

Estimates of productivity and detection probabilities of breeding attempts in the sooty shearwater (*Puffinus griseus*), a burrow-nesting petrel

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Abstract. Monitoring of breeding success in burrow-nesting seabirds is problematic, owing to the difficulties of detecting occupants in complex burrow systems. We summarise 6 years of monitoring the breeding success of sooty shearwater (tīti, muttonbird, *Puffinus griseus*) on two southern New Zealand islands, The Snares and Whenua Hou, with a portable infrared camera system. Breeding attempts were monitored three times during the breeding season, i.e. egg laying, hatching and fledging. Overall breeding success was calculated in two stages. First, we estimated breeding success for each island–site–year combination with a model that allowed for imperfect detection of an egg or chick and accounted for the proportion of the breeding season that was covered by monitoring. The resulting estimates for each island were then analysed with a linear model, to provide a single estimate for that island. Breeding success was found to be highly variable and non-synchronous between islands, with the average proportion of eggs successfully fledging on The Snares (0.35, 0.20–0.52; mean and 95% creditable interval) being considerably lower and more variable than that on Whenua Hou (0.76, 0.70–0.82). Probability of detecting a breeding attempt was higher on The Snares whereas correcting for the proportion of the season monitored had a variable effect, reducing The Snares and Whenua Hou estimates by 27% and 7% respectively. The implications of these findings with respect to the demographic modelling of burrow-nesting species are discussed.

Introduction

Knowledge of the magnitude and variability of annual reproductive output is crucial for understanding the dynamics of any wildlife population. For seabirds, measuring annual breeding success is an integral part of most long-term population-monitoring programs and some form of reproductive rate is typically reported for most studies. For many petrel species, a large amount of variability in breeding success has been reported among breeding seasons, geographic locations, colonies and even individual breeding pairs (Wooller *et al.* 1992; Cobley *et al.* 1998; Furness and Tasker 2000; Cuthbert and Davis 2002; Dunlop *et al.* 2002; Jenouvrier *et al.* 2003). Chick mortalities can be attributed to a range of factors such as nest flooding, predation, by-catch of parents, conspecific disturbance, parental quality, lack of food supply, climate, habitat and observer-related disturbance effects (Thompson and Furness 1991; Carter 1997; Inchausti *et al.* 2003; Jones *et al.* 2003; Nel *et al.* 2003; Smithers *et al.* 2003; Blackmer *et al.* 2004; Priddel *et al.* 2006).

Accurate reporting the proportion of all eggs laid that successfully depart as fledging chicks from a colony is particularly problematic in burrow-nesting species where an egg-laying event or unsuccessful fledging may easily miss detection. Furthermore, exact definitions of breeding success

vary significantly, making direct comparisons among studies difficult. Increasingly, studies use burrowscopes to follow the fate of nesting attempts; however, detection of occupants is often imperfect and reliant on observer ability (Cuthbert and Davis 2002; McKechnie *et al.* 2007). Often issues of detectability are either ignored (Major *et al.* 2006) or compensated for in a rudimentary manner, e.g. Granadeiro *et al.* (2006) estimated tentatively that they missed 15% of breeding attempts when searching Cory's shearwater (*Calonectris diomedea*) colonies and subsequently corrected the estimates of breeding success for this error. The burrows of sooty shearwater can be long (regularly >2 m), convoluted, branched and interconnected (Hamilton 2000; McKechnie 2004). This observed complexity has led to concern over potential bias in correctly determining occupancy, either by missing or double-counting individual breeding attempts. McKechnie *et al.* (2007) investigated the ability of the burrowscope to correctly detect breeding attempts and showed that it rapidly decreases with increasing distance between the occupant and the burrow entrance; we make use of this estimated 'detection function' in our analysis.

Additionally, studies often report only partial breeding rates such as hatching or fledging success and few studies have reported the fate of eggs from laying to fledging, using large long-term

datasets (Warham 1990). Estimates of breeding success are often acknowledged to be biased towards high values because monitoring fails to cover the entire breeding period (Major *et al.* 2006; Wrege *et al.* 2006), although some do attempt to compensate for this issue. For example, Granadeiro *et al.* (2006) assumed 25% of Cory's shearwater clutches had already been lost before their first check early in the incubation stage, owing to high estimated losses at that time (32%). As a consequence of these issues, studies of the breeding success of burrowing seabirds are potentially constrained by inaccurate and imprecise estimates that provide poor resolution and low statistical power. In the present study, we report improved breeding success calculated after correction of burrowscoping data for known detection biases and to allow for the proportion of the breeding season covered by the monitoring period.

The chicks of sooty shearwater (typically referred to as 'tūū' or 'muttonbirds', although these names are synonymous with those of several other medium-sized petrels that have been historically harvested in New Zealand) are exclusively harvested at or just before fledging by Rakiura Māori, New Zealand's southernmost Māori tribe, as one of the few large-scale customary harvests remaining in New Zealand today, and are the subject of a long-term research partnership between Rakiura Māori and the Department of Zoology at the University of Otago (Moller *et al.* 1999). A key component of the program is the monitoring of the populations of sooty shearwater in areas with and without harvesting, to detect temporal trends and estimate key demographic parameters of the population. These will be used to construct baseline unharvested-population models and to then test various management scenarios relating to the cultural harvest. Estimating the key demographic parameters of the population in long-lived vertebrates such as the sooty shearwater is reliant on long-term monitoring programs because of the importance of estimating temporal variation. This information was not readily available at the instigation of the research project, so a preliminary population model was constructed with parameter estimates from a long-term study (50+ years) of the short-tailed shearwater (*Puffinus tenuirostris*), a closely related species (Hunter *et al.* 2000). Elasticity analysis of this early model indicated that correct estimation of breeding success is of intermediate importance in terms of the model's ability to accurately predict population dynamics. Breeding success was ranked third among the 12 parameters when 5% mortality was used in an elasticity analysis (Hunter *et al.* 2000). However, the importance of breeding success is elevated when considered in terms of management options, because the two higher-ranked parameters (breeder survival and probability of staying to breed) are both parameters that are not so conducive to manipulation for management (or experimental) purposes.

We report here on the variability in breeding success of sooty shearwater colonies on two unharvested southern New Zealand islands (The Snares and Whenua Hou/Codfish Island) measured across a 9-year period between 1997 and 2005. The specific objectives of the study were to (i) evaluate the effectiveness of correction factors to improve overall breeding-success estimates, and (ii) gain baseline information on breeding success in sooty shearwater populations, including quantifying the variability in breeding success between years and islands.

