

AGE AT FIRST RETURN TO THE BREEDING COLONY AND JUVENILE SURVIVAL OF SOOTY SHEARWATERS

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Abstract. Using mark–recapture, we estimated the age at first return and survival of juveniles of the Sooty Shearwater (*Puffinus griseus*), a medium-sized burrow-breeding procellariiform, at two New Zealand breeding colonies, Taiaroa Head and The Snares. Sooty Shearwaters were first observed at the colony between 2 and 10 years after being banded as chicks, with a mean of 5.7 years at Taiaroa Head and 5.4 years at The Snares. After accounting for imperfect detectability with a mark–recapture model, we estimate the mean age at first return as 4.8 years. Extrapolation from observed delays between arrival and breeding of the Short-tailed Shearwater (*P. tenuirostris*) suggests that the mean age at first breeding was 7.7 years. Annualized estimates of survival from 0 to 2 years were 0.54 at Taiaroa Head and 0.41 at The Snares. Overall estimates of the generation time and maximum rate of population growth were 13.1 years and 7.7%, respectively. Many published estimates of age at first return and age at first breeding are biased because they implicitly assume perfect detectability of individuals. Such an assumption in turn leads to bias in estimation of generation time and maximum rate of population growth. A generic population model for the Procellariiformes, in which the parameters are scaled against generation time, could prove to be a useful tool in guiding management of bycatch and sustainable harvest.

Key words: mark–recapture, Procellariiformes, Sooty Shearwater, recruitment, sustainable harvest management, transience, fisheries bycatch.

Edad al Momento del Primer Retorno a la Colonia Reproductiva y Supervivencia de los Juveniles de *Puffinus griseus*

Resumen. Usado métodos de marca–recaptura, estimamos la edad al momento del primer retorno y la supervivencia de los juveniles de *Puffinus griseus*, un procelariforme de tamaño medio que anida en huecos, en dos colonias reproductivas en Nueva Zelanda, Taiaroa Head y los Snares. Los individuos de *P. griseus* fueron observados por primera vez en la colonia entre 2 y 10 años luego de haber sido anillados como pichones, con una media de 5.7 años en Taiaroa Head y 5.4 años en los Snares. Luego de tener en cuenta la detectabilidad imperfecta que supone un modelo de marca–recaptura, estimamos la edad media al momento del primer retorno en 4.8 años. La extrapolación de las demoras observadas entre el arribo y la reproducción en *P. tenuirostris* sugiere que la edad media de la primera reproducción fue de 7.7 años. Las estimaciones anuales de la supervivencia de 0 a 2 años fueron 0.54 en Taiaroa Head y 0.41 en los Snares. Las estimaciones globales del tiempo generacional y la tasa máxima de crecimiento poblacional fueron de 13.1 años y 7.7%, respectivamente. Muchas estimaciones publicadas de la edad al momento del primer retorno y de la edad de la primera reproducción están sesgadas debido a que implícitamente asumen una detectabilidad perfecta de los individuos. Este supuesto a su vez lleva a un sesgo en la estimación del tiempo generacional y de la tasa máxima de crecimiento poblacional. Un modelo poblacional genérico para los Procelariformes, en el cual los parámetros están ajustados por el tiempo generacional, podría ser una herramienta útil para guiar el manejo de la captura incidental y de la cosecha sustentable.

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INTRODUCTION

In many species of colonial seabirds, the young leave their natal colony after fledging and do not return to it for several years (Lebreton et al. 1990, 1992, Nichols et al. 1990, Cooke and Francis 1993, Clobert et al. 1994). Individuals return to the colony and start breeding over a range of ages, particularly in longer-lived species such as those of the order Procellariiformes (Duncan and Monaghan 1977, Greenwood and Harvey 1982, Bradley and Wooller 1989). Estimates of age at first return (AFR) and age at first breeding (AFB) are important for understanding recruitment, but the length of the studies required means that relatively few robust estimates of these variables have been reported.

Many studies that report AFR do so by simply stating the age at which birds are first *observed* arriving at the colony. This is accurate only if the probability of detecting an individual at the colony is equal to one, but for many species this is not true, making the observed AFR an overestimate of the true AFR because some individuals will not be detected until one or more years after arriving. In such cases, it will be preferable to use a mark–recapture model to estimate the probability of detection and so estimate AFR more accurately. Even then, the study needs to be long enough to avoid bias caused by the end of the study truncating the maximum age at which birds of later cohorts can first be observed to return. This bias acts in the other direction, in that it will lead to an estimate of AFR lower than would be obtained from a longer study.

Juveniles that cannot be captured between fledging and return to the colony can be thought of as temporary emigrants. A natural approach would therefore be to use Pollock's robust design, which allows estimation of temporary emigration (Pollock 1982, Kendall et al. 1997). However, many studies do not follow the robust design of primary and secondary periods of sampling and so cannot use this approach. Clobert et al. (1994) showed how standard mark–recapture data (not recorded by the robust design) could be used to estimate both juvenile survival and what they termed age-specific breeding probabilities. For further discussion of alternative methods of analysis and different parametrizations of the recruitment process, see Pradel and Lebreton (1999), Schwarz and Arnason (2000) and Link and Barker (2005).

The Sooty Shearwater (*Puffinus griseus*) is called *tūi* by the Rakiura Māori, New Zealand's southernmost group of indigenous people, who traditionally harvest chicks each year from islands around Stewart Island (Wilson 1979, Stevens 2006). Māori culture places great importance on this harvest; cultural regulations prohibit the harvest of adults, restrict access to the islands and timing of the harvest, and include provisions to protect habitat (Kitson and Moller 2008). Recent perceived changes in population status and classification of the population as “near threatened” (Scott et al. 2008) have led to research into the customary harvest's sustainability

(Moller 1996, 2006, Taiepa et al. 1997, Hunter and Caswell 2005, Moller et al. 2009b).

The primary purpose of this paper is to use a multi-state mark–recapture model to obtain estimates of AFR and survival of juvenile Sooty Shearwaters, following the approach of Spindelov et al. (2002). We then use an estimate of the time between AFR and AFB for a closely related species, the Short-tailed Shearwater (*P. tenuirostris*) to estimate AFB for the Sooty Shearwater. We also consider the potential bias in the observed AFR caused by imperfect detectability of individuals and the effect this can have on estimation of generation time and maximum rate of population growth.

