

Estimates of adult survival rate for three colonies of Sooty Shearwater (*Puffinus griseus*) in New Zealand

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Abstract. The Sooty Shearwater (*Puffinus griseus*), also known in New Zealand as tītī or muttonbird, is an abundant, long-lived, trans-equatorial migrant that breeds in colonies in the southern hemisphere during the austral summer and migrates to and forages in the North Pacific Ocean during the boreal summer. That populations of Sooty Shearwaters have been declining has been indicated by falling oceanic counts, and reduced burrow density and declining rates of chick harvest of Rakiura Māori muttonbirders. Accurate estimation of adult survival rate of Sooty Shearwaters is vital if we wish to use a demographic model to help understand the decline and manage the population. Mark–recapture studies were carried out at three breeding colonies: Taiaroa Head, Whenua Hou and The Snares, all in southern New Zealand. Analysis of the data generally involved the use of models in which both transience and trap-dependence were allowed for. In addition, birds were split into two groups, according to whether they had been caught on the surface or under an inspection hatch that was placed over a breeding chamber. Our estimates of the level of transience suggest that a large portion of the population at each colony is composed of juvenile and pre-breeding birds. Model-averaged estimates of the survival rate for resident birds were 0.917 (95% C.I.: 0.860–0.973) at Taiaroa Head, 0.966 (0.933–0.997) at Whenua Hou, and 0.961 (0.706–0.996) at The Snares. A combined estimate for The Snares and Whenua Hou is 0.952 (0.896–0.979). Our estimates are higher than earlier estimates of survival for Sooty Shearwaters and congeners, presumably because transience has been more adequately accounted for than in earlier mark–recapture models.

Additional keywords: Mark–recapture modelling, Procellariiformes, tītī, transience

Introduction

The Sooty Shearwater (*Puffinus griseus*), also known to the New Zealand Māori as tītī or muttonbird, is considered to be one of the most abundant seabirds of the southern hemisphere (Richdale 1963). Within New Zealand (NZ), the largest known breeding colonies of Sooty Shearwater are on islands around Rakiura (also known as Stewart Island) (Richdale 1965; Warham and Wilson 1982). The colony at The Snares is the largest, with ~2 million shearwater burrow entrances, with an estimated occupancy rate of 61% (Scofield 2001). Although many colonies existed along the coast of the both the North and South Islands historically, few remain. Relict colonies occur primarily along the eastern coast of the South Island but most are small and are threatened with local extinction owing to predation by introduced mammals (Jones 2000). Internationally, colonies are reported on the southern coast of Chile and, although the size of these colonies is not known, the population at Isla Guafo was estimated by Clark *et al.* (1984) to consist of at least 200 000 birds during September–October (early breeding season). Smaller colonies occur off Tasmania, Australia (Wood-Jones 1936; Brothers 1979; Lane and White 1982).

Breeding birds return to the southern hemisphere for the austral summer, laying a single egg within excavated burrows (Richdale 1944; Warham 1990; Shaffer *et al.* 2006). Typically,

seabirds exhibit delayed breeding, low reproductive output and high survival rate of breeding birds relative to other bird taxa (Ashmole 1971; Jouventin and Weimerskirch 1991; Wooller *et al.* 1992). The period of monitoring necessary to detect long-term population trends in seabirds is thus comparatively long. In combination with their long reproductive span, this means that long-term trends in survival rate or abundance are subject to time lags outside the scope of most field studies (Wooller *et al.* 1992). Recent shifts in the abundance of the Sooty Shearwater on the western seaboard of North America, have highlighted potential dramatic impacts of climate change on marine ecosystems (Veit *et al.* 1997; Wahl and Tweit 2000; Oedekoven *et al.* 2001; Hyrenbach and Veit 2003).

A customary harvest of Sooty Shearwater chicks by Rakiura Māori occurs just before fledging on the Tītī Islands adjacent to Rakiura, NZ. Rakiura Māori were keen to assess whether the harvest is sustainable in the long-term, given climatic fluctuations, by-catch (Uhlmann 2002) and social and technological change (Lyver and Moller 1999), all of which may be having an impact on population dynamics. Systematic banding of chicks and adult birds was undertaken as part of the Kia Mau te Tītī mo Ake Tōnu Atu ('Keep the Tītī Forever') Project (Moller *et al.* 1999) in order to ascertain vital rates for estimating population trends and harvest sustainability.

Sensitivity and elasticity analyses are now commonly used to highlight the key vital rates when modelling population trajectories (Hamilton and Moller 1995; Heppell *et al.* 2000). In long-lived vertebrates, including birds, survival of breeders is one of the parameters that has greatest influence on population growth rate (Saether and Bakke 2000). Hunter *et al.* (2000) used elasticity and uncertainty analyses to provide a preliminary assessment of the research priorities for the Kia Mau te Tīti mo Ake Tōnu Atū Project. They made use of demographic estimates from a conspecific of the Sooty Shearwater, the Short-tailed Shearwater (*Puffinus tenuirostris*) (Wooller *et al.* 1988, 1989, 1990). That preliminary analysis (Hunter *et al.* 2000) highlighted that population models and predictions of harvest sustainability rely on accurate estimation of survival of breeding Sooty Shearwaters, which is therefore the main aim of this paper.

Methods

Captures of Sooty Shearwater

The estimates of survival rate that we obtain are based on mark–recapture studies of birds of unknown age at three locations: Taiaroa Head, Whenua Hou (Codfish Island) and The Snares (see below for location details). The Sooty Shearwater returns to the southern islands for pair formation and copulation, burrow prospecting and preparation in early October, and all young fledge by the end of May (Richdale 1954). When banding activities began before laying, banding stopped temporarily during the incubation period, and recommenced after the hatching phase. We avoided handling during incubation because researcher-disturbance during the laying phase has been associated with reduced colony attendance in the Short-tailed Shearwater and may also discourage birds from breeding (Serventy and Curry 1984; Bradley *et al.* 1999). Birds were caught at night on the surface, either as they landed or when they were found resting on the surface. Hatch-caught birds were removed from their burrows via a hatch covering. Typically a hatch-covering is a plywood or ceramic tile placed over the nesting area of the burrow to facilitate researcher access to the nesting bird. A few birds were captured at the entrance to a burrow, rather than from beneath a hatch; each of these was considered to be associated with the burrow as a breeding bird, and was therefore regarded as equivalent to a hatch-bird. Most birds were weighed and measured during handling. A single numbered stainless steel band (National Museum of New Zealand, Wellington) was applied to the tarsus.

Study populations

Two of the study locations, Whenua Hou and The Snares, are island colonies, where mark–recapture began in the 1995 and 1996 seasons respectively (Moller *et al.* 1999). Banding at the mainland colony of Taiaroa Head provides the longest data series, of 14 breeding seasons, with banding occurring between 1992 and 2005. Throughout the paper we use the term ‘location’ to refer to the whole colony on an island, and ‘site’ to refer to a particular study area within a location (Fig. 1). In addition, we define an adult bird to be one that is at least two years old (the youngest age at which individuals have been observed to return to their natal colony).

Before our study, other monitoring programs had banded a total of 6728 Sooty Shearwaters throughout NZ (Cossee 1993), including some at the three locations considered here, but few banded birds were recaptured in this study period. For example, at Taiaroa Head only five birds have been recaptured from among those banded at the colony between 1973 and 1984. In order to avoid complications in the analysis, capture histories for birds with prior banding were taken to begin at their first capture during our study period. Very few birds that were recaptured in this study were prior bandings from elsewhere. At Taiaroa Head, there were 11 birds captured that had been banded in six other known locations: for these birds their capture history was also considered to start at their first capture during this study. Although some banding effort continued until May, we removed all April and May bandings from this part of the analysis, as there was the potential for mistakenly identifying fledglings as adults during this late stage of the season.