Methods

Study sites and sampling design

Several long-term study sites were established on North-east Island in The Snares group (280 ha, 48°01'S, 166°36'E) located ~75 km to the south of Rakiura (Stewart Island) and Whenua Hou (1396 ha, 46°45'S, 167°38'E), located approximately 4 km off the north-east coast of Rakiura (Fig. 1), in southern New Zealand. Both islands are free of introduced predator species. Study plots (containing ~100 breeding pairs) and permanent transects (2-m-wide strips containing 20 burrow entrances) were established on both islands. Permanent plots were established on The Snares (four plots) and Whenua Hou (three plots) in 1997. The plots on Whenua Hou encompassed almost entirely three known colonies close to the Sealers Bay hut whereas the four plots on The Snares were randomly located within ~300 m of the research hut and within the extensive colony that covers the island. In all, 48 transects were established randomly over the wider island on The Snares and a further 15 transects within known colonies on Whenua Hou. These sites were monitored with variable effort across three breeding seasons on The Snares and six breeding seasons on Whenua Hou (Table 1).

Monitoring breeding attempts

Sooty shearwaters lay a single egg, in late November/early December, following a 2–3-week partial exodus (or 'honeymoon') from the colony (Warham 1990). Eggs typically hatch in mid- to late January, with chicks fledging in late April or May (Heather and Robertson 1996). Three main stages for checking burrows were identified as part of the monitoring design. The 'egg' stage (checked after laying was assumed to

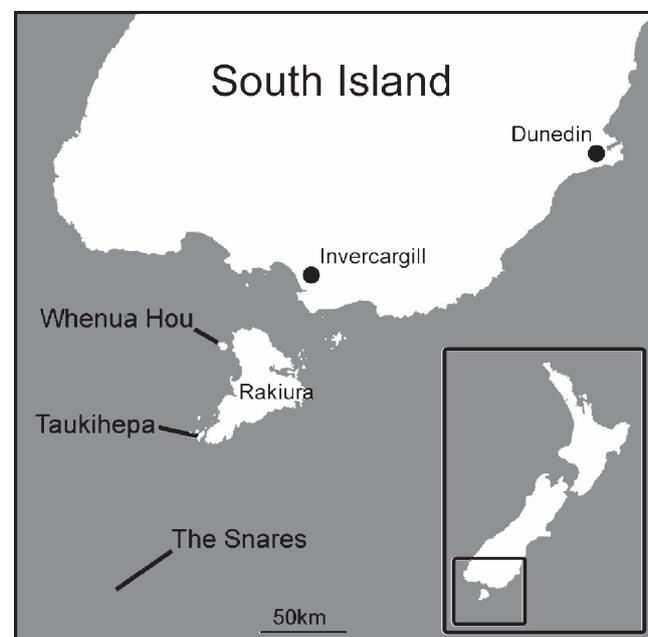


Fig. 1. Location of the islands in southern New Zealand, where breeding attempts of sooty shearwaters were monitored.

Table 1. Number of breeding attempts monitored for each site-year combination on The Snares and Whenua Hou between 1997 and 2005

The Snares			Whenua Hou								
Year	Site	Breeding attempts	Year	Site	Breeding attempts						
1997	A	257	1997	A	78						
	Fern	143		Tran	112						
	Open	241		Total	190						
	Poa	206		1998	A	73					
	Total	847			B	52					
1998	A	113	1998	C	52						
	Fern	62		Tran	111						
	Open	173		Total	288						
	Poa	104		1999	A	63					
	Total	452			B	51					
1999	A	52	1999	C	24						
	B	123		Tran	86						
	C	27		Total	224						
	D	38		2003	A	82					
	Total	240			B	60					
						C	78				
						Tran	74				
						Total	294				
						2004	A	93			
							B	40			
C			50								
2005			Tran			88	2005	A	115		
			Total			271		B	58		
						A		88		C	88
						Tran		104		Tran	104
	Total	365	Total	365							
Grand total		1539	Grand total		1632						

be completed but before hatching started – from the earliest date a survey team started monitoring each season until 3 January), ‘chick’ stage (checked as soon as practically possible once hatching was completed – between 16 January and 18 February) and ‘fledging’ stage (checked as late in the season as possible but before chicks began to emerge from burrows – between 26 March and 20 April). Some stages were not checked in every year and a minimal number of checks fell outside the planned dates. Table 1 summarises the sampling effort across the 9 years of the study on The Snares and Whenua Hou. The lowest number of breeding attempts monitored on either island in any year was 224 and, in total, >1500 breeding attempts were monitored on each island during the duration of the study.

Nest checks were made with a burrowscope – a camera with infrared lights mounted on the end of a 3-m tube which is inserted into burrows to detect adults, eggs and chicks (for a more complete description of this technique see Lyver *et al.* (1998)). Where possible, all entrances within the site were checked for occupants, regardless of whether or not an occupant was recorded in prior checks, although on some occasions site checks were incomplete or limited to only rechecking known breeding attempts because of unforeseen circumstances, or time or logistical constraints.

Reproductive rates defined

Hatching Success (HS) was defined as the probability that an egg eventually hatched. *Fledging Success (FS)* was defined as the probability that a hatched chick eventually fledged. *Breeding Success (BS)* was defined to be the product of *HS* and *FS*, i.e. the probability that an egg eventually became a fledged chick.

Data sorting and interpretation

Data were sorted by the individual burrow number and then scored as either containing a detected breeding attempt (‘1’), searched but nothing found (‘0’) or not checked (‘X’) for each of the three stages within each season to create individual breeding histories. Because some burrows were not checked in all three stages and some occupants were missed when burrows were checked, breeding histories such as 010 or X11 were possible, and sometimes recorded. No ‘back-corrections’ were made for any detection of a breeding attempt with the burrowscope at a later stage. This potential bias was corrected for the analysis described below.

Analysis

The first stage involved modelling the observed ‘detection histories’ for all the burrows, with a model similar to those employed in the analysis of mark–recapture data (Pollock *et al.* 1990). For each combination of site and year on an island, this involved specifying the probability of each distinct detection history, in terms of *HS*, *FS* and the probability of detecting an egg/chick, given that an egg/chick was present in the burrow. This probability was specified to be a linear-logistic function of the mean distance to the occupant, across all stages for which this distance was recorded. When no occupant was detected, this distance could not be recorded. We are therefore assuming that any occupant of a burrow was at the same distance from the entrance during every stage. Furthermore, the intercept and slope of this ‘detection function’ were both allowed to vary across the three stages (egg, hatching, fledging), as well as across sites and years. The work of McKechnie *et al.* (2007) provided us with prior information on the intercept and slope of this detection function. This information was readily incorporated into our analysis by adopting a Bayesian approach, with all calculations being carried out in Winbugs (Lunn *et al.* 2000). One can incorporate prior information by using a likelihood framework, whereas Bayesian methods naturally allow for the use of prior information, and we would expect the two approaches to lead to very similar results.

