Survival and age-at-first-return estimates for grey-faced petrels (*Pterodroma macroptera gouldi*) breeding on Mauao and Motuotau Island in the Bay of Plenty, New Zealand

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Abstract We estimated apparent annual survival of adult and young grey-faced petrels (*Pterodroma macroptera gouldi*) and age of first return to the natal colony of young birds from 2 colonies in the Bay of Plenty, New Zealand, between 1991 and 2008. We analysed the capture histories of 5844 adult birds and 928 chicks in a mark-recapture framework. The apparent adult annual survival rate was 0.89 after accounting for transience effects, which were greater at the mainland site (Mauao, Mount Maunganui) than on the island colony (Motuotau, Rabbit Island). Annual survival of young birds between fledging and 2 years of age was 0.844 for Mauao and 0.865 for Motuotau. Around 50% of fledglings that returned to their natal colony did so by 4 years of age, and by age 6, the probability of a fledgling returning was approximately 1.0. These are the first reliable estimates of these parameters for grey-faced petrels and are vital for models aimed at predicting the effects of natural perturbations or management interventions on breeding populations.

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INTRODUCTION

Population models of long-lived vertebrates typically emphasise the importance of adult survival in the dynamics of the population (Hunter *et al.* 2000; Saether & Bakke 2000). This is particularly so for long-lived seabird species, which typically show life histories with delayed sexual maturity, low

reproductive output and high rates of adult survival, and are thereby considered *K*-selected species (Croxall & Rothery 1991; Russell 1999; Weimerskirch 2002). Also common to long-lived seabirds is the absence of juvenile birds from natal colonies for a number of years following fledging (Greenwood & Harvey 1982; Nichols *et al.* 1990; Weimerskirch 2002). This absence can make estimation of juvenile survival rate and true age of first return (*AFR*) to the colony, as opposed to age of first *observed* return,

problematic. Reliable estimates of these parameters are vital for population models and for predicting the effects of natural perturbations or management interventions on seabird populations.

The grey-faced petrel (*Pterodroma macroptera gouldi*) is a gadfly petrel (average adult body mass 550 g) that breeds on headlands and on islands primarily off the east coast of northern New Zealand (Heather & Robertson 2005). The species is a winter breeder that lays eggs in burrow nests during Jun and Jul, with fledging of chicks in Dec and early Jan. Grey-faced petrels are of cultural significance to the northern *iwi* (Māori tribes, *e.g.,* Hauraki, Ngāti Awa, Ngāti Wai) of New Zealand who traditionally harvested pre-fledging chicks. This practice has largely ceased due to *rahui* (temporary harvest bans) imposed by iwi authorities following concerns over reported declines in the numbers of chicks over the last 30 years (Lyver *et al*. 2008). The total New Zealand population of grey-faced petrels has been estimated at over 1 million birds and the species is classified accordingly as 'not threatened' by the Department of Conservation (Taylor 2000). Abundant seabirds may be considered 'keystone' species in maintaining vital ecosystem processes and their careful management and conservation is therefore pivotal to managing wider ecological communities (Furness 1991; Wardle *et al*. 2009).

In this paper, we estimate adult and juvenile survival and *AFR* of grey-faced petrels using mark-recapture analyses of an 18-year banding record from 2 colonies, one on the mainland and one on an adjacent island, in the Bay of Plenty, New Zealand.

METHODS
Study sites and banding programme
Birds were banded at 2 sites: (i) Mauao (Mount Maunganui), and (ii) Motuotau (Rabbit I). Mauao is a 232 m high coastal rhyolite dome at the entrance to Tauranga Harbour (37° 37.75′ S; 176° 10.21′ E). Most of the area of this hill is contained in the Mauao Historic Reserve, comprising ~76 ha, which has unrestricted access and is heavily used by the public. Grey-faced petrel burrows were located mainly on the lower slopes, in some cases within a few metres of walking tracks. Vegetation cover in areas where burrows were located consists primarily of a mixture of native pohutukawa (*Metrosideros excelsa*) with kawakawa (*Macropiper excelsum*), māhoe (*Melicytus ramiflorus)* and hangehange (*Geniostoma rupestre*). Some areas also include introduced weed species such as gorse (*Ulex europaeus*), and exotic grasses. Some petrel burrows were found in grazed pasture areas. The Mauao study site was adjacent to an urban area that has undergone significant redevelopment over the past 20 years and there