The other main breeding colonies in NZ are managed under The Tīti (Muttonbird) Island Regulations 1978, for harvest purposes by Rakiura Māori (these colonies contain an estimated 59% of New Zealand birds; Bragg *et al.* 2007). Not only was this portion of the population of greater relevance to harvest management than the three locations we studied, owing to ongoing research on the sustainability of harvest, it was also logistically easier and less expensive to obtain information from these colonies. Unfortunately, access to these colonies was not permitted during the periods required for mark–recapture.

Taiaroa Head (45°49.80'S, 170°43.20'E)

The study area is situated within the last remaining substantial mainland colony, at Taiaroa Head, on the Otago Peninsula (Hamilton *et al.* 1997). It consists of ~2 ha of grazed exotic grassland growing in a fragile sandy substrate, with ~2100 burrows (Lyver 2000; McKechnie 2004). All birds captured



Fig. 1. The three study locations: Taiaroa Head, Whenua Hou and The Snares, New Zealand.

here were caught on the surface. Taiaroa Head is the only one of the three study locations where the threat of predation by introduced mammals still exists. The persistence of this colony is probably due to the high level of predator control at the nearby colony of northern Royal Albatross (*Diomedea epomophora*) (Jones 2000). Predation by mustelids, particularly Stoats (*Mustela erminea*), is the primary threat to mainland colonies, though cats (*Felis catus*) and rats (*Rattus* sp.) also take a large toll (Lyver 2000). Common Brushtailed Possums (*Trichosurus vulpecula*), which are also present within the colony, may depredate eggs and disturb nesting birds.

Whenua Hou (Codfish Island) (46°45'S, 167°38'E)

The Whenua Hou colony is the largest population of unharvested birds in proximity to the harvested birds on the Tītī Islands (Moller *et al.* 1999). Although it is only 40–50 km from the Tītī Islands, its vegetation (pakihi bogs (poorly drained soils, low in nutrients and fed by rainwater), scrubby coastal assemblages and tall mixed podocarp forests) and underlying geology differ from those on the Tītī Islands (D. Scott, unpubl. data). Pacific Rat (or Kiore, *Rattus exulans*) were eradicated from the island in 1998, during the fourth field season of this study, while both Weka (*Gallirallus australis*) and Common Brushtailed Possum had been removed by 1987 (McClelland 2002). The New Zealand Wildlife Service eradicated the Common Brushtailed Possum from Whenua Hou between 1984 and 1987 and Stewart Island Weka (*Gallirallus australis scottii*) in 1984. The Department of Conservation banded several birds throughout the 1980s (Hamilton *et al.* 1996), although none were recaptured during this study. Banding of adults in our study spanned 10 breeding seasons, between 1996 and 2005. Mark–recapture effort occurred within three spatially separate sites on the eastern side of the island. The three sites differed in area, vegetation and topography: Site A (2226 m²) was low-lying and near a small area of sandy beach; Site B (513 m²) was slightly inland and elevated; while Site C (1040 m²) was situated on and around the neck of a small peninsula. Few birds were captured in more than one site on the island, either within or between years.

The Snares (48°01'S, 166°36'E)

The Sooty Shearwater population of The Snares is one of the largest known seabird breeding colonies in the world. There were estimated to be ~2750000 burrow-holding pairs in the island group in the period 1969–71 (Warham and Wilson 1982). The Snares have never been permanently inhabited by humans and are one of the least modified habitats in the NZ region. The Sooty Shearwater is also the most abundant species on The Snares. The vegetation of the island is strikingly uniform and depauperate, with most of the island primarily vegetated with *Olearia lyalli* surrounded by a coastal fringe of tussock grasslands (Miskelly *et al.* 2001). Field effort was concentrated at three sites on North East Island, the main island of the group: (A) of 472 m², (B) of 413 m² and (D) of 613 m², each ~200 m apart. The sites were located within one large essentially contiguous colony that covers most of the island. As the study sites were not spatially distinct from other areas of the colony, some birds will have landed and passed through to adjacent areas in which they were nesting. For this reason an 'edge effect' is anticipated, both within seasons (as they land and move within the

colony) and between seasons (as they move burrows). This phenomenon may be reflected in the apparent survival rate for surface-caught birds in their first year after banding.

Estimating annual survival rate

The standard Cormack–Jolly–Seber (CJS) model incorporates variability in survival and capture over time but assumes that these parameters do not vary between individuals (Pollock *et al.* 1990). Heterogeneity in either capture rate or survival rate will generally lead to bias in the estimates of annual survival rate, if it is not allowed for in the analysis (Pradel *et al.* 1997a). We therefore consider the factors that might influence such heterogeneity, with a view to allowing for them in our statistical model.

Bird-type: Surface-bird v. hatch-bird

On The Snares and Whenua Hou, birds were caught both on the surface and underground, from within the nest chamber of the burrow, via a hatch. In the rest of the paper, we consider two bird-types: those that were caught only on the surface and those that were caught at least once in a burrow over the whole period of the study. We refer to these as 'surface-birds' and 'hatch-birds' respectively. Note that our definition of a hatch-bird implies that in some years such a bird may have been caught on the surface only.

Most birds caught were surface-birds, for which breeding status was difficult to determine: they will therefore consist of a mixture of pre-breeders, breeders and non-breeders. Even for a hatch-bird found in a burrow, we were not always able to determine its breeding status. For Short-tailed Shearwaters, most prospecting pre-breeders are found on the surface, with only a few exploring unoccupied burrows (Serventy 1967). This suggests that very few of the hatch-birds will be pre-breeders, but some may be non-breeders. Like their conspecific the Short-tailed Shearwater, we expect that breeders exhibit high site-fidelity (Bradley *et al.* 1999), resulting in their apparent survival estimate being higher than that for pre-breeders, as many of the latter will permanently emigrate within a year or two of being captured (see the section on Transience below). This suggests that we should model survival rate differently for the two bird-types; we therefore consider models in which survival rate depends upon bird-type.

As the hatches were also used to estimate breeding success, they will have been checked several times within a breeding season. This means that hatch-birds are also likely to have a higher capture rate than surface-birds; we therefore consider models in which capture rate depends upon bird-type.

Non-breeders

A non-breeder is a bird that has bred before but fails to initiate a breeding attempt in the current year, a phenomenon known as skipping. In the Short-tailed Shearwater, 14% of breeders are known to skip breeding attempts and be absent from the colony, with a further 15% of males and 13% of females being present but not in association with an egg (Bradley *et al.* 2000). Non-breeders are likely to visit the colony less often than breeders, or not to visit the colony at all that year. If we assume that breeders and non-breeders have the same mortality rate and the same

capture rate, skipping will generally lead to underestimation of survival rate.

A non-breeder that does not visit the colony, in any one year, can be thought of as a temporary emigrant. If the study has involved the use of a 'robust design', one can use a model that directly estimates the amount of temporary emigration to ensure that survival rate is not underestimated (Kendall *et al.* 1997). Our studies did not involve use of the robust design; we therefore make use of an alternative approach that indirectly allows for temporary emigration. This involves use of a 'trap-dependence' model, in which the probability of capture depends on whether or not that individual was caught in the previous year (Sandland and Kirkwood 1981; Pradel 1993). Such a model can allow for the possibility that a bird may not be captured for two or more years in succession even though it is still alive: without such a model, this sequence of non-captures would tend to indicate that the bird has died or permanently emigrated.