We illustrate the model for site *i* and year *j*, by considering the detection history 101, i.e. a burrow where we detected an egg, did not detect a chick at the hatching stage, but did detect one at the fledging stage. Suppose that the mean distance to an occupant in this burrow was *x*. As we are only considering those burrows where we detected an egg or chick at least once, the probability of this history can be written as

$$\Pr(101, i, j, x) = p_1(i, j, x) s_1(i, j) (1 - p_2(i, j, x)) s_2(i, j) \times p_3(i, j, x) / (1 - \Pr(000, i, j, x)),$$

where the notation is as follows:

$s_1(i, j)$ = probability that an egg hatches (*HS*),

$s_2(i, j)$ = probability that a hatched chick fledges (*FS*),

$p_1(i, j, x)$ = probability that an egg is detected, given that one is present at a distance x from the entrance of the burrow,

$p_2(i, j, x)$ = corresponding probability for the hatching stage, and

$p_3(i, j, x)$ = corresponding probability for the fledging stage.

The probability of not detecting an egg or chick at any stage is given by

$$\begin{aligned} \Pr(000, i, j, x) &= (1 - p_1(i, j, x))(1 - s_1(i, j) + s_1(i, j)) \\ &\quad \times (1 - p_2(i, j, x))(1 - s_2(i, j) + s_2(i, j)) \\ &\quad \times (1 - p_3(i, j, x)) \end{aligned}$$

and the detection probabilities are given by

$$\log\left(\frac{p_k(i, j, x)}{1 - p_k(i, j, x)}\right) = a_k(i, j) + b_k(i, j)x \quad (k = 1, 2, 3).$$

For each stage ($k = 1, 2, 3$), the prior distribution for $[a_k(i, j), b_k(i, j)]$ was taken to be a bivariate normal, with mean and covariance matrix given by the estimates and covariance matrix derived from the analysis used in McKechnie *et al.* (2007). We used a *Beta*(0.5, 0.5) as a vague prior distribution for $s_k(i, j)$ ($k = 1, 2$).

The probabilities for all the other distinct detection histories were derived in a similar fashion. Each detection history was modelled as the successful outcome of a Bernoulli trial. For example, consider again the detection history 101 at site i in year j , for which the mean distance to an occupant was x . This observation was modelled as the successful outcome of a Bernoulli trial with probability given by $\Pr(101, i, j, x)$.

The timing of burrowscope checks for each stage varied considerably from year to year and from site to site and never covered the complete breeding season (i.e. from point of lay to point of fledge). Therefore, we employed a 'date-correction factor' at each site and year, to allow for the proportion of the entire season covered by the burrowscope checks. In doing so, we calculated a daily 'survival' probability for an egg or chick by using the formula

$$s_k^d(i, j) = s_k(i, j)^{1/t_k(i, j)} \quad (k = 1, 2),$$

where $t_k(i, j)$ is the number of days between burrowscope checks during stage k at site i in year j . We then extrapolated the daily probabilities across the entire duration of each of the two stages (egg to hatch and hatch to fledge) to give 'date-corrected' values for *HS* and *FS* as follows:

$$S_k(i, j) = s_k^d(i, j)^{T_k},$$

where T_k is the entire duration of stage k ($k = 1, 2$). From the scant information available it appears that laying peaks about the last week of November (Warham *et al.* 1982; Heather and Robertson 1996), although it may vary in timing from island to island (Richdale 1963). For the purposes of this correction, the laying date was set to 25 November each year and the laying to fledging period was set as 150 days (Heather and Robertson 1996).

The final part of the first stage involved calculation of *BS*, both 'uncorrected' and date-corrected, as follows:

$$s_{12}(i, j) = s_1(i, j)s_2(i, j)$$

and

$$S_{12}(i, j) = S_1(i, j)S_2(i, j).$$

The second stage of the analysis involved analysis of the resulting date-corrected estimates of *HS*, *FS* and *BS*, to obtain an overall estimate (across all sites and years), separately for Whenua Hou and The Snares. In doing so, we assumed the following linear-logistic model:

$$\log\left(\frac{S_k(i, j)}{1 - S_k(i, j)}\right) = Y_k(i, j) \quad (k = 1, 2, \text{ or } 12),$$

$$Y_k(i, j) = \mu_k + \alpha_k(i) + \beta_k(j) + \varepsilon_k(i, j) + e_k(i, j),$$

$$\varepsilon_k(i, j) \sim N(0, \sigma_k^2),$$

$$e_k(i, j) \sim N(0, v_k),$$

where (for $k = 1, 2$, or 12) the notation is

μ_k , an overall effect;

$\alpha_k(i)$, the effect of site i (with $\alpha_k(1)$ arbitrarily set to zero);

$\beta_k(j)$, the effect of year j (with $\beta_k(1)$ arbitrarily set to zero);

$\varepsilon_k(i, j)$, 'process error' for site i in year j ; and

$e_k(i, j)$, 'estimation error' for site i in year j .

The distinction between the two types of error terms was needed to allow for the uncertainty in the estimation of *HS* from the first stage of the analysis: v_k is the error variation that arises from the uncertainty involved in estimating $S_k(i, j)$ in the first stage of the analysis; σ_k^2 is the error variation that would appear in the model if the $S_k(i, j)$ were known perfectly, i.e. if v_k were zero.

In performing this analysis, we set $Y_k(i, j)$ and v_k equal to the mean and variance, respectively, of the posterior distribution for $Y_k(i, j)$ that was obtained from the first stage. We used the following vague priors for all other terms in the model:

$$\mu_k \sim N(0, 100^2),$$

$$\alpha_k(i) \sim N(0, 100^2) \quad (i = 2, 3, \dots),$$

$$\beta_k(j) \sim N(0, 100^2) \quad (j = 2, 3, \dots), \text{ and}$$

$$\sigma_k \sim \text{Uniform}(0, 20).$$

To assess the effect of the date correction, we also carried out the above analysis for the uncorrected versions of *HS*, *FS* and *BS*.

After a preliminary check for autocorrelation and convergence by monitoring the Brooks–Gelman–Rubin diagnostic (Brooks and Gelman 1998), we ran each of the 36 first-stage models as a single chain for a burn-in phase of 10 000 iterations, followed by 100 000 iterations sampled at every 10th value (thin = 10). For the second-stage models, we ran the Markov chain Monte Carlo (MCMC) algorithm with three chains for a burn-in phase of

50 000 iterations, followed by 100 000 iterations, again sampled at every 10th value.