METHODS

STUDY SITES AND FIELD WORK

The Sooty Shearwater is a medium-sized procellariiform that nests in burrows primarily on offshore islands of New Zealand and Chile (small colonies also occur in Australia and the Falkland Islands). It lays at most one egg each breeding season. We used banding data from two colonies in New Zealand: Taiaroa Head (45° 48' S, 170° 44' E), on the tip of Otago Peninsula 36 km northeast of the city of Dunedin; and at The Snares (48° 01' S, 166° 36' E), a group of small subantarctic islands lying 105 km south-southwest of Stewart Island.

Taiaroa Head. Over 14 breeding seasons, between April 1992 and May 2005, we banded 1175 chicks and 2088 adults (Appendix 1; available at <http://dx.doi.org/10.1525/cond.2013.110150>). Throughout the paper we use the labels 91, 92, ..., 04 to denote the breeding seasons of 1991/92, 1992/93, ..., 2004/05, respectively. Most field effort took place between late September and mid-November, just after the return of breeding adults (Shaffer et al. 2006), as any handling after this period might have led to an increase in failure of breeding. In some years, we also banded adults after chicks had hatched. We captured chicks when they emerged from their burrows between mid-April and mid-May to exercise wing muscles, lose down, and fledge.

The Snares. From 1996 to 1999, we banded 2770 chicks and 4495 adults (Appendix 1). In the early years of the study we made three visits to the islands to study egg-laying, hatching, and fledging, but later shortened this to one or two trips. Where possible, trips were timed to coincide with late incubation and hatching or with fledging (Newman et al. 2009a). The data used in our analyses were from sites A, B, and D, described by Clucas et al. (2008). Sites A (472 m²), B (413 m²), and D (613 m²) are approximately 200 m apart on North East Island, the main island of the group. Study sites were located within one large essentially contiguous colony that covers most of the island under a low forest dominated by *Tūpare* (*Olearia colensoi* Hook.). They were not spatially distinct from other areas of the colony, and some birds will have landed in them and passed through to adjacent areas in which

they were nesting. For this reason we anticipated some disappearances of banded individuals that nevertheless survived to return to breed, both within a season (as they land and move within the colony) and in successive seasons (as they move burrows). The density of burrow entrances is much higher at The Snares than at Taiaroa Head (Moller et al. 2009a, Newman et al. 2009b).

The number of birds banded or recaptured in each year and the year that they were next captured (if they were) are given in Appendix 1, separately for those birds banded as chicks and those banded as adults. This tabulation is referred to as an “m-array” by Lebreton et al. (1992). The data on banded adults provides information on transience and adult survival; its inclusion in the analysis therefore leads to more reliable estimation of AFR and juvenile survival than we would have obtained from the data on banded chicks alone. A detailed analysis of transience and adult survival per se is given in Clucas et al. (2008).

MULTI-STATE MODELING TO ESTIMATE JUVENILE SURVIVAL AND AFR

Our multi-state model had two states: *young* (chick or juvenile) and *adult* (pre-breeder, breeder or nonbreeder). We defined a juvenile as a bird that has fledged but has not yet returned to the colony, an adult as a bird that has returned to the colony and is a pre-breeder, breeder, or non-breeder. The model involved three types of parameter: probabilities of survival and recapture for each state and the probabilities of transitions between states. Juveniles are thought of as being temporary emigrants, so *young* individuals were assigned a recapture probability of zero. Likewise, a transition from *adult* to *young* is impossible, so we set its probability to zero.

When a multi-state model is fitted to a large data set it is not uncommon for there to be issues with convergence of the estimation process due to sparseness in the data (Kendall et al. 2003:1063). The only results we report are for those models in which convergence was achieved.

The model required specifying a minimum age *k* (years) at which first return can occur and an age *m* (years) by which it is assumed that all individuals that eventually return will have done so. A natural choice for *k* is the minimum observed AFR (Spendelov et al. 2002), which was 2 years. To allow for the possibility that individuals might return at age 1 year, we compared models with *k* = 1 and *k* = 2. We considered values of *m* between 2, the minimum possible value given our choice of *k*, and 10, the maximum observed AFR. For individuals banded as chicks, age in subsequent years is known. Thus we can specify the probability of transition from young to adult as age-dependent. We defined $\alpha^{(v)}$ to be the probability that a bird of age *v* will be present at the colony in any given year (given that the bird is alive in that year, has not previously returned to the

colony, and will return to the colony at some stage in its lifetime). In all models, we set $\alpha^{(v)}$ to 0 for *v* < *k* and 1 for *v* ≥ *m*, corresponding to the assumption that no individual returns to the colony before age *k* and all individuals will have returned by age *m*. We did not consider models in which values of $\alpha^{(v)}$ were time-dependent (varied by annual cohort) because fitting these led to problems with convergence (the final estimates depending on the initial values), suggesting that they are too complex to fit to the data. We considered three types of model for $\alpha^{(v)}$. In the first, the values of $\alpha^{(v)}$ were fully age-specific, in the other two the relationship between $\alpha^{(v)}$ and age *v* (*v* = 2, ..., *m* - 1) was given by one of the following linear-logistic functions:

$$\log\left(\frac{\alpha^{(v)}}{1-\alpha^{(v)}}\right) = a + bv \tag{1}$$

and

$$\log\left(\frac{\alpha^{(v)}}{1-\alpha^{(v)}}\right) = a' + b' \exp(v) \tag{2}$$

Eq. 1 is a classic logistic regression equation with age as the predictor variable (Spendelov et al. 2002). Eq. 2 was an alternative that was motivated by preliminary analyses in which we plotted

$\log\left(\frac{\hat{\alpha}^{(v)}}{1-\hat{\alpha}^{(v)}}\right)$ versus *v* for the model in which $\alpha^{(v)}$ was fully age-specific. Note that Eqs. 1 and 2 both imply that $\alpha^{(v)}$ is a strictly increasing function of age.