Transience

The phenomenon of transience is common in seabird mark-recapture studies, especially among pre-breeders (Reed *et al.* 1998; Barbraud and Weimerskirch 2001; Oro *et al.* 2004; Grosbois and Thompson 2005). We define a 'transient' bird to be one that arrives at a colony and possibly stays for only one year; all other birds are regarded as 'residents'. One obvious mechanism for this is that the bird is a pre-breeder that has not yet attained site fidelity, and is therefore 'prospecting'. Not allowing for transience will lead to underestimation of the survival rate for resident birds, especially when the capture rate is low (Pradel *et al.* 1997a).

A common method of allowing for transience is to use a model where the survival rate in the year following first capture (ϕ^1) is different from the survival rate in all subsequent years (ϕ^{2+}) (Pradel *et al.* 1997a). This can be thought of as a model in which survival is age-dependent, where 'age' here means the number of years since first capture (we adopt this definition for age throughout the rest of the paper). Use of such a model also allows us to estimate the proportion of transients in the population as

$$1 - \frac{\hat{\phi}^1}{\hat{\phi}^{2+}}$$

where $\hat{\phi}^1$ and $\hat{\phi}^{2+}$ are the estimates of ϕ^1 and ϕ^{2+} (Pradel *et al.* 1997a). Note that age-dependence in the true adult survival rate will affect this estimate of the proportion of transients, to an extent that will depend upon the age distribution of newly banded birds.

The primary purpose of using a model in which survival rates are age-specific is to help reduce bias in estimates of adult survival. An important issue with these estimates of transience is that they may in turn be biased, owing to the timing of fieldwork, for reasons we now describe. For many seabirds, migration is truly age-dependent, with juveniles and pre-breeders returning to the colony slightly later than breeders (Halley *et al.* 1995; Dittmann and Becker 2003). Short-tailed Shearwater presence at the colony is related to both age and breeding status: pre-breeders arrive with the breeders but leave earlier, while birds that are 2–4 years old arrive up to 4 months later and leave earlier (Marshall and Serventy 1956; Serventy 1967). Little is

known about the temporal variation in the population structure at Sooty Shearwater colonies, but it is reasonable to assume a similar pattern to the one for Short-tailed Shearwater. Migration into Sooty Shearwater colonies appears to be highly synchronised, with a sample of 19 electronically tagged breeders in 2005 being found to cross the equator within 10 days of 7 October (Shaffer *et al.* 2006). An age-structured migration will result in a changing population structure in the colony throughout the breeding season. Study populations at different locations can be expected to exhibit different rates of transience if field effort is not spread evenly across the season or consistently between sites and locations. We considered the timing of the capture of birds caught just once to determine when the peak influx of transients was and compared this with the timing of fieldwork.

Sites

Very few individuals were observed at more than one site within a location, precluding the use of a multi-site model. At Whenua Hou, over the entire period of the study, only 15 birds (1.5%) were seen at more than one site and of these only five birds (0.05%) were seen at more than one site within a single season. At The Snares, only 19 birds (0.04%) were seen at different sites between years, and none seen at more than one site within a year. For simplicity, we arbitrarily assigned birds that were captured at more than one site to the site of their first capture. As sites may have differed in ways that affected the capturing process, we considered models in which capture rate was site-dependent.

Model selection

Estimation of survival (ϕ) and recapture (p) followed the general modelling approach described by (Lebreton *et al.* 1992) and was implemented in Program MARK (White and Burnham 1999; White 2005). We included time-dependence in capture rate for all the models that we considered, as banding effort varied over time. Goodness-of-fit (GoF) tests (Chastel *et al.* 1993) were carried out using the software UCARE (Choquet *et al.* 2005). We report the directional tests (Test3.SR, Test3.SM, Test2.CT and Test2.CL) and use the non-directional test for calculating the effect of structural model adjustments. Test3 checks the assumption that all birds banded alive at (i) have the same probability of surviving to ($i + 1$) and Test2 whether those birds known to be alive between (i) and ($i + 1$) have equal catchability (Cooch and White 2005). An estimate of over-dispersion (\hat{c}) was calculated from the overall GoF statistic and from each component of this statistic; over-dispersion is more likely to be present when the value of \hat{c} is approximately the same for each component, while lack of consistency in the different \hat{c} indicates a need to alter the model structure (Pradel *et al.* 1997b). The value of \hat{c} is used to inflate the standard errors of the parameter estimates and reduces the risk of falsely identifying a model factor as important (Lebreton *et al.* 2003).

Model selection was based on the small-sample version of Akaike's Information Criterion (AIC_c); when over-dispersion was present, we used $QAIC_c$ instead (Burnham and Anderson 2002). We also calculated AIC_c (or $QAIC_c$) model weights, and performed model-averaging using these weights (Burnham and Anderson 2002). We used the 'variance components' option

within Program MARK to estimate mean parameter values over time (White and Burnham 1999).

Finally, to obtain an overall estimate of Sooty Shearwater survival that could be used in a population model, we calculated the weighted mean of the overall (model-averaged) estimates from the individual locations (Burnham 1987). Where survival was site-dependent the weighted mean across sites within a location was first derived, then across bird-types, before the between-location weighted mean was calculated.

Model notation

For both The Snares and Whenua Hou, the notation we use to represent the different models is as follows. For the survival part of the model, we have the following four basic parameters, determined by 'age' and bird-type:

- ϕ_S^1 , probability of survival for a surface-bird in the first year after banding;
- ϕ_S^{2+} , probability of survival for a surface-bird in all subsequent years;
- ϕ_H^1 , probability of survival for a hatch-bird in the first year after banding; and
- ϕ_H^{2+} , probability of survival for a hatch-bird in all subsequent years.

Each of these parameters can vary by site or by time or both, in which case we amend the notation as follows. For any one of the parameters, denoted ϕ_Y^X ($X = 1$ or $2+$; $Y = S$ or H), we write $\phi_Y^X(s)$, $\phi_Y^X(t)$ or $\phi_Y^X(s \times t)$ to denote the fact that ϕ_Y^X depends upon site, time or both site and time, respectively. If it does not depend upon either site or time, we simply write it as ϕ_Y^X . In some models we set two or more of the ϕ_Y^X equal, in which case we write this explicitly. For example, consider a model in which ϕ_S^{2+} and ϕ_H^{2+} are independent of both site and time, and are equal; we write this part of this model as $\phi_S^{2+} = \phi_H^{2+}$.

For the capture part of the model, we have two basic parameters, determined by bird-type:

- p_S , probability of capture for a surface-bird; and
- p_H , probability of capture for a hatch-bird.

Each of these parameters can vary by site or time or both, in which case we amend the notation in the same way as for the survival parameters. For example, if p_S is site- and time-dependent, we write $p_S(s \times t)$. In addition, we use the superscript *TD* to denote the fact that the probability of capture depends on whether or not the individual was captured in the previous year. The formulation of trap-dependence that we used was one in which the probability of capture (p) is modelled using

$$\log\left(\frac{p}{1-p}\right) = a + bx$$

where x is an indicator variable, taking the value 1 if the individual was captured in the previous year and 0 otherwise. In addition, we chose to allow the parameter a to be site or time-dependent, or both, and to make b constant in all models containing trap-dependence (Pradel 1993), e.g. for the probability of capture of surface birds, $p_S^{TD}(t)$ implies that a is time-dependent.

For Taiaroa Head, the notation is simpler, as there is no dependence on bird-type or site. We therefore have two basic survival parameters, determined by 'age': ϕ^1 and ϕ^{2+} . Both of these parameters can be time-dependent. For the capture part of the model, we have just one basic parameter, the probability of capture, which is assumed to be time-dependent.

Results

Taiaroa Head

Of the 2085 adults banded at Taiaroa Head between 1992 and 2005, 44% were subsequently recaptured (Table 1). The overall GoF statistic for the CJS model was highly significant ($\chi^2 = 152.76$, with 85 d.f., $P < 0.001$), as were the directional Test3.SR and Test2.CT statistics. The Test3.SR result implies that we need to allow for transience, while the Test2.CT result suggests a need to include trap-dependence in the model.