Results

Overall island estimates

Prior to date correction, overall hatching success (mean and 95% credible interval) was estimated to be 0.72 (0.49–0.90) on The Snares and 0.92 (0.87–0.95) on Whenua Hou (Fig. 2). Date correction reduced The Snares estimate to 0.59 (0.31–0.84), a reduction of 18%, and the Whenua Hou estimate to 0.88 (0.82–0.93), a 4% reduction. Similarly, before date correction overall fledging success was estimated to be 0.72 (0.56–0.85) on The Snares and 0.98 (0.95–0.99) on Whenua Hou (Fig. 3). Date correction reduced The Snares estimate by 8%, to 0.66 (0.44–0.84), and the Whenua Hou estimate to 0.97 (0.94–0.99), a reduction of <1%.

The overall date-corrected breeding success on the Snares was estimated to be 0.35 (0.2–0.52; Fig. 4). This was a 27% reduction from the overall estimate without date correction (0.49, 0.35–0.61). By comparison, on Whenua Hou the overall date-

corrected breeding success was estimated to be 0.76 (0.70–0.82), a 7% reduction from the uncorrected estimate (0.82, 0.77–0.87).

The probability of detecting a breeding attempt was similar at each burrowscope check on Whenua Hou (egg 0.73, 0.71–0.76, hatch 0.73, 0.71–0.76; fledge 0.74, 0.73–0.75; Fig. 5); however, these figures were lower than on The Snares (egg 0.80, 0.72–0.86, hatch 0.80, 0.76–0.85; fledge 0.84, 0.81–0.86) where the probability of detection was highest at the fledge check (Fig. 4).

Inter-site and inter-annual variability

We found considerable inter-annual variability in breeding success on each island (Fig. 6). Although there was also some inter-site variability within each island–year combination, for the most part estimates of breeding success for each site in any given year were similar on each island. Combining all available data from Whenua Hou for the same 3 years that data was available on The Snares (1997–1999) produced a lower date-corrected estimate of breeding success of 0.59 (0.31–0.84) on Whenua Hou than that on The Snares.

Large differences in the estimated daily survival rates for eggs and chicks were also found between islands and years

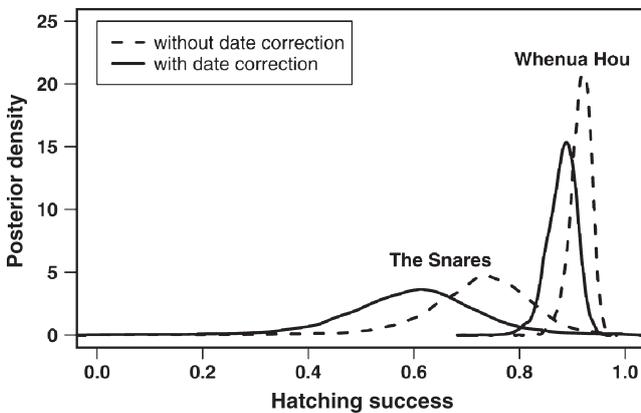


Fig. 2. Posterior density estimates of overall mean hatching success of sooty shearwater breeding attempts on The Snares and Whenua Hou, before and after date correction.

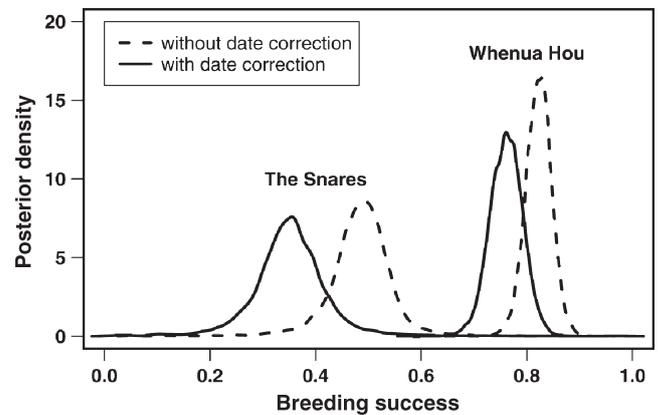


Fig. 4. Posterior density estimates of overall mean breeding success of sooty shearwater breeding attempts on The Snares and Whenua Hou, before and after date correction.

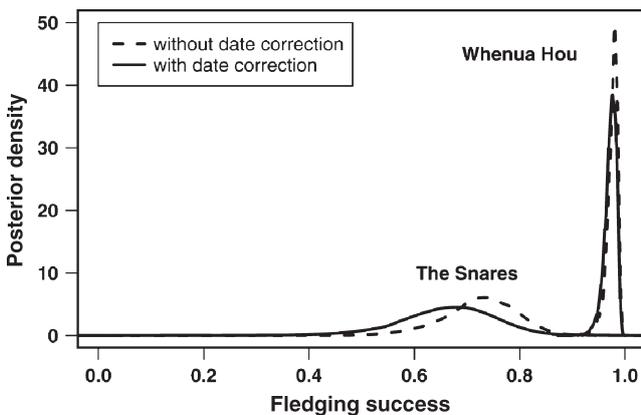


Fig. 3. Posterior density estimates of overall mean fledging success of sooty shearwater breeding attempts on The Snares and Whenua Hou, before and after date correction.

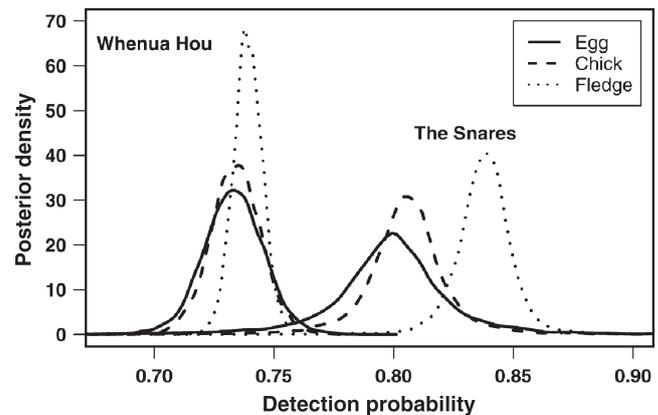


Fig. 5. Posterior density estimates of the mean probability of detecting a sooty shearwater breeding attempt during each monitoring period (egg, hatch and fledge) on The Snares and Whenua Hou.

