chicks were likely to have left their breeding burrow. We removed individual chicks from the nesting chamber during the day and weighed them to the nearest 10 g, using 2 kg Pesola scales. The  $\alpha$  level for all confidence intervals and statistical tests was set at 0.05.

## RESULTS

### The influence of vegetation type on tūī density

Mean burrow entrance density was higher in transects with closed understorey vegetation (“closed transect”) than in transects with an open understorey (“open transect”) on four of the five manu when transects were established and differences remained consistent throughout the monitoring period (Table 2, Fig. 2). After the initial year, higher densities were also detected on closed transects on the fifth manu. There was no evidence of any differences between closed and open transects in the slopes of regressions of entrance density against successive years over the monitoring period (Table 2), so differences in entrance between vegetation types probably remained stable over our study period.

Burrow occupancy was higher on open than closed transects on each manu in 1997. These differences remained over the monitoring period and occupancy was still statistically significantly higher on open transects in 2005 (Fig. 3, Table 2). Only minor differences were observed between closed and open transects in the slopes of regressions of occupancy over the monitoring period (Table 2). Although there were differences in chick density between closed and open transects, the nature of these differences varied between the individual manu. The magnitude of these differences was generally lower than for the other abundance measures, and had an increased tendency for the relationship to change over the monitoring period (Fig. 4). The slope of regressions of chick density over the monitoring period were similar between open and closed understorey vegetation types (Table 2).

In 1998 the mean ground cover on closed transects was 51% (SD = 18%,  $n = 25$ ) and 0.9% (SD = 2.8%,

$n = 29$ ) on the open transects. There were significant changes in the ground cover within transects between 1998 and 2005 (Table 3). The direction of these changes differed, depending on the transect's original vegetation class, but not manu (Table 3). Ground cover decreased dramatically on the closed transects ( $-39\%$ ,  $SD = 12\%$ ,  $n = 21$ ) and increased on the open transects ( $+16\%$ ,  $SD = 12\%$ ,  $n = 26$ ) over this time. All transects had similar ground cover by 2005, regardless of their initial classification (open transects  $17\%$ ,  $SD = 12\%$ ,  $n = 27$ ; closed transects  $12\%$ ,  $SD = 12\%$ ,  $n = 28$ ).

The proportion of manu consisting of the closed habitat type varied between 0.50 and 0.89 on the different manu (Table 4), with the amount remaining relatively stable over the study period at three out of the four manu surveyed (Table 4). At the fourth (manu IV) the proportion of circular plots classified as closed declined by 0.2 (log likelihood ratio goodness of fit test statistic,  $G = 21.00$ ,  $P = <0.001$ ; Sokal & Rohlf 1995).

**Population size and harvest intensity in 2005**

Our overall three-dimensional surface area estimate for Putauhinu is  $1\,356\,071\text{ m}^2$ . However, approximately 5% of this area ( $71\,746\text{ m}^2$ ) consists of the cushion bog "pākihi" vegetation community (Johnson 1982), which is not used by tītī for breeding. The estimated surface area of all sooty shearwater breeding habitat, including the unharvested interior, was  $1\,284\,325\text{ m}^2$ . The sizes of individual manu varied between  $99\,154$  and  $165\,187\text{ m}^2$ , and the unharvested centre was estimated to be  $445\,640\text{ m}^2$  (Table 1).

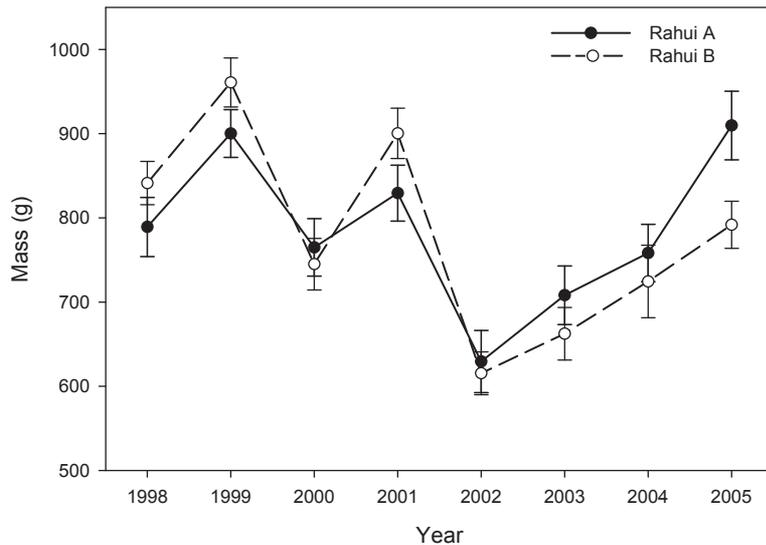
Mean chick densities on the six manu in 2005 varied between 0.31 and 0.46 per  $\text{m}^2$ , while the density in the unharvested centre was considerably lower at 0.12 per  $\text{m}^2$  ( $95\% \text{ CI} = 0.10\text{--}0.14$ ). This resulted in a population size of chicks of 275 905 ( $\text{CI} = 196\,789\text{--}355\,021$ ) on the harvested manu and 373 601 ( $\text{CI} = 272\,821\text{--}474\,381$ ) for the island as a whole (Table 5).