Removing the Test3.SR and Test2.CT components led to a GoF statistic that no longer showed any evidence of lack-of-fit (last column of Table 2). Use of $\hat{c} = 1.05$ would be appropriate

Table 1. Summary of Taiaroa Head mark-recapture data for adult Sooty Shearwaters over 14 seasons, 1992 to 2005

Dates	Year	Newly banded	All birds captured	All birds captured then recaptured
May 1992	1991–92	6	6	4
1 Nov. 1992 – 13 May 1993	1992–93	122	122	77
29 Oct. 1993 – 09 May 1994	1993–94	339	370	212
06 Oct. 1994 – 09 May 1995	1994–95	242	367	236
01 Oct. 1995 – 11 May 1996	1995–96	261	473	216
03 Oct. 1996 – 13 May 1997	1996–97	63	172	87
13 Oct. 1997 – 13 May 1998	1997–98	170	311	141
3 Dec. 1998 – 10 May 1999	1998–99	178	292	123
6 Oct. 1999 – 08 May 2000	1999–2000	277	444	217
28 Oct. 2000 – 13 May 2001	2000–01	67	382	105
01 Oct. 2001 – 09 May 2002	2001–02	89	169	42
01 Oct. 2002 – 13 May 2003	2002–03	123	218	26
15 Oct. 2003 – 06 May 2004	2003–04	79	138	6
13 Oct. 2004 – 11 May 2005	2004–05	69	114	0
Totals		2085	3578	1492

Table 2. Goodness-of-fit tests for adult Sooty Shearwater mark-recapture at Taiaroa Head
P values in bold are not significant

Taiaroa Head	Overall	TEST3.SR removed	TEST2.CT removed	TEST3.SR and TEST2.CT removed
χ^2	152.76	109.17	109.76	66.16
d.f.	85	74	74	63
\hat{c}	1.80	1.48	1.48	1.05
P	0.00	0.00	0.00	0.37

if we could be sure that allowing for transience and trap-dependence in our model would soak up all the lack-of-fit associated with Test3.SR and Test2.CT. As we could not be sure of this, a choice of $\hat{c} > 1.05$ is appropriate. In addition, we know that our choice of \hat{c} should be < 1.80 , the value we might use if we were not making any adjustment for transience or trap-dependence (Table 2). We therefore chose to use $\hat{c} = 1.48$, as a compromise between 1.05 and 1.80. This selection of \hat{c} reduced the standard error around the point estimate slightly, without altering the model ordering, relative to a \hat{c} of 1.80.

Based on the GoF tests, we considered only models that included age-dependence in survival, in order to allow for transience (Table 3). In order to simplify and speed up the process of model selection, we initially considered models in which there was no trap-dependence in capture rate, and then added trap-dependence to the best of these models. The best model had a constant estimate of $\phi^1 = 0.734$ (95% confidence interval 0.685–0.777; subsequent figures in parenthesis are 95% confidence intervals (C.I.) unless stated) and a mean value (over years) for ϕ^{2+} of 0.917 (0.860–0.973) (Fig. 2). For the second-best model, the mean value (over years) for ϕ^1 was 0.782 (0.683–0.881) with a constant estimate of $\phi^{2+} = 0.886$ (0.850–0.916). These values are slightly low for shearwaters but may be realistic for the location, given mammalian predation has driven most mainland colonies to extinction.

Table 3. Program MARK model comparison for Taiaroa Head
#Par, number of model parameters. The two best models are discussed in the text

Model	$\Delta QAIC_c$	Model weight	#Par
$\phi^1, \phi^{2+}(t), p^{TD}(t)$	0	0.874	22
$\phi^1(t), \phi^{2+}, p^{TD}(t)$	4.32	0.101	25
$\phi^1, \phi^{2+}, p^{TD}(t)$	7.12	0.025	15
$\phi^1(t), \phi^{2+}(t), p^{TD}(t)$	18.98	0.000	36

^ATop-ranking models discussed in the text.

For the top-ranked model, trap-dependence was such that the mean recapture rate (over years) for a bird that was captured in the previous year was 0.25 (0.16–0.33), compared with 0.17 (0.10–0.24) for a bird not captured in the previous year.

Whenua Hou

Of the 967 adults banded between 1995 and 2005, 35% were subsequently recaptured (Table 4). Of these, 43% of birds were banded at site A, 27% at site B, and 30% at site C. In total, 47% of birds that were banded were hatch-birds, whereas 76% of the birds that were recaptured were hatch-birds.

We originally intended to carry out GoF tests separately for each of the six combinations of site and bird-type, but this resulted in some very low observed values for surface-birds. We therefore performed the tests in two stages: first separately for each bird-type (ignoring site) and then separately for each site (ignoring bird-type).

For both bird-types, the directional Test3.SR was highly significant. Omitting this component led to there being no further evidence for lack-of-fit, either overall or for any of the groups (Table 5). This suggested that we should consider models involving age-specific survival, in order to allow for transience, and that there was no need to include trap-dependence.

Of the models with non-negligible model weights, none showed evidence of time-dependence in survival (Table 6). The

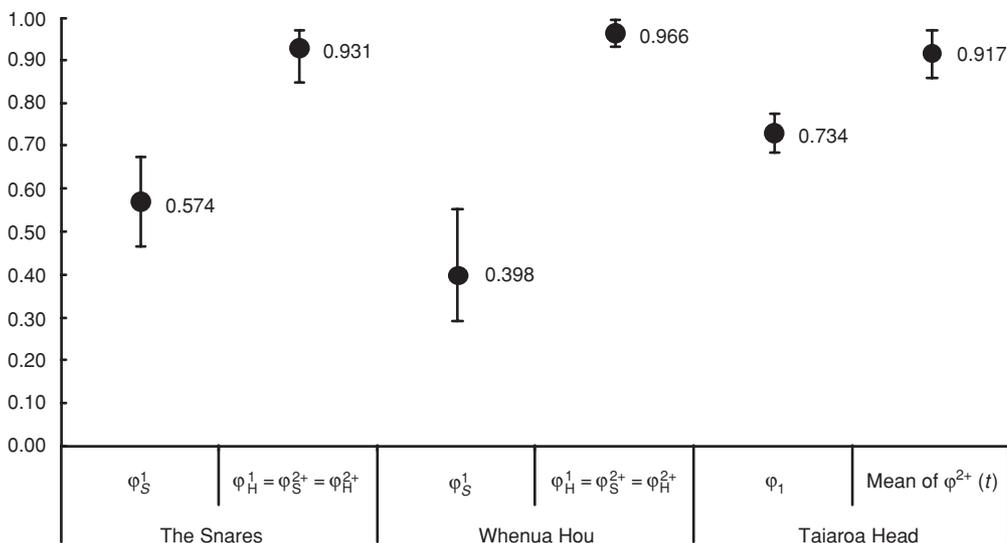


Fig. 2. Survival estimates, using the top-ranked model, for The Snares, Whenua Hou and Taiaroa Head. The parameter notation is given in the text.