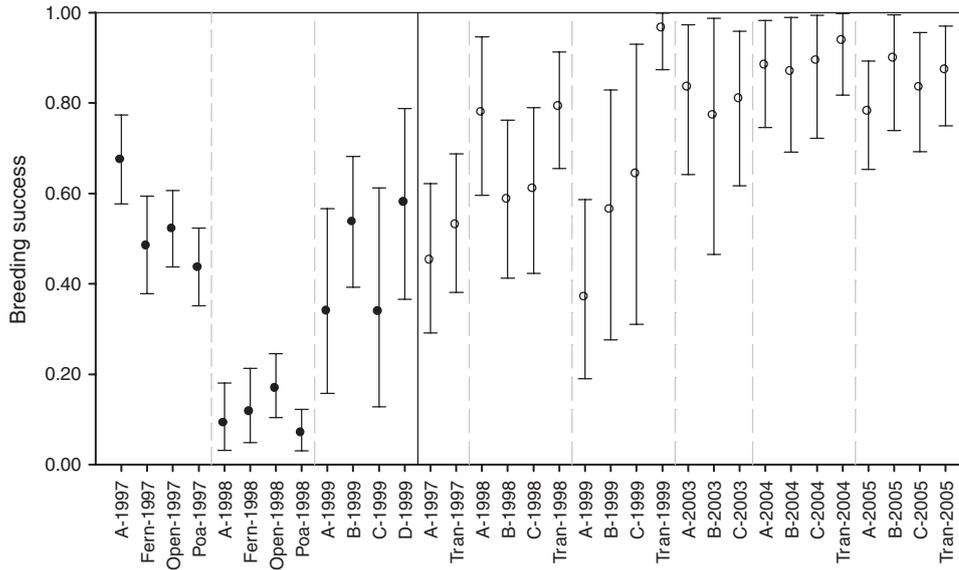


Fig. 6. Estimates of mean breeding success of sooty shearwaters for each site-year combination on The Snares (●) and Whenua Hou (○). Error bars show 95% credible intervals.

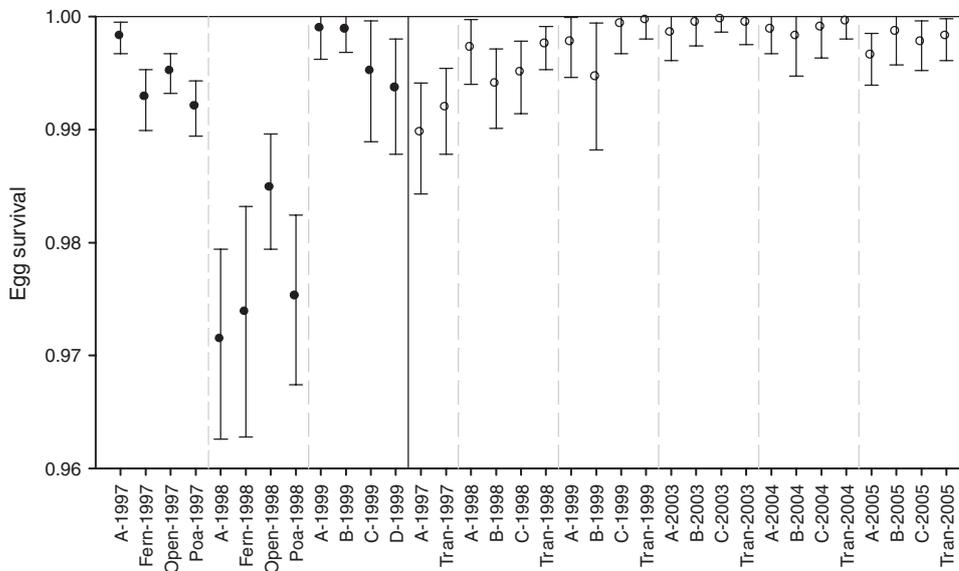


Fig. 7. Estimates of daily egg survival of sooty shearwaters for each site-year combination on The Snares (●) and Whenua Hou (○). Error bars show 95% credible intervals.

(Figs 7 and 8). However, survival rates for eggs and chicks were not always synchronised between the two islands from year to year. For example, in 1998 survival rates for both eggs and chicks were particularly low on The Snares but not on Whenua Hou; in 1999, fledging survival was low on Whenua Hou whereas egg survival was not.

Discussion

The merit of applying correction factors

Detection of eggs or chicks will always be a confounding factor when a burrowscope is used to measure breeding success, unless

each complete burrow system can be prospected with absolute confidence (Hamilton 1998a; Cuthbert and Davis 2002). This issue can be circumvented only if it can be demonstrated that a subset of burrows, such as those under inspection hatches, are representative of the population of interest as a whole. However, the sole use of inspection hatches may represent a biased subset of all breeding attempts in the sooty shearwater because the hatches are typically installed in shallow burrows close to the surface, where easy access to the nesting chamber is possible (Warham *et al.* 1982). In addition, unless the option of monitoring the fate of each egg from laying to fledging is feasible, some form of adjustment must be made for the proportion of the breeding

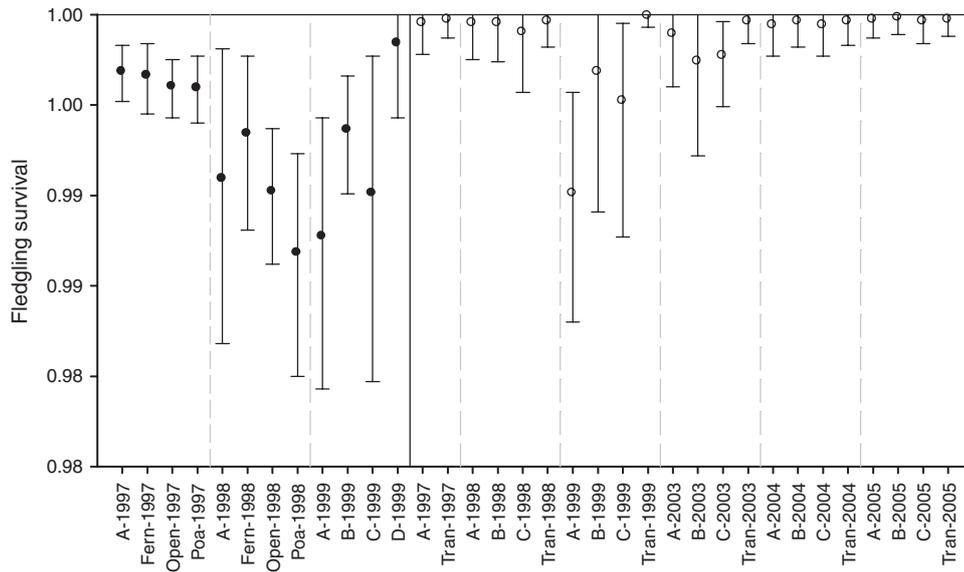


Fig. 8. Estimates of daily chick survival of sooty shearwaters for each site-year combination on The Snares (●) and Whenua Hou (○). Error bars show 95% credible intervals.

season missed by the monitoring program if the true breeding success is to be estimated. These issues have been highlighted only occasionally when breeding-success values in other burrowing species have been reported (Hamilton 1998b; Jones *et al.* 2003; Priddel *et al.* 2006).