Twenty-six harvesters present on the island in 2005 took 31 280 chicks in total or 11% ( $\text{CI} = 8.8\text{--}16\%$ ) of the available chicks on the five harvested manu. Once the unharvested ground is included, overall 8.4% ( $\text{CI} = 6.6\text{--}12\%$ ) of the chicks available on Putauhinu in 2005 were harvested. On average, 6256 chicks

**Table 2** Results of two-way ANOVA testing differences in tītī abundance between manu and vegetation cover type each year between 1997–99, and 2003–05, and differences in the slope of regressions between vegetation cover types over the entire monitoring period, on four manu on Putauhinu. Values in brackets are degrees of freedom.

Source	1997		1998		1999 <sup>a</sup>		2003		2004		2005		Slope	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Entrance density														
Manu	1.41(3)	0.256	2.19(3)	0.110	3.37(2)	0.049	0.99(3)	0.409	2.13(3)	0.113	1.21(3)	0.320	1.72(3)	0.180
Vegetation	6.04(1)	0.019	4.01(1)	0.055	5.34(1)	0.028	5.68(1)	0.022	4.07(1)	0.051	11.31(1)	0.002	0.02(1)	0.895
Manu × veg.	0.65(3)	0.589	1.06(3)	0.383	1.00(2)	0.381	0.28(3)	0.842	0.51(3)	0.680	1.03(3)	0.392	0.06(3)	0.982
Error	(38)		(29)		(28)		(38)		(36)		(36)		(36)	
Occupancy														
Manu	0.98(3)	0.411	0.51(3)	0.679	4.13(2)	0.027	1.34(3)	0.277	5.90(3)	0.002	2.10(3)	0.117	1.93(3)	0.143
Vegetation	13.56(1)	0.001	2.95(1)	0.096	3.84(1)	0.060	1.62(1)	0.211	3.22(1)	0.081	4.46(1)	0.042	0.00(1)	0.996
Manu × veg.	2.30(3)	0.092	0.46(3)	0.712	7.00(2)	0.003	2.17(3)	0.107	1.32(3)	0.285	0.75(3)	0.527	0.06(3)	0.982
Error	(39)		(30)		(28)		(38)		(36)		(36)		(35)	
Chick density														
Manu	2.25(3)	0.098	2.01(3)	0.134	8.15(2)	0.002	1.61(3)	0.202	4.67(3)	0.007	1.31(3)	0.285	0.60(3)	0.621
Vegetation	1.32(1)	0.257	0.21(1)	0.653	0.19(1)	0.667	0.07(1)	0.798	0.02(1)	0.889	0.23(1)	0.631	0.39(1)	0.537
Manu × veg.	3.44(3)	0.026	0.20(3)	0.896	4.02(2)	0.029	1.66(3)	0.193	0.65(3)	0.591	0.81(3)	0.496	1.32(3)	0.284
Error	(38)		(29)		(28)		(38)		(36)		(36)		(36)	

<sup>a</sup>Values for manu V in the early period were measured in 1999.



**Fig. 6** Annual changes in mean mass (g) of tītī chicks in burrow at two rahui (non-harvested) sites just prior to fledging, between 1998 and 2005. Error bars are standard errors.

**Table 3** Results of a two-way ANOVA testing the change in ground cover on transects from five manu between 1998 and 2005. Transects were classified as either open or closed habitat based on their percentage ground cover in 1998.

Source	d.f.	<i>F</i>	<i>P</i>
Manu	4	0.45	0.771
Habitat	1	83.44	< 0.001
Manu × habitat	4	0.37	0.826
Error	37		

were harvested per individual manu in 2005 (CI = 1746–11 103). Harvest intensities on individual manu varied considerably, but averaged 12% (CI = 1.8–17%) in 2005, with minimum and maximum values across individual manu of 4.3 and 22%, respectively, over the monitoring period.