Table 4. Summary of Whenua Hou 1996–2005 mark–recapture data for adult Sooty Shearwaters
S/H refers to surface-only captured (S) and hatch-captured (H) birds released both newly banded and banded on a prior occasion

Dates	Year	Newly banded	All birds captured S/H	All birds captured then recaptured S/H
29 Feb. 1996 – 10 Mar. 1996	1995–96	11	5/6	11/60
15 Feb. 1997 – 5 May 1997	1996–97	76	36/40	12/40
30 Nov. 1997 – 4 May 1998	1997–98	136	72/77	23/53
30 Nov. 1998 – 6 May 1999	1998–99	155	70/118	15/82
19 Jan. 2000 – 18 Apr. 2000	1999–2000	120	54/108	10/69
5 Jan. 2001 – 3 May 2001	2000–01	229	148/217	21/121
10 Jan. 2001 – 28 Apr. 2002	2001–02	107	62/213	9/47
11 Dec. 2002 – 5 May 2003	2002–03	56	70/26	7/6
19 Jan. 2004 – 4 May 2004	2003–04	62	69/41	1/6
28 Jan. 2005 – 19 Apr. 2005	2004–05	14	17/37	0
Total		967	603/883	109/430

best model showed evidence for a difference between bird-types in ϕ^1 , but not in ϕ^{2+} (Table 6). This model implies that the degree of transience is about the same for all three sites but different for the two bird-types. A difference in the proportion of transients between surface- and hatch-birds was expected, with few hatch-birds expected to be transient. This model results in a survival rate estimate for resident birds of 0.966 (0.933–0.997) (Table 7 and Fig. 2) and allows for differences in capture rate between sites and between bird-types; the mean recapture rate for surface birds was 0.17, while that for hatch-birds was 0.24.

Table 5. Goodness-of-fit tests for adult Sooty Shearwater mark–recapture at Whenua Hou

Grouping refers to Bird-type and Site groupings. *P* values in bold are not significant

	Grouping	Overall	TEST3.SR removed	TEST2.CT removed	TEST3.SR and TEST2.CT removed
χ^2	A	64.29	29.93	56.34	23.78
	B	18.67	5.35	16.43	2.42
	C	19.16	9.73	17.91	5.95
	Surface	61.02	19.20	49.43	15.10
	Hatch	34.47	22.55	29.04	17.12
d.f.	A	34	26	27	19
	B	16	11	12	7
	C	19	13	14	8
	Surface	26	19	19	12
	Hatch	32	25	25	18
\hat{c}	A	1.89	1.15	2.09	1.25
	B	1.17	0.49	1.37	0.35
	C	1.01	0.75	1.28	0.74
	Surface	2.35	1.01	2.60	1.26
	Hatch	1.08	0.90	1.16	0.95
<i>P</i>	A	0.00	0.27	0.00	0.20
	B	0.29	0.91	0.17	0.93
	C	0.45	0.72	0.21	0.65
	Surface	0.00	0.44	0.00	0.24
	Hatch	0.35	0.60	0.26	0.52

The model-averaged estimate of ϕ^{2+} for the two bird-types differed by less than 0.01, but the 95% C.I. for ϕ^{2+} hatch-birds were tighter than those for surface-birds. Model-averaging resulted in slightly different survival rate estimates for ϕ^{2+} across sites. For hatch-birds, the estimates are 0.969 (0.903–0.991) at site A, 0.967 (0.879–0.992) at site B and 0.964 (0.805–0.994) at site C. The weighted mean across sites and bird-type on Whenua Hou is 0.968 (0.935–0.984).

The Snares

Altogether 4514 adult birds were banded on The Snares between 1996 and 2005, with 28% of these being recaptured (Table 8). In total, 82% of all birds banded were surface-birds, a higher proportion than on Whenua Hou, where more intensive efforts were made to check breeding success. Of all birds banded, 30% were banded at site A, 45% at site B and 25% at site D.

Changes in the study design through time, caused by logistical problems, resulted in the potential for greater problems with capture heterogeneity on The Snares than at Taiaroa Head and Whenua Hou. During the period 1998–99 to 2001–02, the three sites were each split in half and surface banding continued in only one of these halves: in 2002–03 surface banding recommenced throughout each site. Hatch checks were undertaken throughout the whole of each site for the entire study period. This meant that birds captured in the first two seasons on the half of a site where banding was discontinued for four seasons were less likely to be recaptured during those four years. We tried a variety of approaches to allow for this, involving further splitting of the data before analysis, but

Table 6. Program MARK model comparison for Whenua Hou
#Par, number of model parameters. The four best models are discussed in the text

Model	ΔAIC_c	Weight	#Par
$\phi_S^1, \phi_H^1 = \phi_S^{2+} = \phi_H^{2+}, p_S(s \times t), p_H(s \times t)$	0.00	0.61	48
$\phi_S^1, \phi_S^{2+}, \phi_H^1 = \phi_H^{2+}, p_S(s \times t), p_H(s \times t)$	2.11	0.21	49
$\phi_S^1, \phi_H^1, \phi_S^{2+}, \phi_H^{2+}, p_S(s \times t), p_H(s \times t)$	3.20	0.12	50
$\phi_S^1(s), \phi_H^1, \phi_H^{2+} = \phi_H^{2+}, p_S(s \times t), p_H(s \times t)$	4.58	0.06	52
$\phi_S^1(s), \phi_H^1(s), \phi_H^{2+}(s), \phi_H^{2+}(s), p_S(s \times t), p_H(s \times t)$	14.33	0.00	58

Table 7. Adult Sooty Shearwater survival parameter estimates from the three top-ranking models (weightings >0.10) generated by Program MARK for Whenua Hou 1996–2005

Model	Parameter	Estimate	Lower	Upper
$\phi_S^1, \phi_H^1 = \phi_S^{2+} = \phi_H^{2+}, p_S(s \times t), p_H(s \times t)$	ϕ_S^1	0.398	0.282	0.555
	$\phi_H^1 = \phi_S^{2+} = \phi_H^{2+}$	0.966	0.933	0.997
$\phi_S^1, \phi_S^{2+}, \phi_H^1 = \phi_H^{2+}, p_S(s \times t), p_H(s \times t)$	ϕ_S^1	0.395	0.289	0.560
	ϕ_S^{2+}	0.976	0.860	1.000
	$\phi_H^1 = \phi_H^{2+}$	0.965	0.931	0.997
$\phi_S^1, \phi_H^1, \phi_S^{2+}, \phi_H^{2+}, p_S(s \times t), p_H(s \times t)$	ϕ_S^1	0.395	0.289	0.560
	ϕ_H^1	0.976	0.860	1.000
	ϕ_S^{2+}	0.929	0.804	1.000
	ϕ_H^{2+}	0.980	0.935	1.000

found that none of these led to any improvement in the GoF statistics.

The GoF statistic for the CJS model showed clear evidence of lack-of-fit ($\chi^2 = 358.1$, with d.f. = 177, $P < 0.001$, $\hat{c} = 3.323$) (Table 9). GoF statistics were then calculated separately for each site and for each bird-type (as with Whenua Hou, a breakdown into the six site \times bird-type categories was not possible owing to low observed values in some categories). Surface-birds showed lack-of-fit on TEST3.SR, whereas hatch-birds did not. After removing the TEST3.SR component, the overall GoF statistic was still highly significant for surface-birds, with consistently high \hat{c} values across subcomponent tests indicating the presence of over-dispersion (Table 9). For hatch-birds TEST2.CT was highly significant and the subcomponent tests indicated that allowing for trap-dependence would be adequate. There was lack-of-fit in both Test3.SR and Test2.CT at sites B and D, whereas at site A lack-of-fit was also evident in Test3.SM and Test2.CL. Transience was allowed for in all the models and trap-dependence was added to the capture part of the model once the survival structure of the model was determined. The over-dispersion parameter $\hat{c} = 3.323$ was calculated from the full CJS model, and its use in calculating the QAIC_c altered the order of the two top ranking models.

The model that had survival depending on just bird-type was better than one involving just site or bird-type \times site, while removing both bird-type and site led to a poorer model; in addition, there was no evidence of time-dependence in survival (Table 10). The model for the survival probability was then

further refined, resulting in the survival for hatch-birds becoming independent of age. The structure of the recapture probabilities was then examined, with the result that site differences were again removed. The differences in recapture rates between hatch-birds and surface-birds, as well as between birds captured or not captured in the previous year are summarised in Fig. 3.