Although both of the correction factors applied here have merit, there are several underlying assumptions that need validation. Our model allowed the detection function to vary in all three stages in the present study, and on each island. Our results showed a lower detection of breeding attempts on Whenua Hou than on The Snares, presumably owing to the average depth of breeding attempts being higher on Whenua Hou. Our analyses also indicated that fledglings were easier to detect than hatched chicks or eggs on The Snares, whereas detection probabilities for all three stages were similar on Whenua Hou. Serventy and Curry (1984) and Jones (1986) also found some evidence for stage-dependant detection functions. We have specified detection probability to be a function of the mean distance to an occupant, the mean being calculated across those stages for which an occupant was detected. It is possible that this is an underestimate of the mean distance to an occupant across all stages, because detection probability decreases with distance to occupant and undetected occupants, therefore, tend to be located deeper in the burrow. It is therefore possible that we have slightly overestimated the detection probability for unobserved occupants, and so slightly underestimated 'survival'. A further investigation of how the detection of the breeding attempt varies with island or stage would be worthwhile.

In most petrel species, losses during the egg stage are thought to be higher than those during the chick stage (Warham 1990; Cuthbert and Davis 2002), although the evidence for this appears limited. In the present study, we found that hatching and fledging success were remarkably similar within both islands (Fig. 4). Our initial checks during the egg stage were sometimes in late December and never before 28 November (Table 1), so it is

possible that very early losses may have been missed entirely by our burrowscoping teams (provided no evidence of a breeding attempt remained). In the absence of any functions that adequately describe mortality across the breeding season we had to assume constant mortality across each stage. Hatching success could therefore be overestimated on some occasions if losses are particularly high just after laying. Any sampling near the time of egg laying is likely to be highly disruptive to breeding success when sooty shearwaters are thought to be highly susceptible to observer-induced breeding failures (Warham 1990). During the season where intensive monitoring of inspection hatches was undertaken on The Snares, observer-induced failures were noted on several occasions – although it was not possible to calculate their true extent. Equally, the actual installation and maintenance of inspection hatches in dense colonies with soft, easily disturbed soil is problematic in itself. By comparison, disturbance is likely to be minimal when a burrowscope is used to check for occupants.

Inter-annual variability in fledging rates may also have been buffered because of a potential bias that may have operated towards the end of the breeding season when chicks detected with the burrowscope during the 'fledge' stage were classified as 'fledging' and until the final departure of the chicks from the island would be missed, leading to an inflated estimate of the fledging rate. This potential bias is likely to be considerable in years of poor food availability because chicks are capable of surviving long periods between provisioning and have been observed moving around above ground, late in the season, at exceptionally low weights (<180 g; J. Newman, pers. obs.). Chicks of this size have a very small chance of departing the island as successful fledglings (Sagar and Horning 1998). The chicks of sooty shearwater remain on the islands for some time after leaving their natal burrows, often spending up to a week on the surface losing down and exercising their wings before their departure from the colony (Richdale 1963). During this stage,

they may roost in numerous burrows, sometimes moving considerable distances each night (H. Moller, pers. obs.). The final burrowscope check during the 'fledging' stage was deliberately timed to occur before any movement of chicks among nests, to avoid confusion caused by inter-burrow chick movement. Some estimate of this bias could be made from the observed mortality of chicks above ground late in the season, although many chicks may also die underground and it is harder to know how to correct for this bias. From a demographic perspective, this bias is not serious because it would be compensated for by a reduction in the estimate of juvenile survival rate, leaving the overall recruitment rate unchanged.

The effect of applying the date-correction factor

Hunter *et al.* (2000) investigated the sensitivity of population-model output to changes in vital rates by using the closely related short-tailed shearwater as a surrogate for sooty shearwaters. These authors used a breeding success for the short-tailed shearwater of 0.61 (s.e. = 0.02; data from Wooller *et al.* 1990) in their analyses and concluded that the elasticity of population growth rate to this parameter is relatively low and its importance certainly ranks below parameters such as adult and juvenile survival. However, the reductions in the estimates of breeding success of 0.14 (The Snares) and 0.06 (Whenua Hou), when applying a date-correction factor, appear to be large enough to have a meaningful influence on population growth rate. A deterministic matrix model with a structure similar to that constructed by Hunter *et al.* (2000), and parameterised with estimates of vital rates for sooty shearwater (H. Moller, unpubl. data), predicts that changes in the mean breeding success of these magnitudes will decrease the finite population growth rate (λ) by 1.25 and 0.28 percentage points on The Snares and Whenua Hou respectively. This signals a warning that the development and application of similar correction factors should be considered when estimating breeding success for other burrow-nesting species where similar biases are likely to exist. In addition, even when model elasticity analyses rank breeding success as low priority, large fluctuations such as these can influence population dynamics considerably (Jenouvrier *et al.* 2003).

Temporal and spatial variability in breeding success

Correctly determining breeding success in any burrow-nesting species that is prone to disturbance is always going to be challenging and problematic. It was not possible to test for interactions formally between year and island. Nevertheless, our results indicate that some interaction did occur. For example, 1998 was observed to be a particularly poor year for breeding success on The Snares, whereas it was no way near as extreme on Whenua Hou (Fig. 6). Overall, our estimates of hatching success on each island were lower than those of fledging success. Lower hatching success has been reported for other petrel species (Cuthbert and Davis 2002). Inter-annual variation in hatching and fledging rates could easily be caused by several different mechanisms, including pre-laying condition of breeding birds, differential food availability during the incubation or provisioning phase or even local climatic conditions such as flooding events occurring at different stages

of the breeding season (Thompson and Furness 1991; Furness and Tasker 2000; Smithers *et al.* 2003).

Our estimates of the overall breeding success for the two islands differed significantly; the estimates from the full dataset (with the detection and date corrections) on Whenua Hou (0.76, 0.70–0.82) were more than twice those for The Snares (0.35, 0.20–0.52). Previous reports on estimates of breeding success for sooty shearwaters are rare. Warham *et al.* (1982) recorded a hatching-success range of 33–58% across 2 years on The Snares, which is comparable to our estimates; however, these authors acknowledged that they were using a biased subset of burrows and considered that observer disturbance had lowered their estimates. Jones *et al.* (2003) estimated overall breeding-success rates for 2 years at a range of coastal colonies from stage-specific survival rates and found significantly different rates across the four colonies, ranging from 48% to zero. The authors attributed much of their observed low breeding success to predation, with the highest rates being recorded on a small predator-free offshore island (Tuhawaiki I.) and a heavily trapped mainland colony (Taiaroa Head).