We converted the final estimates of $\alpha^{(v)}$ to a distribution for AFR by the following formula, which follows from the fact that an individual that first arrives at the colony at age *x* > *k* clearly must have “not arrived at the colony” between ages *k* and *x* - 1 inclusive (Pradel and Lebreton 1999):

$$\Pr(AFR = x) = \begin{cases} \alpha^{(k)} & x = k \\ \alpha^{(x)} \prod_{v=k}^{x-1} (1 - \alpha^{(v)}) & x = k + 1, \dots, m \end{cases} \tag{3}$$

We needed to assume that each individual had the same probability of survival from age *k* onward. Thus the probability of survival of juveniles of age ≥ *k* was the same as that for adults. The annual survival probabilities for a juvenile of age < *k* cannot be estimated separately. We therefore estimated the probability of surviving from age 0 to age *k*, $\phi^{(0)}$, and converted this to an effective annual survival probability between ages 0 and *k* with the formula $[\phi^{(0)}]^{1/k}$. We did not consider models in which $\phi^{(0)}$ is time-dependent because these again led to problems with convergence.

Given our previous experience with analyzing mark-recapture data for this species, and the literature for other seabirds, we expected that we would need to allow for both “transience” and “trap-dependence” (Spendlow et al. 2002). A “transient model” allows for the fact that some prospecting pre-breeders appear at a site for one season only and are never seen again (Richdale 1963, Warham 1996). A “trap-dependence model” can allow for some forms of temporary emigration of adults.

To allow for the transience effect, we defined two survival probabilities for individuals of age $\geq k$:

- $\theta^{(k+)}$ probability that an unmarked adult captured in year i survives until year $i + 1$ and remains in the population (assumed the same for all years)
- $\phi^{(k+)}$ probability that a marked bird (juvenile or adult) of age $\geq k$, alive in year i , survives until year $i + 1$ and remains in the population (assumed the same for all years)

Initial analysis again revealed problems with convergence when we fitted models in which either $\theta^{(k+)}$ or $\phi^{(k+)}$ was time-dependent; we therefore consider only models in which these are both constant.

We defined the probability of recapture of an adult, $p_i^{(k+)}$, to be the probability that a marked adult alive and in the study population at year i is captured in year i . To allow for trap-dependence, we assumed $p_i^{(k+)}$ to depend on whether or not the individual was captured (as an adult) in year $i - 1$; note that use of this model for $p_i^{(k+)}$ is not meant to reflect a behavioral response caused by the capture process (Pradel 1993). We specified the probability of recapture of individual j in year i as

$$\log\left(\frac{p_{ij}^{(k+)}}{1 - p_{ij}^{(k+)}}\right) = c_i + dx_{i-1,j} \quad (4)$$

where $x_{i-1,j} = 1$ if individual j was captured in year $i - 1$ and $x_{i-1,j} = 0$ otherwise. We allowed the intercept (c_i) to vary with time because a number of factors contribute to annual variation in the birds’ catchability, including variation in field effort caused by other research needs. It is not possible to fit a model in which both the intercept and d vary with time (Pradel 1993). In all models, we specified parameters c_i and d as site-dependent because of differences between sites in field effort and expected differences in temporary emigration.

We used the following three-step process for model selection. First, we determined a suitable model for $\alpha^{(v)}$ by setting $m = 10$ (the largest value that we considered) and for each of the 16 models in which $\phi^{(0)}$, $\theta^{(k+)}$, $\phi^{(k+)}$, and $\alpha^{(v)}$ were either site-dependent or not, and we compared the fit of that model when $\alpha^{(v)}$ was fully age-specific with the same model but with $\alpha^{(v)}$ given by Eq. 1 or 2. Second, having chosen a model for $\alpha^{(v)}$, we determined the value of m for which the estimates of $\alpha^{(v)}$ were equal to 1 for all $v \geq m$. Finally, having chosen a model for $\alpha^{(v)}$ and a value for m , we compared the fit of the 16 models in which $\phi^{(0)}$, $\theta^{(k+)}$, $\phi^{(k+)}$, and $\alpha^{(v)}$ were either site-dependent or not.

All models were fitted by the multi-state modeling option in program Mark (White and Burnham 1999), and we performed a multi-state lack-of-fit test in UCare (Choquet et al. 2009). We

summarized the fit of each model with AIC_c , adjusted for any overdispersion evident from the lack-of-fit test, and used model averaging to obtain final estimates of the parameters (Burnham and Anderson 2002). Where appropriate, estimates of parameters are followed by 95% confidence intervals in parentheses.

BIAS IN AFR FROM NOT ACCOUNTING FOR DETECTION PROBABILITY

We estimated the amount of bias that might be expected if detection probability is ignored and the mean observed AFR is used to estimate the true mean (μ_{AFR}). The positive bias caused by not observing individuals for one or more years after they first return should decrease when detection probability increases. The negative bias caused by the end of the study effectively truncating the data should be greater for later cohorts, with a corresponding greater negative bias for cohorts combined in longer studies. Appendix 2 gives details of the calculations used to estimate the expected mean observed AFR, both for individual cohorts and overall.

We gauged the effect of bias in the mean observed AFR on management decisions by considering the resulting bias in estimation of the logarithm of maximum population growth rate ($r_{max} = \log \lambda_{max}$, where λ_{max} is maximum population growth rate; Niel and Lebreton 2005). This is the growth rate we would expect in a small population under ideal conditions. Sustainable harvest and limits for accidental bycatch are sometimes chosen to be proportional to r_{max} (Hunter and Caswell 2005, Niel and Lebreton 2005, Dillingham and Fletcher 2008). Niel and Lebreton (2005) used allometric relationships to provide a formula for λ_{max} that should be reliable for most bird species. This formula is

$$\lambda_{max} = \exp[1/T^{(opt)}], \quad (5)$$

where $T^{(opt)}$ is generation time for a population experiencing optimal conditions. There are several definitions of generation time, a natural one being the mean age of mothers at child-birth. If the reproductive rate and survival probability are the same for all adults, this leads to

$$T^{(opt)} = \mu_{AFB}^{(opt)} + \phi_A^{(opt)} / [\lambda_{max} - \phi_A^{(opt)}], \quad (6)$$

where $\mu_{AFB}^{(opt)}$ and $\phi_A^{(opt)}$ are assumed “optimal” values of μ_{AFB} and ϕ_A (Gaillard et al. 2005). Eqs. 5 and 6 can be solved iteratively for λ_{max} . Now, $\mu_{AFB} = \mu_{AFR} + \mu_p$ where μ_p is the mean time spent as a pre-breeder, between arrival at the colony and first breeding. An estimate of μ_p is not easy to obtain for the Sooty Shearwater (Section 1), so we used the estimate given by Bradley et al. (1999) for the Short-tailed Shearwater.