#### Temporal variation in chick availability, chick size and harvest intensity

Moderate fluctuations in the number of chicks available for harvesting were observed on each manu (CV = 15–22%) across the monitoring period and was relatively synchronous across manu (Fig. 5). The 1999 breeding season in particular appeared to be favourable for chick numbers on most manu. Although the number of chicks taken on each manu also showed variation (CV = 11–39%; Fig. 5), fluctuations in this variable did not appear to correspond closely with the number of chicks

available (Fig. 5), nor the size of the chicks measured under inspection hatches. Harvest intensity differed substantially between years (CV = 26–56%; Fig. 5), as a consequence of variation in both the magnitude of the harvest and the number of chicks available.

Substantial temporal variation in chick mass was detected at both rahui sites (Fig. 6; Rahui A, CV = 12%; Rahui B, CV = 15%). Variation in mass was highly correlated between the two rahui sites ( $r = 0.84$ ,  $P = <0.01$ ). The highest average mass was observed at Rahui B in 1999 (mean = 961 g, SD = 170,  $n = 34$ ) and the lowest mass in 2002, also at Rahui B (mean = 615 g, SD = 153,  $n = 36$ ).

## DISCUSSION

### The influence of vegetation on tītī abundance measures

Our results do not support the TEK construct of many muttonbirders that differences in sooty shearwater chick abundance measures exist between vegetation types. No consistent overall difference in chick abundance was found between open and closed habitats, though occupancy was higher in open areas. Counteractive differences in the two measures that multiply to give chick density, namely burrow entrance density and burrow occupancy, lead to evening out in chick abundance between habitats. This result also contradicts the general premise that thick vegetation cover precludes breeding by

seabirds (Warham 1990), and the negative correlation observed between ground cover and tītī abundance on other Tītī Islands (Charleton et al. in press; Moller et al. 2009c). However, the coarseness of our division into open and closed transects, coupled with overall low ground cover (average 51%) could have obscured detection of such an exclusion effect in extremely densely vegetated micro-sites. Collectively, our studies have revealed only weak and sometimes inconsistent predictive models between vegetation, habitat and location factors and burrow entrance density (Newman et al. 2008; Scott et al. 2008). Relationships between burrow entrance density and site-specific vegetation and location factors are complex, and present challenges for predictive modelling. Lack of concordance between TEK and our science result in this instance is unusual—more normally science and TEK have agreed strongly about what is happening, even though they often differed on why a particular pattern was observed (Newman & Moller 2005). In this case, it could be that the birders based their judgement on burrow occupancy being higher in open ground while not

fully compensating for the overall lower entrance density there.

Tītī are proficient at burrowing and rapidly form new burrows if the ground is disturbed (McKechnie et al. 2008), but the presence of ground vegetation may facilitate burrow entrance formation and burrow persistence. Entrances were often observed against the raised base of ground ferns. This supports the notion that petrels, where possible, use depressions in the ground to initiate burrowing. Sooty shearwaters often dig a circular burrow completely around the base of the ferns predominating on Putauhinu. Multiple entrances are present in these short lengths of burrow, whereas wide and open “gallery” spaces are created in open ground without ferns present, especially in locations with high tītī density, such as The Snares (Hamilton et al. 1998; McKechnie et al. 2007).

Mean burrow occupancy was lower in closed than open transects on all manu in the year monitoring was initiated. Beyond that year the relationship showed some variation, although on three of the manu this difference remained consistent. Due to

**Table 4** Change in proportion of circular plots classified as closed ( $\geq 30\%$  vegetation cover below chest height) between the early and late stages of tītī monitoring on four manu on Putauhinu. *G* is the test statistic of the log likelihood ratio test of goodness of fit (Sokal & Rohlf 1995).

Manu	Start of study			End of study			<i>G</i>	<i>P</i>
	Year	Proportion closed	<i>n</i>	Year	Proportion closed	<i>n</i>		
I	1998	0.63	153	2003	0.62	242	0.05	0.815
II	1998	0.54	151	2003	0.59	229	0.87	0.350
IV	1998	0.89	157	2004	0.69	238	21.00	< 0.001
V	1999	0.50	108	2004	0.46	261	0.40	0.525

**Table 5** Summary of the population size of tītī burrow entrances and chicks magnitude on different sections of Putauhinu in 2005. Bounds are the lower and upper 95% confidence limits.