Although such a considerable inter-island difference as we report here may seem surprising, several recent examples of inter-population differences in demographic parameters have been reported for other species. Frederiksen *et al.* (2005) described inter-population differences in kittiwakes by comparing nine published studies, whereas Nel *et al.* (2003) reported similar for wandering albatross. Frederiksen *et al.* (2005) also argued that rather than being a nuisance, such differences are valuable for understanding population dynamics, suggesting that such effects are rarely reported because few species are studied in sufficient detail over wide-enough geographic ranges. The two main islands used for the present study also differ markedly in many biotic and abiotic features. The Snares has some of the highest densities of sooty-shearwater burrows recorded (Scofield 2001), and contains an estimated 2 million breeding pairs – the largest population in New Zealand (Warham and Wilson 1982). The island is also inhabited by high densities of other seabird species and contains a greatly reduced set of flora and fauna, with a mono-specific canopy of *Olearia* over >60% of the main island (North-east Island) (Warham and Wilson 1982; Hay *et al.* 2004). The Snares could be considered a classic seabird-dominated ecosystem. By comparison, Whenua Hou is an island containing considerably more diverse ecotypes and has a larger list of flora and fauna more typical of the nearby Rakiura (Stewart Island). The entrance density for the sooty shearwater on Whenua Hou is amongst the lowest reported (Scott 2005) and colonies occupy only a small proportion of the entire island. However, a likely mechanism could be some form of density dependence where high-density sites such as on The Snares suffer reduced breeding success because of disturbance and crowding from such a high density and absolute number of birds present. The Snares had lower estimates of breeding success and higher estimates of detection probabilities (owing to shallower breeding attempts) than did Whenua Hou. This suggests that some form of nest-site selection may be operating, with deeper burrows being preferred and being more productive than shallow ones. The fact that breeding success was significantly lower in a large, dense colony signals a warning to anyone reporting breeding success from small or low-density sites and extrapolating them to other populations. It is reasonable

to expect that those vital rates to which population growth rate is least sensitive (such as breeding success) are more free to vary in space and time, although the true sensitivity of these rates may have been underestimated (Jenouvrier *et al.* 2003).

Conclusion

We consider burrowscoping to be currently the most appropriate method for determining breeding success in a burrow-nesting species such the sooty shearwater, especially when large-scale spatial replication is required. After 9 years of monitoring sooty shearwater breeding with a burrowscope on two southern islands, we conclude that breeding success is highly variable and site dependant. Because of the problems inherent in attempting to monitor breeding success in a burrow-nesting species, we consider the application of detection and date-correction factors valid improvements to naïve burrowscope estimates and recommend the future development of these correction techniques. The possibility that breeding success is being regulated in a density-dependant fashion is also worthy of investigation. These findings will have important implications for our proposed method of using The Snares and Whenua Hou as comparable non-harvested treatment populations for the purposes of comparing populations on harvested and non-harvested islands. The considerable difference between the rates reported here for Whenua Hou and The Snares highlights the need for extreme caution when selecting values for demographic models.

Acknowledgements

We thank the Rakiura Tīti Islands Administering Body for guidance throughout the study, and the New Zealand Department of Conservation for permission to undertake the experiment on The Snares and Whenua Hou. Over the duration of this study, a large number of people, too numerous to list here, assisted with this research; we gratefully thank all those involved. Thanks go also to Grant Blackwell for reviewing this manuscript and to Suzanne Bassett for editing. Financial assistance was given by the Foundation for Research, Science and Technology, University of Otago, New Zealand Aluminum Smelters Ltd, and South-west Helicopters Ltd. This research was carried out under the approval of the University of Otago Animal Ethics Committee # F02/001. We thank two anonymous reviewers for their constructive comments.

References

- Blackmer, A. L., Ackerman, J. T., and Nevitt, G. A. (2004). Effects of investigator disturbance on hatching success and nest-site fidelity in a long-lived seabird, Leach's storm-petrel. *Biological Conservation* **116**, 141–148. doi: 10.1016/S0006-3207(03)00185-X
- Brooks, S. P., and Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* **7**, 434–455. doi: 10.2307/1390675
- Carter, J. (1997). Nest-site selection and breeding success of wedge-tailed shearwaters *Puffinus pacificus* at Heron Island. *Australian Geographical Studies* **35**, 153–167. doi: 10.1111/1467-8470.00016
- Cobley, N. D., Croxall, J. P., and Prince, P. A. (1998). Individual quality and reproductive performance in the grey-headed albatross *Diomedea chrysostoma*. *Ibis* **140**, 315–322. doi: 10.1111/j.1474-919X.1998.tb04395.x
- Cuthbert, R., and Davis, L. S. (2002). Adult survival and productivity of Hutton's shearwaters. *Ibis* **144**, 423–432. doi: 10.1046/j.1474-919X.2002.00071.x
- Dunlop, J. N., Long, P., Stejskal, I., and Surman, C. (2002). Inter-annual variations in breeding participation at four Western Australian colonies of the wedge-tailed shearwater *Puffinus pacificus*. *Marine Ornithology* **30**, 13–18.
- Frederiksen, M., Harris, M. P., and Wanless, S. (2005). Inter-population variation in demographic parameters: a neglected subject? *Oikos* **111**, 209–214. doi: 10.1111/j.0030-1299.2005.13746.x
- Furness, R. W., and Tasker, M. L. (2000). Seabird–fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* **202**, 253–264. doi: 10.3354/meps202253
- Granadeiro, J. P., Dias, M. P., Rebelo, R., Santos, C. D., and Catry, P. (2006). Numbers and population trends of Cory's shearwater (*Calonectris diomedea*) at Selvagem Grande, northeast Atlantic. *Waterbirds* **29**, 56–60. doi: 10.1675/1524-4695(2006)29[56:NAPTOC]2.0.CO;2
- Hamilton, S. (1998a). A test of burrow occupancy of sooty shearwaters (*Puffinus griseus*) using chick response to sound. *Notornis* **45**, 64–66.
- Hamilton, S. (1998b). Determining burrow occupancy, fledging success and land-based threats to mainland and near-shore island sooty shearwater (*Puffinus griseus*) colonies. *New Zealand Journal of Zoology* **25**, 443–453.
- Hamilton, S. A. (2000). How precise and accurate are data obtained using an infra-red scope on burrow-nesting sooty shearwaters *Puffinus griseus*? *Marine Ornithology* **28**, 1–6.
- Hay, C. H., Warham, J., and Fineran, B. A. (2004). The vegetation of The Snares, islands south of New Zealand, mapped and discussed. *New Zealand Journal of Botany* **42**, 861–872.
- Heather, B. D., and Robertson, H. A. (Eds) (1996). 'The Field Guide to the Birds of New Zealand.' (Viking Books: Auckland.)
- Hunter, C. M., Moller, H., and Fletcher, D. (2000). Parameter uncertainty and elasticity analyses of a population model: setting research priorities for shearwaters. *Ecological Modelling* **134**, 299–323. doi: 10.1016/S0304-3800(00)00344-6
- Inchausti, P., Guinet, C., Koudil, M., Durbec, J. P., Barbraud, C., Weimerskirch, H., Cherel, Y., and Jouventin, P. (2003). Inter-annual variability in breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of Avian Biology* **34**, 170–176. doi: 10.1034/j.1600-048X.2003.03031.x
- Jenouvrier, S., Barbraud, C., and Weimerskirch, H. (2003). Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Animal Ecology* **72**, 576–587. doi: 10.1046/j.1365-2656.2003.00727.x
- Jones, M. J. (1986). Breeding synchrony of Cory's shearwater *Calonectris diomedea* on Selvagem Grande. *Ibis* **128**, 423–426. doi: 10.1111/j.1474-919X.1986.tb02693.x
- Jones, C., Bettany, S. M., Moller, H., Fletcher, D. J., Lyver, P. O. B., and de Cruz, J. (2003). Burrow occupancy and productivity at coastal sooty shearwater (*Puffinus griseus*) breeding colonies, South Island, New Zealand: can mark–recapture be used to estimate burrow accuracy? *Wildlife Research* **30**, 377–388. doi: 10.1071/WR01050
- Lunn, D. J., Thomas, A., Best, N., and Spiegelhalter, D. (2000). WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* **10**, 325–337. doi: 10.1023/A:1008929526011
- Lyver, P. O., Hamilton, S. A., Mc Kenzie, M., Dickson, I., Dooher, T., Broad, T., and Moller, H. (1998). A burrowscope for examining petrel nests in burrows. Conservation advisory science notes 209. The New Zealand Department of Conservation, Wellington, New Zealand.
- Major, H. L., Jones, I. L., Byrd, G. V., and Williams, J. C. (2006). Assessing the effects of introduced Norway rats (*Rattus norvegicus*) on survival and productivity of Least auklets (*Aethia pusilla*). *The Auk* **123**, 681–694. doi: 10.1642/0004-8038(2006)123[681:ATEOIN]2.0.CO;2