RESULTS

GOODNESS OF FIT

For both sites, the overall goodness-of-fit test for the Jolly–Movement model (the multi-state version of the Cormack–Jolly–Seber model; Pradel et al. 2005) showed clear evidence

of lack of fit (Taiaroa Head: $\chi^2_{82} = 111.0$, $P = 0.02$; The Snares: $\chi^2_{49} = 143.8$, $P < 0.001$). After the component of this test that corresponds to transience was removed, the fit was satisfactory for both sites (Taiaroa Head: $\chi^2_{71} = 69.0$, $P = 0.54$, $\hat{c} = 0.97$; Snares: $\chi^2_{42} = 44.1$, $P = 0.38$, $\hat{c} = 1.05$). We included transience in all our models, so we made no adjustment for overdispersion to the AIC_c values.

COMPARISON OF MODELS

In the first step of the selection of models, for each of the 16 models in which $\phi^{(0)}$, $\theta^{(k+)}$, $\phi^{(k+)}$, and $\alpha^{(v)}$ were either site-dependent or not, use of Eq. 2 provided a better fit than either Eq. 1 (ΔAIC_c ranging from 8.4 to 11.4) or fully age-specific $\alpha^{(v)}$ (ΔAIC_c ranging from 0.3 to 4.6). For each of the 16 models using Eq. 2, the estimates of $\alpha^{(v)}$ were equal to 1 for $v \geq 6$, so we set $m = 6$. Likewise, for each of these models, use of $k = 2$ led to a better fit than did $k = 1$, so we focus solely on models with $k = 2$. Table 1 provides a summary of the fit of the final set of models, in which $\phi^{(0)}$, $\theta^{(k+)}$, $\phi^{(k+)}$, and $\alpha^{(v)}$ were either site-dependent or not, where the subscript s indicates site-dependence in that parameter. No single model stood out as the best, but the sum of the weights of the top four models was 0.927, suggesting that the juvenile survival and transience parameters are site-dependent. Conversely, the data appear not to be sufficient for an assessment of whether there is site dependence in adult survival or AFR.

AGE-SPECIFIC PROBABILITIES OF FIRST RETURN

Figure 1 shows the model-averaged estimates of $\alpha^{(v)}$ for each site, together with model-averaged estimates from the same set of models but with $\alpha^{(v)}$ fully age-specific. Note that the latter estimates are shown only for ages 2, 4, and 5, because the estimates for age 3 from individual models were unreliable, often having confidence intervals spanning the range from 0 and 1. As with lack of convergence of the estimation process, it is not uncommon for reliable estimation of one or more parameters to be difficult when a multi-state model is fitted to sparse data (Kendall et al. 2003). At Taiaroa Head, the mean of the estimated AFR distribution is 4.7 years, while that for The Snares is 4.9 years.

For each site, the distribution of the estimated AFR (derived by Eq. 3) and the corresponding observed AFR are shown in Fig. 2. For both sites, the distribution of the estimated AFR is shifted to the left of that of the observed AFR, representing some birds returning one or more years before being observed. At Taiaroa Head, the mean of the observed AFR is 5.7 years ($n = 66$), a positive bias of one year, while at The Snares, it is 5.4 years ($n = 93$), a positive bias of 0.5 years.

PROBABILITIES OF SURVIVAL AND RECAPTURE

The estimates of $\phi^{(0)}$ were 0.29 (0.21–0.37) for Taiaroa Head and 0.17 (0.12–0.22) for The Snares, corresponding to annualized estimates $[\phi^{(0)}]^{1/2}$ of 0.54 (0.46–0.61) and 0.41 (0.35–0.47), respectively. The estimates of $\theta^{(2+)}$ were 0.75

TABLE 1. Comparison of models by AIC_c . Δ is the difference between the AIC_c for the model and that for the model with the lowest AIC_c ; w is the AIC_c weight of that model; K is number of parameters; Dev is the model's deviance; $\phi^{(0)}$ is the probability of surviving from age 0 to age 2; $\theta^{(2+)}$ is the probability that an unmarked adult captured in year i survives until year $i + 1$ and remains in the population; $\phi^{(k+)}$ is the probability that a marked bird of age ≥ 2 that is alive in year i survives until year $i + 1$ and remains in the population; $\alpha^{(v)}$ is the probability that a bird of age v will be present at the colony in any given year, given that the bird is alive in that year, has not previously returned to the colony, and will return to the colony at some stage in its lifetime. Use of the subscript s signifies site dependence in that parameter. In all models we specified the relationship between $\alpha^{(v)}$ and v as in Eq. 2, with $k = 2$ and $m = 6$.

Model	Δ	w	K	Dev
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	0.00 ^a	0.391	31	21580.7
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	0.36	0.327	33	21577.0
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	2.46	0.114	32	21581.1
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	2.86	0.094	30	21585.5
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	6.31	0.017	32	21585.0
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	6.53	0.015	31	21587.2
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	6.55	0.015	30	21589.2
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	7.10	0.011	32	21585.8
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	8.62	0.005	31	21589.3
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	8.73	0.005	29	21593.4
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	10.31	0.002	31	21591.0
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	10.44	0.002	30	21593.1
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	12.55	0.001	30	21595.2
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	13.24	0.001	29	21597.9
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	15.10	0.000	29	21599.8
$\{\phi_s^{(0)} \theta_s^{(2+)} \phi_s^{(2+)} \alpha_s^{(v)}\}$	15.64	0.000	28	21602.3

^a $AIC_c = 21642.8$.

(0.69–0.79) for Taiaroa Head and 0.65 (0.60–0.70) for The Snares, while those for $\phi^{(2+)}$ were 0.88 (0.85–0.90) and 0.91 (0.87–0.94), respectively. The transience effect that we had expected is borne out by $\theta^{(2+)}$ being less than $\phi^{(2+)}$ at the same site (Pradel et al. 1997). At Taiaroa Head the annual recapture probabilities ranged from 0.00 to 0.40 (mean = 0.20) for a bird seen in the previous year, and from 0.00 to 0.36 (mean = 0.17) for a bird not seen in the previous year; at The Snares, they ranged from 0.08 to 0.38 (mean = 0.18) and from 0.07 to 0.33 (mean = 0.15), respectively.