For the survival component of the model, the best three models were identical to those obtained for Whenua Hou, with their model weights also being close to those for Whenua Hou (Table 6 v. Table 10). For the best model, the estimate of ϕ^{2+} was 0.931 (0.848–0.971) (Fig. 2), while for the second-best model it was 0.906 (0.798–0.960) for surface-birds and 0.961 (0.706–0.996) for hatch-birds. The model-averaged estimates of ϕ^{2+} were: 0.921 (0.816–0.968) for surface-birds and 0.943 (0.791–0.987) for hatch-birds. The weighted mean across bird-type for The Snares was 0.928 (0.896–0.951).

Overall estimate of survival rate

In producing an overall estimate of survival rate that could be used in a population model, we chose to omit the estimate for Taiaroa Head, as predation by introduced mammals is likely to be producing a low survival rate. The model-averaged estimates for the different sites at Whenua Hou were combined to produce a weighted mean for each bird-type. We then calculated the weighted mean of these two estimates to produce an overall estimate for Whenua Hou. Likewise, we combined the two estimates of survival for each bird-type at The Snares to produce an overall estimate. Finally, we calculated the weighted mean from

Table 8. Summary of The Snares mark–recapture data for adult Sooty Shearwaters 1996–2005
S/H refers to surface-birds (S) and hatch-birds (H) released both newly banded and banded on a prior occasion

Dates	Year	Newly banded	All birds captured S/H	All birds captured then recaptured S/H
8 Oct. 1996 – 9 May 1997	1996–97	730	616/109	210/107
18 Dec. 1997 – 11 May 1998	1997–98	340	215/187	87/120
19 Nov. 1998 – 12 May 1999	1998–99	890	819/331	235/208
6 Jan. 2000 – 4 May 2000	1999–2000	583	568/327	136/161
9 Jan. 2001 – 14 May 2001	2000–01	423	515/183	126/82
6 Jan. 2002 – 9 Feb. 2002	2001–02	340	402/202	101/70
9 Jan. 2003 – 4 Mar. 2003	2002–03	552	658/120	127/27
22 Nov. 2004 – 14 Feb. 2004	2003–04	333	541/83	49/7
10 Jan. 2005 – 14 Feb. 2005	2004–05	323	318/5	0/0
Total		4514	4652/1542	1071/782

Table 9. Goodness-of-fit tests for adult Sooty Shearwater mark-recapture at The Snares

Grouping refers to Bird-type and Site groupings. *P* values in bold are not significant

	Grouping	Overall	TEST3.SR removed	TEST2.CT removed	TEST3.SR and TEST2.CT removed
χ^2	A	123.21	88.17	112.25	56.59
	B	97.24	62.62	86.71	33.98
	D	140.24	83.80	123.16	26.91
	Surface	202.01	125.21	139.39	62.59
	Hatch	73.82	63.65	31.12	20.95
	d.f.				
d.f.	A	43	36	37	30
	B	42	35	36	29
	D	42	35	36	29
	Surface	44	37	38	31
	Hatch	39	32	33	26
	\hat{c}	A	2.87	2.45	3.03
B		2.32	1.79	2.41	1.17
D		3.34	2.39	3.42	0.93
Surface		4.59	3.38	3.67	2.02
Hatch		1.89	1.99	0.94	0.81
<i>P</i>		A	0.00	0.00	0.00
	B	0.00	0.00	0.00	0.24
	D	0.00	0.00	0.00	0.58
	Surface	0.00	0.00	0.00	0.00
	Hatch	0.00	0.00	0.56	0.74

the two locations to produce a single overall estimate of survival. The weighted mean of the model-averaged estimates for The Snares and Whenua Hou was 0.952 (0.896–0.979).

Transience

The estimate of ϕ^1 from each of the top-ranking models (Fig. 2) allowed us to calculate the estimated proportion of birds that are transient at each location. Over both bird-types these were 0.16 (0.13–0.19) at Taiaroa Head, 0.59 (0.43–0.75) at Whenua Hou, and 0.38 (0.35–0.42) at The Snares. When broken down between bird-types, the proportion of transients is much higher for surface-birds than for hatch-birds, at both The Snares and Whenua Hou (Fig. 4). The lower proportion of transients at Taiaroa Head can in part be explained by the degree of sampling effort at that colony early in the season (Fig. 5). Assuming the

Table 10. Program MARK model comparison for The Snares
#Par, number of model parameters. The two best models are discussed in the text

Model	ΔQAIC_c	QAIC_c Weight	#Par
$\phi_S^1, \phi_H^1 = \phi_S^{2+} = \phi_H^{2+}, p_S^{\text{TD}}(t), p_H^{\text{TD}}(t)$	0.00	0.56	20
$\phi_S^1, \phi_S^{2+}, \phi_H^1 = \phi_H^{2+}, p_S^{\text{TD}}(t), p_H^{\text{TD}}(t)$	1.15	0.32	21
$\phi_S^1, \phi_H^1, \phi_S^{2+}, \phi_H^{2+}, p_S^{\text{TD}}(t), p_H^{\text{TD}}(t)$	3.11	0.12	22
$\phi_S^1, \phi_H^1 = \phi_S^{2+} = \phi_H^{2+}, p_S(t), p_H(t)$	22.63	0.00	18
$\phi_S^1, \phi_S^{2+}, \phi_H^1 = \phi_H^{2+}, p_S(t), p_H(t)$	22.64	0.00	19
$\phi_S^1, \phi_H^1, \phi_S^{2+}, \phi_H^{2+}, p_S(t), p_H(t)$	24.26	0.00	20

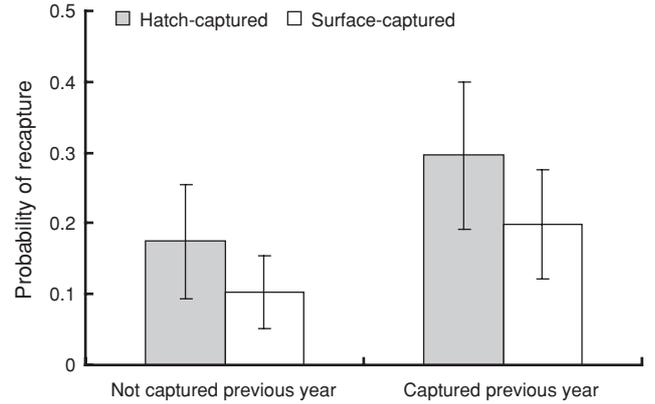


Fig. 3. Average probabilities of recapture at the The Snares between hatch-captured and surface-captured birds, and between birds captured and not captured in the previous year, generated using the top-ranked model.

age-structure of the population varies in a similar way to that of the Short-tailed Shearwater, capture effort at this colony dipped during the seasonal high attendance by juvenile birds, in contrast to Whenua Hou and The Snares where effort peaked during the same period.

Fig. 6 shows the proportion of surface birds banded at each of the three locations, in a particular month, that were never recaptured. For both Taiaroa Head and The Snares, this proportion is consistently lower early on in the breeding season and appears to peak in December. This pattern is consistent with our hypothesis that pre-breeders and juveniles arrive later than breeders. If this is so, greater banding effort early in the season, as occurred at Taiaroa Head (Fig. 5), will result in a lower estimate of transience, relative to locations where the effort occurs during the influx of pre-breeders and juveniles. There appears to be a comparatively lower number of once-seen birds at Taiaroa Head (Fig. 6) compared with The Snares and Whenua Hou. However, the rate of recapture, which is lower at The Snares than for Taiaroa Head, may be responsible for this apparent difference.