- McKechnie, S. J. D. (2004). Sooty shearwater burrow systems: detection of occupants, site selection and recovery from disturbance. M.Sc. Thesis, The University of Otago, Dunedin, New Zealand.
- McKechnie, S., Fletcher, D., Moller, H., Scott, D., Newman, J., and Bragg, C. (2007). Estimating and correcting for bias in population assessments of sooty shearwaters. *Journal of Wildlife Management* **71**, 1325–1335. doi: 10.2193/2006-018
- Moller, H., de Cruz, J., Fletcher, D., Garrett, K., Hunter, C., *et al.* (1999). 'Kia Mau Te Titi Mo Ake Tōnu Atu: Goals, Design and Methods.' (The University of Otago: Dunedin, New Zealand.)
- Nel, D. C., Taylor, F., Ryan, P. G., and Cooper, J. (2003). Population dynamics of the wandering albatross *Diomedea exulans* at Marion Island: Longline fishing and environmental influences. *African Journal of Marine Science* **25**, 503–517.
- Pollock, K. H., Nichols, J. D., Brown, C., and Hines, J. E. (1990). Statistical inference for capture–recapture experiments. *Wildlife Monographs* **107**, 1–97.
- Priddel, D., Carlile, N., Fullagar, P., Hutton, I., and O'Neill, L. (2006). Decline in the distribution and abundance of flesh-footed shearwaters (*Puffinus carneipes*) on Lord Howe Island, Australia. *Biological Conservation* **128**, 412–424. doi: 10.1016/j.biocon.2005.10.007
- Richdale, L. E. (1963). Biology of the sooty shearwater *Puffinus griseus*. *Proceedings of the Zoological Society of London* **141**, 1–117.
- Sagar, P. M., and Horning, D. S. (1998). Mass-related survival of fledgling sooty shearwaters *Puffinus griseus* at The Snares, New Zealand. *Ibis* **140**, 329–331. doi: 10.1111/j.1474-919X.1998.tb04397.x
- Scofield, P. (2001). Sooty shearwater (*Puffinus griseus*) survival of unharvested populations. Ph.D. Thesis, The University of Otago, Dunedin, New Zealand.
- Scott, D. S. (2005). Burrow entrance densities of sooty shearwaters and mottled petrels on Whenua Hou. Postgraduate Diploma of Science Thesis, The University of Otago, Dunedin, New Zealand.
- Serventy, D. L., and Curry, P. J. (1984). Observations on colony size, breeding success, recruitment and inter-colony dispersal in a Tasmanian colony of short-tailed shearwaters *Puffinus tenuirostris* over a 30-year period. *Emu* **84**, 71–79.
- Smithers, B. V., Peck, D. R., Krockenberger, A. K., and Congdon, B. C. (2003). Elevated sea-surface temperature, reduced provisioning and reproductive failure of wedge-tailed shearwaters (*Puffinus pacificus*) in the southern Great Barrier Reef, Australia. *Marine and Freshwater Research* **54**, 973–977. doi: 10.1071/MF02137
- Thompson, K., and Furness, R. (1991). The influence of rainfall and nest-site quality on the population dynamics of the Manx shearwater *Puffinus puffinus* on Rhum. *Journal of Zoology* **225**, 427–437.
- Warham, J. (1990). 'The Petrels: Their Ecology and Breeding Systems.' (Academic Press Ltd.: London.)
- Warham, J., and Wilson, G. (1982). The size of the sooty shearwater population at the Snares Islands, New Zealand. *Notornis* **29**, 23–30.
- Warham, J., Wilson, G. J., and Keeley, B. R. (1982). The annual cycle of the sooty shearwater *Puffinus griseus* at the Snares Islands, New Zealand. *Notornis* **29**, 269–292.
- Wooller, R., Bradley, J. S., Skira, I. J., and Serventy, D. L. (1990). Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. *Journal of Animal Ecology* **59**, 161–170. doi: 10.2307/5165
- Wooller, R., Bradley, J. S., and Croxall, J. P. (1992). Long-term population studies of seabirds. *Trends in Ecology & Evolution* **7**, 111–114. doi: 10.1016/0169-5347(92)90143-Y
- Wrege, P. H., Shuford, W. D., Winkler, D. W., and Jellison, R. (2006). Annual variation in numbers of breeding California gulls at Mono lake, California: the importance of natal philopatry and local and regional conditions. *The Condor* **108**, 82–96. doi: 10.1650/0010-5422(2006)108[0082:AVINOB]2.0.CO;2

Manuscript received 16 June 2006, accepted 28 October 2008