BIAS IN AFR FROM NOT ACCOUNTING FOR DETECTION PROBABILITY

Figure 3 shows the relationship between the mean observed AFR for each cohort and detection probability (assumed to be constant) for a 20-year study in which the distribution of AFR estimated for Taiaroa Head is used as the true AFR (true mean AFR = 4.7). For simplicity of presentation, we show the results for only half of the cohorts. For all cohorts with at least 6 years between banding and the end of the study, the mean observed AFR decreases when

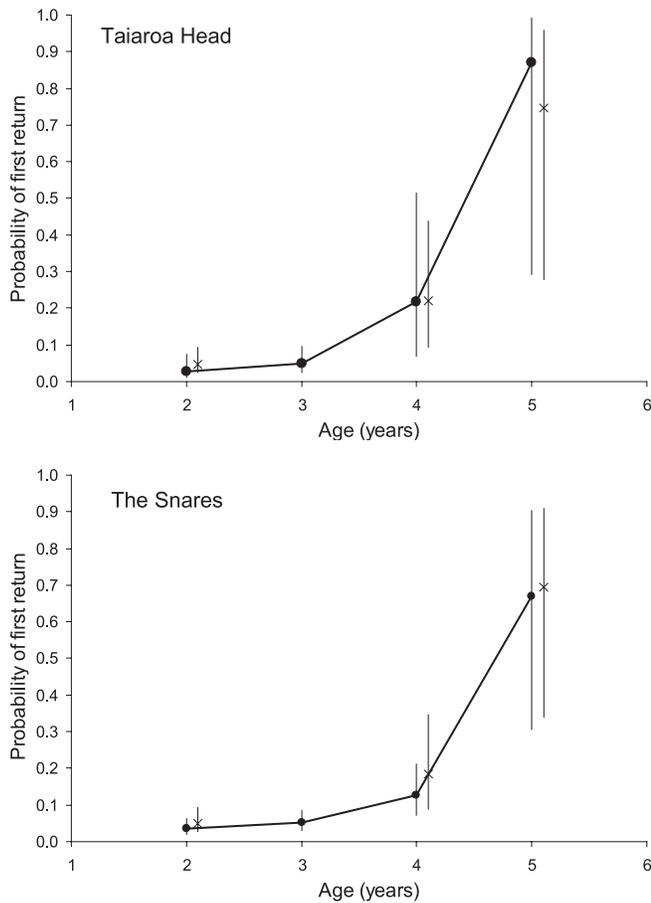


FIGURE 1. Model-averaged estimates and 95% confidence intervals for $\alpha^{(v)}$, the probability of first return at age, v , of Sooty Shearwaters at Taiaroa Head and the Snares, based on a model in which $\alpha^{(v)}$ has a linear-logistic relationship with e^v (black circles) or one in which $\alpha^{(v)}$ is fully age-specific (crosses; shifted to the right of the relevant age for presentation).

detection probability increases (Fig. 2). The strong positive bias caused by the detection probability being less than 1, evident for early cohorts, is moderated by the negative bias caused by the end of the study truncating the maximum age at which birds of later cohorts can first be observed breeding. The benefit from increasing the detection probability is greatest for the earlier cohorts. For cohorts with less than 6 years between banding and the end of the study, the negative bias caused by truncation of the data completely outweighs the effect of the detection probability.

We now consider the overall mean observed AFR, using data from all cohorts. Figure 4 shows the relationship between this mean and detection probability for a 10, 15 or 20-year study with cohorts of equal size, again assuming that the distribution for the true AFR is the same as that estimated for Taiaroa Head. The bias is generally positive, decreasing when the detection probability increases, and becoming slightly negative when the detection probability approaches one. In addition, the mean increases when

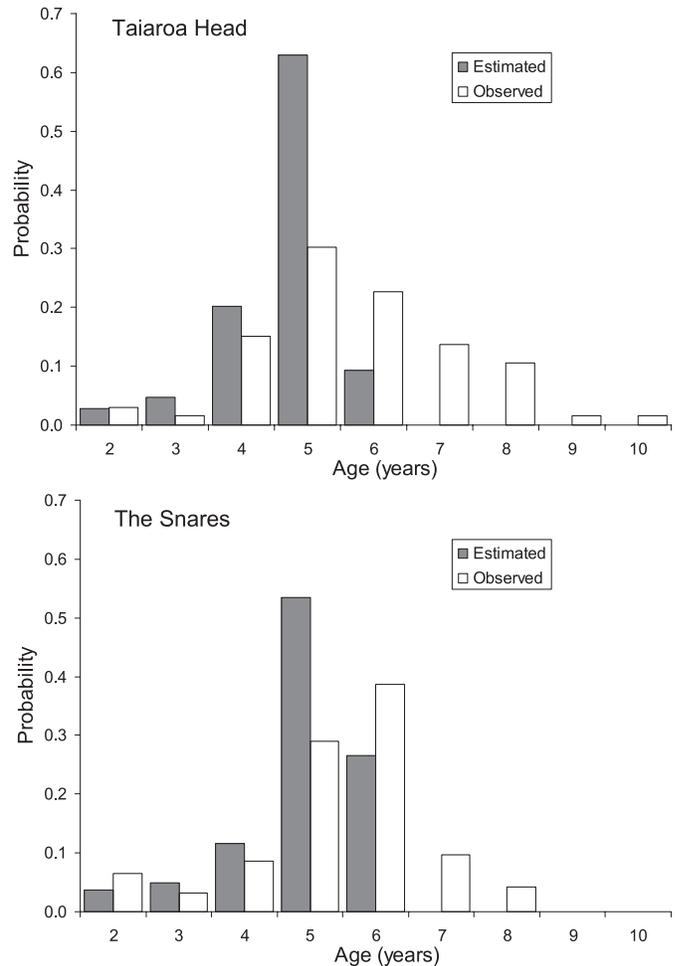


FIGURE 2. Estimated and observed distributions of AFR of Sooty Shearwaters at Taiaroa Head and The Snares.

t increases, with bias greatest for a 20-year study with a low detection probability; for shorter studies the truncation bias cancels out some of the bias caused by low detection probability (Fig. 3).