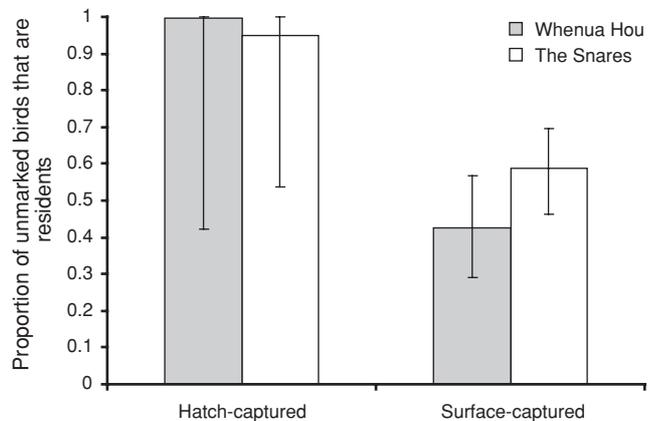


Fig. 4. Estimated proportion of unmarked birds at Whenua Hou and The Snares that are residents, in each case using the best-fitting model that allows a comparison between surface- and hatch-captured birds $\{\phi_S^1, \phi_H^1, \phi_S^{2+}, \phi_H^{2+}, p_S(s \times t), p_H(s \times t)\}$.

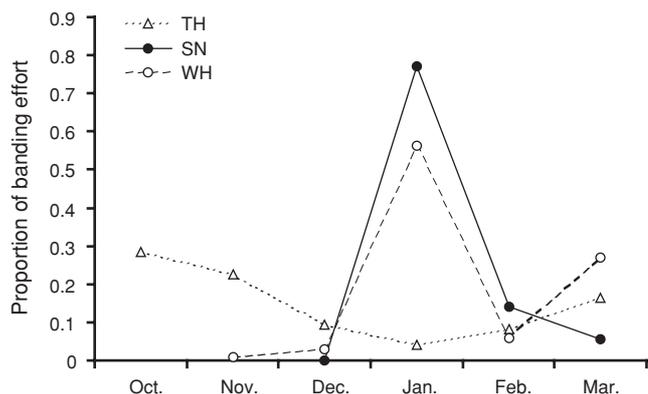


Fig. 5. Proportion of banding effort (birds banded) undertaken during different months of the breeding season over all years of the study at Tairaroa Head (TH), The Snares (SN) and Whenua Hou (WH).

Discussion

Transience and trap-dependence

The need to allow for transience and trap-dependence is common in mark–recapture studies of seabird populations (Dunnet and Ollason 1978; Barbraud and Weimerskirch 2001; Votier *et al.* 2005) although few have addressed these concerns. We adjusted for trap-dependence in our models because of the temporary emigration that occurs when individuals skip breeding for one or more years and because of possible capture heterogeneity relating to effort. Our goodness-of-fit tests indicated a need to include trap-dependence in the models for both Tairaroa Head and The Snares, but not Whenua Hou. As skipping is a phenomenon that we expected to occur to some degree at all three locations, the result for Whenua Hou was surprising but could be a consequence of the colonies at Whenua Hou being small and discrete with comparatively low burrow densities. If skipping is density-dependent, then we would expect a lower rate at Whenua Hou.

Our models also suggest that at Tairaroa Head a bird was 1.5 times more likely to be recaptured if it had been captured in the

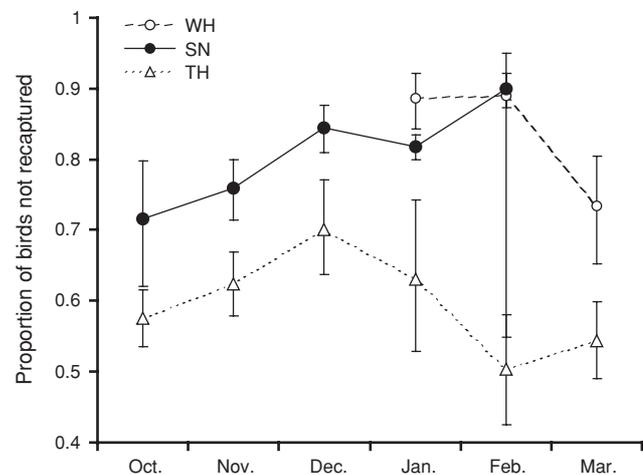


Fig. 6. Proportion of surface-birds banded and never recaptured on Tairaroa Head (TH), The Snares (SN) and Whenua Hou (WH).

previous year, while at The Snares this ratio was 1.9 for surface-birds and 1.7 for hatch-birds. In addition, hatch-birds on The Snares had a higher recapture rate than surface-birds, regardless of whether or not they were captured in the previous year (Fig. 3). The higher probability of capture for birds captured the previous year was also detected in mark–recapture study of adult Northern Fulmars (*Fulmarus glacialis*: Procellariidae) (Grosbois and Thompson 2005). We also found higher recapture rates for all hatch-birds, regardless of which island they were from, and whether or not they had been captured in the previous year (Fig. 3). This was expected as hatch-birds were more prone to recapture as there was greater effort in recapturing birds from hatches (owing to other research, on breeding success, being done). Also hatch-birds are more likely to be breeders with repeated nest-attendance.

Our estimate of the proportion of transient birds, at each location, gives an indication of the level of prospecting by juveniles. If transience is not allowed for in the modelling, it creates a negative bias in the estimate of survival for the resident birds (Pradel *et al.* 1995, 1997b). We expected most hatch-birds to be residents or older pre-breeders (with site fidelity), and most surface-birds to be transients (Richdale 1963). At The Snares, however, the sites are only small sections of a much larger colony, and surface-birds could therefore be residents from another part of the colony that are resting or moving through the study site. At both The Snares and Whenua Hou, the estimated proportion of transients among surface-birds was considerably higher than amongst hatch-birds. We had expected a higher rate of transience among surface-birds at The Snares, compared with Whenua Hou, but we found the opposite to be the case (Fig. 4).

The estimate of the proportion of transients at Tairaroa Head was lower than for the other two locations. This may partly reflect the timing of field effort relative to the other two locations, as more breeders and returning pre-breeders are likely to have been present at Tairaroa Head during the time when most of the sampling effort occurred. Most of the field work at The Snares and Whenua Hou occurred during the time when numbers of juveniles present was thought to peak. The estimated proportion of transients among the surface-birds at these locations therefore gives an idea of the high proportion of juveniles and young pre-breeders among the birds present at this time (Fig. 4).

Survival rates

The top-ranking models for Whenua Hou and The Snares had equivalent survival structures. The best model at both locations had ϕ^1 differing between surface-birds and hatch-birds, with ϕ^{2+} being the same for the two bird-types. Estimates of ϕ^{2+} for hatch-birds are very similar at Whenua Hou (0.965) and The Snares (0.961), whereas for surface-birds ϕ^{2+} differs markedly between the two locations (0.976 at Whenua Hou, 0.906 at The Snares). Our use of bird-type in conjunction with the age-class model allowed us to differentiate between birds that are largely pre-breeders and those that are primarily adults: using age-class but ignoring bird-type led to a poorer fit. Although top-model estimates of ϕ^{2+} for hatch-birds are very similar at Whenua Hou and The Snares, model-averaging and weighting substantially reduced The Snares estimate compared with that for Whenua Hou (0.928 (0.896–0.951) and 0.968 (0.935–0.984) respec-

tively). The reduced Snares estimate is due to the standard error around the point estimates, in part a product of the use of a large over-dispersion factor, incorporating lack of certainty in the ability of the data to meet the model assumptions. A combination of model-averaging and weighted means across sites (in the case of Whenua Hou) and bird-type (at both locations) have produced an overall estimate of 0.952 (0.896–0.979) that includes not only location, site and bird-type variability but also uncertainty in model selection and any potential bias around the estimates.