Section	Entrances	Lower bound	Upper bound	Chicks	Lower bound	Upper bound
Manu I	77 321	65 501	89 140	42 216	34 432	50 000
Manu II	66 946	60 264	73 627	42 648	35 297	49 998
Manu III	53 254	44 956	61 553	36 876	26 331	47 421
Manu IV	97 116	83 417	110 814	63 987	41 720	86 255
Manu V	113 938	82 771	145 104	75 971	45 305	106 638
Manu VI	98 464	82 784	114 143	51 082	40 035	62 130
Unharvested interior	102 140	88 084	116 197	60 821	49 702	71 939
Total	609 178	507 777	710 579	373 601	272 821	474 381

restrictions on when we could visit the island, it is not possible to attribute the lesser burrow occupancy in the closed habitat to fewer breeding attempts, and/or lower breeding success through to the late chick stage, than in the open habitat. Furthermore, we can only speculate on the mechanisms driving these differences. Sites supporting ground cover vegetation, especially the dominant fern (*Polystichum vestitum*), are likely to be associated with high soil moisture levels. Wet soils and risk of flooding are important determinants of breeding success in burrow-nesting seabirds (Warham 1990; Thompson & Furness 1991).

The relationships between chick abundance measures and vegetation type remained relatively constant throughout the monitoring period, despite marked changes in actual vegetation cover. Vegetation cover increased at the open sites and decreased at the closed sites during our study. This suggests that vegetation is not directly influencing chick abundance. It is more likely that the ecological factors that promote high vegetation coverage during some part of the successional vegetation cycle also influence local abundance at that time.

#### Population size and harvest intensity

The population on Putauhinu appears to be of moderate size for this species, and the second largest on the Rakiura Tītī Islands. Extrapolation from surveys of six manu on Taukihepa (Big South Cape Island) between 1999 and 2005 suggests that it has 147 000 to 188 000 burrow entrances (Newman et al. 2008), at least twice as many as we estimate are on Putauhinu. Lyver (2000) estimated that there were 93 002 (64 544–124 930) and 97 942 (77 962–119 993) chicks available for harvesting on Poutama Island in 1994 and 1995 respectively. Chick densities in that study were lower than those observed on the harvested manu on Putauhinu, and Poutama Island is also considerably smaller (60 ha). Whenua Hou (Codfish island) is much larger than Putauhinu, but even its coastal fringe has low entrance density, so its total number of sooty shearwater burrow entrances (206 000–386 000; Scott et al. 2009, this issue) was about half that on Putauhinu. The largest colony in the New Zealand region is at Northeast Island, The Snares, where about 2 061 000 burrow entrances were estimated to occur (Scott et al. 2008). A recent estimate of about 4 million breeding pairs nesting on Guafo Island, Chile (Reyes-Arriagada et al. 2007) is larger again, and indicates the potential for very large populations in South America which have been little explored by seabird biologists.

Overall, harvesters on Putauhinu took about 11% (CI = 9–16%) of the chicks available on the harvested manu. This is lower than the only other published estimates of 13–24% (15 722 chicks) and 17–28% (22 092 chicks) of chicks taken on Poutama in 1994 and 1995 (Lyver 2000), and 16–21% (105 000 to 173 000 chicks) on Taukihepa (Newman et al. 2008). However, harvest intensity on Putauhinu may be somewhat overestimated, because it does not account for chicks originating in the unharvested centre of the island that are then caught while they migrate through the manu to fledge on the coast. If we consider Putauhinu tītī to consist of a single mictic population, then about 8% (CI = 7–12%) of the total population of chicks was harvested in 2005. Refugia, such as impenetrable patches of vegetated ground within manu, the unharvested centre of the island, some small unharvested islets, will collectively ameliorate localised impacts of harvesting on shearwater density because density-dependent immigration is probably triggering replenishment of depleted areas of manu (Moller et al. 2009d this issue).

#### Temporal variation in chick numbers and harvest intensity

Considerable fluctuations in the number of chicks available for harvesting were detected on all manu. In the most extreme case, the minimum number of chicks present on a manu in 1998 was just 67% of the maximum number observed in the same manu in 1999. There was also substantial variation in the number of chicks harvested by each whānau annually. There was little relationship between harvest and either the abundance or size of available chicks.

Given the variation in chicks available and harvest, it is obvious that variation in harvest intensity will be magnified. Sustainable management of harvesting is more difficult when the resource abundance and harvest intensity fluctuates between seasons (Lande et al. 1995; Engen et al. 1997; Milner-Gulland & Akcakaya 2001). Fortunately, on Putauhinu harvest generally represents a relatively small proportion of the available population. Moreover, harvesting focuses on a life-history stage (chicks) to which population growth rate exhibits low sensitivities and elasticities (Hamilton & Moller 1995; Hunter et al. 2000b; Saether & Bakke 2000; Hunter & Casswell 2005). Research focus will now be directed at combining these estimates of harvest magnitude and temporal variance with demographic models of tītī population dynamics so that the sustainability of current harvests can be assessed.

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