For the Short-tailed Shearwater, Bradley et al. (1999) estimated μ_{AFR} to be 4.1 years and the mean age at first breeding to be 7.0 years. This leads to an estimate for μ_p of 2.9 years. If we combine the estimates of μ_{AFR} from Taiaroa Head and The Snares, we have an estimate of μ_{AFB} of $(4.7 + 4.9)/2 + 2.9 = 7.7$ years. If we use this as an estimate of $\mu_{AFB}^{(opt)}$ and set $\phi_A^{(opt)} = 0.91$ (the higher of the two estimates of ϕ_A), we have $T^{(opt)} = 13.1$ years and $r_{max} = 7.7\%$. It may be useful to express the estimates of μ_{AFR} and μ_{AFB} in terms of $T^{(opt)}$, for the purpose of comparison across species: they are 0.37 and 0.59 generations, respectively.

If we had used the mean of the observed AFR at the two sites, we would have obtained an estimate of μ_{AFB} of $(5.7 + 5.4)/2 + 2.9 = 8.45$ years, a positive bias of 10%. This in turn would have led to $r_{max} = 7.1\%$, a relative bias of -7% , which would lead to underestimation of the sustainable harvest level

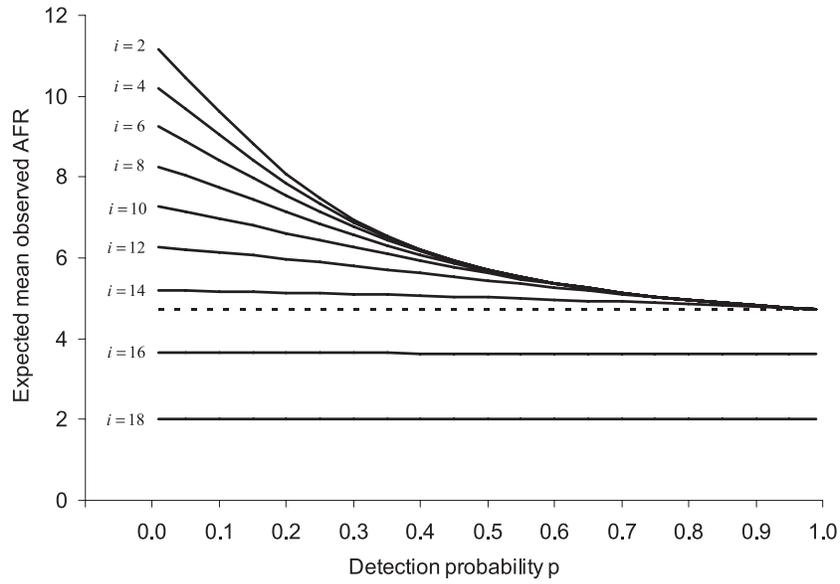


FIGURE 3. Expected mean observed AFR for individual cohorts banded in year i ($i = 2, 4, \dots, 18$) of a 20-year study versus detection probability. The dotted line shows the mean of the true distribution for AFR, which is taken to be the estimated AFR distribution for Taiaroa Head (true mean AFR = 4.7).

by the same amount (Hunter and Caswell 2005). Figure 5 shows the estimate of r_{\max} that would result from using the mean of the predicted distribution for the observed AFR over a range of detection probabilities, for a 10, 15 or 20-year study with cohorts of equal size, assuming that the distribution for the true AFR is the same as estimated for Taiaroa Head and that we set $\phi_A^{(\text{opt})} = 0.91$. Note that the bias calculations given here ignore possible bias in estimation of μ_p and ϕ_A ; in

particular, a small bias in the latter may have a substantial effect on estimation of r_{\max} .

DISCUSSION

ESTIMATING AFR AND AFB

Published papers on the demography of the Procellariiformes typically report only observed age at first return and/or age at

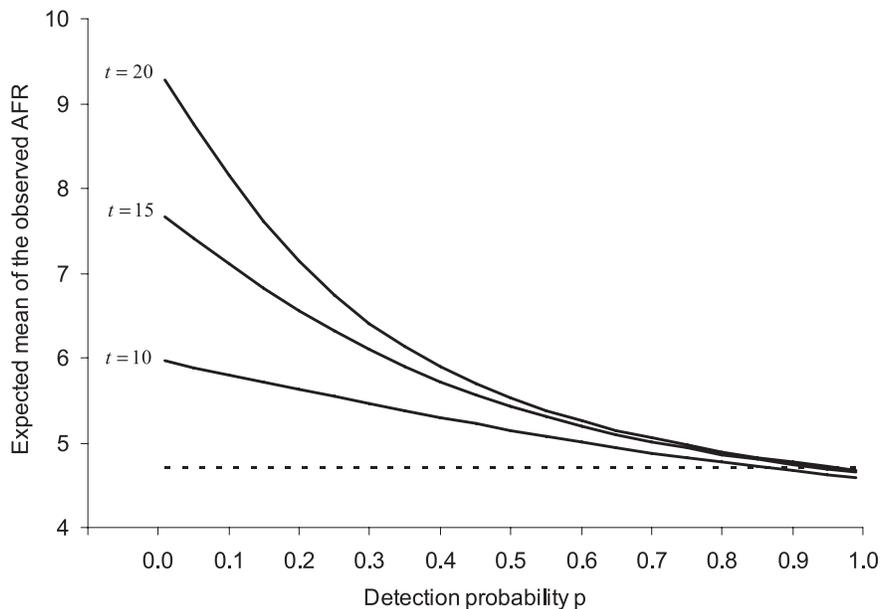


FIGURE 4. Expected mean observed AFR versus detection probability for a study lasting t years ($t = 10, 15, 20$) and with cohorts of equal size. The dotted line shows the mean of the true distribution for AFR, which is taken to be the estimated AFR distribution for Taiaroa Head (true mean AFR = 4.7).