The convergence of survival structures between islands is congruent with the proposition that survival is less of a local phenomenon, as adult birds are affected by factors operating beyond the vicinity of the colony. Broader-scale oceanic conditions are increasingly being recognised as driving synchronous population trends in spatially disparate seabird colonies (Cuthbert *et al.* 2003; Gaston 2003). As we would expect, there were virtually no between-site differences in the survival estimates at Whenua Hou and none at The Snares. The effect of Pacific Rat being present on Whenua Hou before 1999 was not evident in our estimates of survival rates, although their primary impact would be on breeding success (Booth *et al.* 1996) and reduced colony attendance. Their removal would have resulted in a recovery phase during the latter period of study.

The estimate of ϕ^{2+} for the best-fitting model at Taiaroa Head was 0.917, which appears to be low for shearwaters. Our modelling of the data from Whenua Hou and The Snares suggests that ϕ^{2+} for surface-birds is similar to that for the hatch-birds (Tables 3, 10). This indicates that the estimate of ϕ^{2+} at Taiaroa Head should be relatively free of bias from transience. The Taiaroa Head colony is a small remnant colony that appears to be in decline, suffering a 26% reduction in the number of burrows between 1995 and 2002, the duration of this study (McKechnie 2004). Predation by exotic mustelids is likely to have been a key factor in causing the increased mortality rate. Burrow disturbance caused by sheep-grazing may have also led to an increase in the number of failed breeding attempts. As petrels are highly philopatric once they start breeding (Bradley and Wooller 1991), it may be difficult for them to breed elsewhere following several breeding failures. In a study of Short-tailed Shearwater on Fisher Island (Bass Strait, Australia), birds that had bred there, at least once, were not found to breed subsequently elsewhere despite intensive search effort on neighbouring islands (Bradley *et al.* 1991), suggesting that failed breeders may be lost to the breeding population altogether.

We have obtained estimates of adult survival rates from colonies in three very different locations. Unless predation of adults is occurring during the breeding season or there is attrition from the colony (e.g. displacement by another species), we would not expect survival to be colony-dependent. The Snares is the largest of the three study colonies and constitutes a large part of the NZ population (31% of an estimated 37.2 ± 9.3 million birds; Bragg *et al.* 2007). It is unfortunate that changes in the field-effort protocol at this location appear to have precipitated the need for a large over-dispersion factor, reducing accuracy in the estimate of survival at The Snares since the estimates from the other two locations cannot be considered representative. This is especially important when modelling a long-lived species where a small bias in the estimate of survival may have a large impact on projections from a population model.

Comparison with previous estimates

There are few published estimates of adult survival of Sooty Shearwaters. Scofield *et al.* (2001) estimated that survival of breeding Sooty Shearwaters on Whero Island, NZ, was 0.872, based on re-analysis of a detailed dataset collected by L. E. Richdale between 1940 and 1957. While the authors did not allow for transience in their models, they found no significant overall lack-of-fit, even though 40% of birds were never recaptured. It is possible that the GoF tests used lacked statistical power. It would be interesting to know what their estimate of breeder survival would have been if transience had been allowed for in the model, as we would expect survival to increase once transience is incorporated. A confounding factor that could also partially explain their unexpectedly low estimate is that at the time of monitoring, the population was in decline and succeeded by a colony of Stewart Island Shag (*Phalacrocorax chalconotus*) (Scofield 2001).

The Short-tailed Shearwater is the closest relative of the Sooty Shearwater. By 1991 a total of 92 000 Short-tailed Shearwaters had been banded in Australia (Skira 1991). There is considerable variability in the survival estimates reported for this species in the literature, and our estimates exceed these. Croxall (1981), in a review of estimates of survival for petrels, cited 0.94 for the Sooty Shearwater, while Wooller *et al.* (1992) give 0.92; neither gave supporting methodology. Skira (1991), in a review of Short-tailed Shearwater biology, reports male and female mortality rates as 7.8% (s.e. 1.5%) and 10.6% (s.e. 1.8%) in the first year of recorded breeding, decreasing to 6.6% (s.e. 2.1%) and 7.6% (s.e. 2.3%) 9 years after first recorded breeding and rising to 12.7% (s.e. 1.9%) and 15.6% (s.e. 1.8%) after 18 years. Bradley *et al.* (1989) reported an increased rate of mortality of Short-tailed Shearwaters 10 years after the age of first breeding (6–7 years on average), with a further dramatic rise 20 years after first breeding.

Time dependence in survival

At two of our study locations, models in which survival rate was constant were ranked higher than those in which it varied with time. Taiaroa Head was the only location where time dependence was indicated; predominately in the ϕ^{2+} model structure. Predation and habitat degradation at the Taiaroa colony are likely to be causative rather than larger scale effects so we chose to derive an average survival rate for the entire period that incorporated model uncertainty rather than focus on year-to-year variability. Additionally, the period of the study was not adequate to detect a long-term trend as error around the point estimates increased as the study progressed. For a long-lived, slow-reproducing species, we would expect little temporal variation in the adult survival rate as annual variation in food resources is likely to have a greater impact on fecundity than on adult survival (Furness and Camphuysen 1997; Jenouvrier *et al.* 2005). In the case of Whenua Hou and The Snares, it is possible that the variation in survival rate during the period of this study was fairly small. However, an inability to detect such variation may also be caused by a lack of statistical power, owing to the low recapture rate. The size of the overall population, the longevity and generation time of the species, the spatial scale of breeding colonies, and migratory

ability make inference from mark–recapture studies of seabird populations difficult.

In this study, there was an imbalance in study design with regard to effort, both within sites between years and between sites which necessitated our applying time dependence to capture. We potentially lost vital information of a biological basis such as the incorporation of climate indices that impact on breeding. The data were too sparse to apply a site by bird-type by effort interaction able to incorporate varying effort over site and time. Had we been able to do so the inclusion of a climatic variable might have detected a relationship between climatic indices and recapture rates as an indication of breeding proportions. The field effort also varied during different parts of the season and the longest study period was only 14 years, comparatively brief for a long-lived species.

Effect of climate on adult survival

Investigation into the biological impact of recent climatic trends suggests either large-scale shifts in the foraging distribution of Sooty Shearwaters during the boreal summer or dramatic reductions in abundance and survival rate (Ainley *et al.* 1995; Veit *et al.* 1996, 1997; Spear and Ainley 1999; Wahl and Tweit 2000; Oedekoven *et al.* 2001; Hyrenbach and Veit 2003). Regime shifts in the Pacific Decadal Oscillation (Hare and Mantua 2000) and El Niño–Southern Oscillation (ENSO) events have been identified as causative factors in seabird declines having disrupting effects on the pelagic food web (Ainley *et al.* 2005). Observations of direct changes in bird abundance, primarily in the northern hemisphere, were generally outside the period of this study, by which time some recovery may have occurred. By-catch in the northern hemisphere began in the mid-1970s, peaked in 1988, and was effectively removed by 1992, with the 15 years of intense drift-netting having caused an estimated 1.5% decrease in survival rate (Bragg *et al.* 2007). Corroborating these observations is the evidence for population decline on The Snares and some Tītī Islands. Burrow density has decreased over the last 30 years on The Snares by 37% (Scofield 2001) and an annual rate of 1% decline has occurred on some Tītī Islands (H. Moller, pers. comm.).

Our estimates of survival rate are generally high and indicate that the effects of anthropogenic and climatic factors that had been having an impact on the population throughout the 1980s and early 1990s were reduced by the time of this study. Further work involving climate indices as covariates would improve understanding of the responsiveness of the Sooty Shearwater as an apex predator to changing oceanic conditions.

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