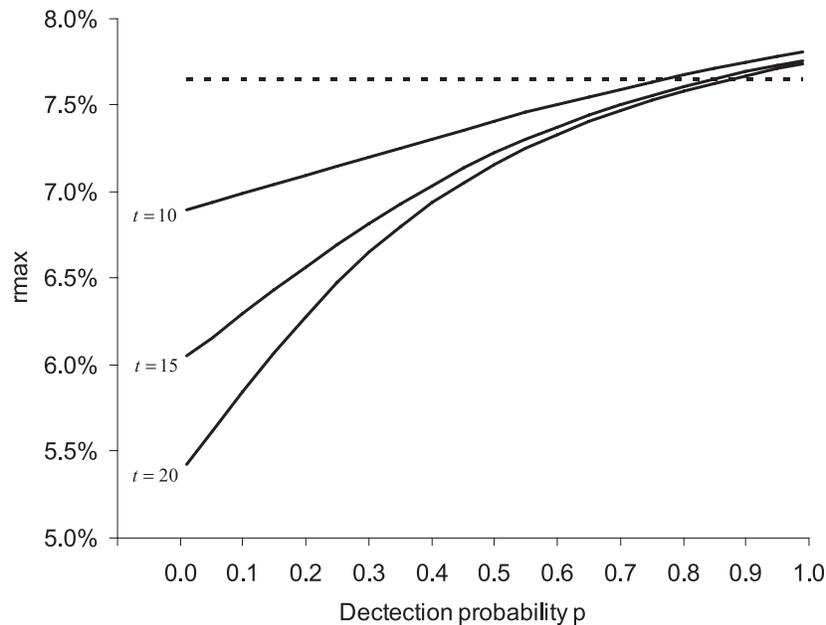


FIGURE 5. Estimated maximum population growth rate (r_{\max}) versus detection probability, with $\phi_A^{(\text{opt})} = 0.91$ and the expected mean observed AFR as an estimate of μ_{AFR} , for a study of duration t years ($t = 10, 15, 20$) and cohorts of equal size. The dotted line shows the estimate of r_{\max} corresponding to the true distribution for AFR, which is taken to be the estimated AFR distribution for Taiaroa Head (true mean AFR = 4.7).

first breeding (e.g., Warham 1996). Use of a mark–recapture model is more reliable, in that it allows for imperfect detectability of adults. In effect, it provides a way of adjusting the observed AFR to allow for the fact that some individuals will have returned one or more years *before* being observed at the colony. It also allows for missing years of data, if recaptures are not made during every year of the study. Nevertheless, there may still be estimation problems. If, as in our study, few birds banded as chicks return to the colony, the uncertainty around age-specific estimates of probabilities of first return may be large. Our choice of a monotonically increasing function to describe the relationship between probability of first return and age can be viewed as a simple default option. We found that a linear-logistic relationship between probability of first return and $\exp(\text{age})$ provided a much better fit than a similar relationship with age, because the latter could not adequately model the apparent sharp increase in this probability between four and five years of age. Given the importance of age at first breeding for fitness and population growth, and the consequent selection pressure assumed to operate on age at first breeding in birds and mammals (Williams 1966, Begon et al. 1990), it is surprising that this topic has received so little attention.

We have illustrated how ignoring the detection probability generally leads to the mean of the observed AFR overestimating the true mean AFR. This bias is larger than the negative bias caused by data truncation in the later cohorts, except in studies that are extremely short relative to the recruitment process, and is actually worse for longer studies.

Our results also suggest that the bias the duration of a study causes in the estimate of mean AFR obtained from a mark–recapture model should be negligible. We therefore recommend that mark–recapture models such as those described here be used in studies of seabird recruitment. The necessarily long duration required for a study of a seabird population, and the complexity involved in estimating the probability functions for first return and first breeding, may explain the lack of such information for seabirds, particularly for long-lived Procellariiformes. Note that this issue will tend to be more important for burrow-nesting seabirds (such as the Sooty Shearwater) than for the larger surface nesters, such as albatrosses, which are more readily detected.

Estimates of the time between AFR and AFB in the Procellariiformes have been reported mainly for the larger, more easily observable albatrosses (Croxall et al. 1990, Weimerskirch 1992, Robertson 1993). This delay between first return and breeding is likely to be related to the species' position along the slow-to-fast demographic continuum (Sæther and Bakke 2000), with delays longer for the slower (larger) albatrosses. Estimates for these species are therefore unlikely to be similar to those for the Sooty Shearwater. Instead we assume that the average 2.9-year delay between AFR and AFB observed for the Short-tailed Shearwater (Bradley et al. 1999) also applies to the Sooty Shearwater. Short-tailed Shearwaters average ~550 g, whereas the average weight of an adult Sooty Shearwater we recorded on The Snares was 850 g (SE = 8 g, $n = 400$). The only other estimate for a species with similar demography (Jenouvrier et al. 2003) is a delay of 3.0 years between AFR

and AFB in the Southern Fulmar (*Fulmarus glacialisoides*; ~1000 g, AFR = 8, SD = 3; AFB = 11, SD = 4). Using the Short-tailed Shearwater's average delay and the mean of our two site-specific estimates for mean AFR leads to an estimate of mean AFB of 7.7 years in the Sooty Shearwater.

It is likely that AFR and AFB are determined by a mix of fixed physiological and behavioral maturation constraints and more labile environmental influences like feeding conditions and site-specific influences on breeding like the availability of mates or nest sites. Lifetime reproductive fitness is probably subject to strong selective pressures (Stearns 1976) that balance the benefits of breeding early (as soon as it is safe and likely to be successful) against the risk of breeding too early (reduced survival of adults or chicks, or impaired future reproductive success). The Procellariiformes have a "prospecting" stage in which prebreeders move around potential breeding sites and when density-dependent effects such as availability of breeding space and mates could hasten or delay onset of breeding, or change rates of immigration or emigration from natal colonies (Warham 1996, Moller et al. 2009a). This suggests a need to allow for variation in this delay in a population model, as well as a need for further estimates of this delay and research into what determines it.

ESTIMATES OF JUVENILE SURVIVAL

Our estimates of the probability of the Sooty Shearwater's annual survival in the first two years of life were 0.54 for Taiaroa Head and 0.41 for The Snares, both lower than that of 0.71 for the Short-tailed Shearwater (multiplying the probability of reappearance from fledging to year 1 and the probability of reappearance from year 1 to year 2, in table 2 of Hunter et al. 2000). Survival of juveniles being lower on The Snares than at Taiaroa Head is consistent with our expectation that juvenile demographic parameters are more site-specific and labile than those for adults. The size and condition of the fledglings affects their probability of return to their natal colony (Sagar and Horning 1997), presumably by determining the probability of successful migration of juveniles to the Northern Hemisphere immediately after fledging. Chicks' body condition varies considerably between colonies, and even between parts of colonies (Bragg et al. 2007). Also the "apparent" survival rate of juveniles is partly determined by probability of juveniles' returning to the natal colony where they were banded (emigrants to other colonies will be counted as dead), and that in turn is probably affected by site-specific factors like availability of mates and nests. In contrast, adults remain at the same site once they begin breeding there, so variation in transience and immigration/emigration do not add local variation to rates of adults' apparent survival. Also, adults move over a huge area to exploit patches rich in food, where density-dependent competition is very unlikely (Shaffer et al. 2009), and adult seabirds conserve their own survival by quickly abandoning chicks if deteriorating ecological conditions risk their long-term reproductive fitness (Warham 1996,

Efford and Edge 2006). It is the vital rates in early life (survival of eggs, chicks, and juveniles, immigration and emigration of pre-breeders) that may be the most density-dependent; these therefore have the greatest potential to trigger compensatory changes to ameliorate the effects of harvest and bycatch (Moller 2006).

Note that if survival of juveniles is estimated empirically, by the proportion of chicks observed to return to the colony, for example, imperfect detectability will lead to underestimation of this parameter, in addition to the overestimation of AFB. If a population growth rate is estimated with a demographic model that involves juvenile survival and AFB, bias in the estimates of these parameters might lead to substantial underestimation of the growth rate. The method by which we estimated the maximum population growth rate (Eqs. 5 and 6) does not require an estimate of juvenile survival, as use of allometric relationships means it is based solely on estimation of AFB and adult survival (Niel and Lebreton 2005).

IMPLICATIONS FOR SOOTY SHEARWATER MANAGEMENT

The Sooty Shearwater is culturally important and listed as "near threatened" because of recent population declines (Scott et al. 2008, Clucas 2011, Clucas et al. 2012), despite numbering in the millions (Warham and Wilson 1982, Miskelly et al. 2001, Newman et al. 2009b). Until this study, the only published estimate of the Sooty Shearwater's AFB was 6 years at Whero Island (Richdale 1963). Preliminary models of the population used the AFB of 6 years from Whero (Hamilton and Moller 1995) or substituted 7.1 years, the estimate for the Short-tailed Shearwater from Fisher Island (Hunter and Caswell 2005), whereas we estimate it to be 7.7 years. Uncertainty analyses show that age at first breeding has a large effect on shearwaters' rate of population growth (Hamilton and Moller 1995, Hunter et al. 2000), so the population-viability models for the Sooty Shearwater will have greatly overestimated the population's resilience to marine catastrophes (Hamilton and Moller 1995), and predicted effects of harvest pressure (Hunter and Caswell 2005) will have been slightly underestimated.

Delayed breeding makes the Sooty Shearwater population relatively slow to respond to management. Models imply that around a third of the population decline since the mid-1970s was driven by mortality due to large-scale drift-net fishing in the northern Pacific Ocean (Bragg et al. 2007, Moller et al. 2010). Cessation of drift netting in 1991 may have triggered a sharp improvement in survival of both juveniles and adults, but estimates of the size of this release are very uncertain (Uhlmann et al. 2005). Our study suggests that it was 8 or 9 years before most of the refreshed cohort of young saved from risk of drowning in drift nets in mid-1991 began breeding in 1999–2000. A further surge in chick production would have been expected in 2007–2008 once most of the offspring of the first refreshed cohort reached breeding age. An indirect test of whether drift-net fishing drove a substantive

part of the Sooty Shearwater's decline will therefore be whether there was an upswing in the number of chicks produced in the late 1990s, and especially whether a geometric upswing in chick numbers occurred around the mid to late 2000s, when the second generation of drift-net survivors entered the breeding population. Similarly the removal of introduced rats and the Weka (*Gallirallus australis*), predators of Sooty Shearwater eggs and chicks, from some breeding colonies in 2006 (McClelland et al. 2011) should not trigger pulses of added recruitment until around 2015 and 2023. In view of the delayed breeding and large annual fluctuations in the Sooty Shearwater caused by large-scale climate variation (Lyver et al. 1999, Bragg et al. 2007, Moller et al. 2010), another 15–20 years of monitoring will be required before conservation managers and Rakiura Māori tītī harvesters can confidently conclude whether or not elimination of fisheries bycatch and removal of introduced predators has been sufficient to reverse decades of population decline.

THE NEED FOR A GENERIC DEMOGRAPHIC MODEL FOR THE PROCELLARIIFORMES

In view of the potential bias in estimates of AFR and AFB discussed above, it is not clear whether the unexplained variation that has arisen in previous attempts to generate predictive relationships between body size and demographic parameters in the Procellariiformes (Warham 1996, Weimerskirch 2002) derives mainly from methodological difficulties or genuine variability in ecological and physiological constraints and conditions. Analyses accounting for phylogenetic inertia in such datasets often result in elevated variation around allometric relationships. Scaling key parameters such as AFR or AFB against an estimate of generation time (Niel and Lebreton 2005, Dillingham and Fletcher 2008) may allow for development of a generic population model for the Procellariiformes, based on a meta-analysis of studies of very different species, families, sizes, and breeding systems (annual and biennial breeders, for example). In this way a larger number individual studies may be combined to predict gaps for species requiring management. A similar approach has been used for mammals both by Barlow and Boveng (1991) and Caswell et al. (1998).

Predictive models to guide conservation and sustainable harvest would be particularly valuable for the Procellariiformes (Moller 1996, Robertson and Gales 1998) because their slow population turnover makes estimation of population parameters for populations and species especially problematic. Despite a large amount of banding and 14 years of exhaustive and expensive field work, our estimates of a subset of early-stage population parameters for the Sooty Shearwater remain approximate. Had a robust generalized model been available, we could have been more confident of preliminary estimates garnered from the congeneric Short-tailed Shearwater. We could then have concentrated more of our effort on estimation of adult survival, which elasticity analyses identified as the most important determinant of sustainable levels of Sooty

Shearwater (Hunter et al. 2000), as well as determination of putative density-dependent effects that might determine harvest compensation (Moller et al. 2009a).

A generalized demographic model standardized by generation time and predicted from allometrics and phylogeny must first be built from the few detailed long-term population studies available and critical examination of biases of the type explored in our study. If such a model successfully predicted outcomes for those well-studied species, even for just some of their population parameters, it may allow preliminary modeling for guiding management of little-studied species. This would be especially helpful for recovery of threatened seabirds for which conservation decisions must be made immediately and long before precise parameter estimates become available. In the meantime, conservation managers can be encouraged by the potential for overestimation of age at first breeding and underestimation of juvenile survival in many past studies, as some demographic models may have underestimated the rate of population increase and the consequent resilience of many Procellariiformes to increasingly serious conservation threats.

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