are records and anecdotal reports of introduced cats (*Felis catus*), mustelids (*Mustela* spp.) and rats (*Rattus* spp.) at the site. Control of some predators took place during most of the latter part of the period reported here. This has been associated with increased chick productivity (Ornithological Society of New Zealand, *unpubl. reports*, 1991-2008). The site is subject to fire, landslips, and stock grazing, though at lower levels than in the past. The Motuotau (Rabbit I) study site was a small (2.5 ha) island, ~800 m offshore from Mauao. It is a steep-sided, flat-topped 45 m high rhyolite dome. The island is a scenic reserve with unrestricted access, but is little used by the public because of poor accessibility and dense vegetation. Grey-faced petrel burrows were mostly located on steep slopes around the higher parts of the island. The vegetation is dominated by pohutukawa with an understorey including *Pseudopanax* spp., *Coprosma* spp. and *Hymenanthera novae-zelandiae*. Mammalian predators are normally absent, although 1 stoat *(Mustela erminea)* was detected and trapped during this study. There are no recent records of traditional harvest of chicks at either site.

Banding of both adults and pre-fledging chicks has been carried out at the sites by volunteers associated with the Waikato Region of the Ornithological Society of New Zealand (OSNZ) since the breeding season of 1991. Work on Motuotau ceased in 2000 due to personnel and logistical constraints. Site visits took place throughout the breeding season with activity mainly focused on: (i) the prospecting period (Apr-May), during which adult birds return to the colonies to establish or reaffirm pair bonds and prepare burrows for incubation (range: 3-15 visits per year at Mauao; 2-6 visits per year at Motuotau); (ii) the early incubation period (Jul-Aug), when breeding adults frequently attend the colony (range: 3-9 visits per year at Mauao; 1-5 visits per year at Motuotau), and; (iii) the pre-fledging period (Dec-Jan) when chicks emerge from breeding burrows at night (range 2-10 visits per year at Mauao; 2-5 visits per year at Motuotau). Colonies were visited from just before dusk and birds banded on their return soon after. Effort per night varied between nights reflecting the voluntary nature of the banding project. Other occasional site trips took place outside of these periods. Adult birds were banded during all site visits, but in the immediate pre-fledging period the emphasis was on banding chicks. Sites were divided into a series of sections, which were visited sequentially throughout a night's banding, though not always in the same sequence. Limitations imposed by the availability of volunteers, and occasionally by deterioration in weather during the night, meant that not all sections were visited on all nights.

Banding took place just after dusk. Adults were captured by hand and placed in a cloth bag for ease and safety of handling and for weighing using a spring balance. Unbanded birds had a single, numbered stainless steel E-series band applied to the tarsus and the band number of previously banded birds was recorded when these were recaptured.

Apparent survival of adults

We used Cormack-Jolly-Seber (CJS) mark-recapture models (Cormack 1964; Jolly 1965; Seber 1965) implemented in Program MARK (White & Burnham 1999) to estimate apparent survival of adults. Note that the term 'apparent survival' is used because the complement (1 – apparent survival) includes losses due to both mortality and permanent emigration (Sandercock 2006). For estimating survival rates, it is necessary to define sampling occasions; survival rates are then estimated for the time periods between sampling occasions. Input data consisted of individual capture histories in which an annual sampling 'occasion' represented the combined prospecting and early incubation periods for each breeding season. Any data from outside of this period were excluded. Use of this 4-month capture period violates one of the standard assumptions of open mark-recapture models: that capture occasions are of negligible duration relative to the period between them and that mortality is negligible during the capture occasion (Pollock et al. 1990). Violation of this assumption is common as researchers attempt to maximise sample sizes and enhance what are often sparse data sets (O'Brien et al. 2005). Simulation of the effects of violating this assumption has shown that induced bias is minimal when survival rates during the occasion are high (Smith & Anderson 1987; Hargrove & Borland 1994; O'Brien et al. 2005). As petrel species are typically long-lived, with annual survival rates of around 0.9 for many species, we considered that short-term survival rates were unlikely to be so low as to violate this assumption for grey-faced petrels.

Standard CJS models also assume homogeneity of both survival and capture probabilities among individuals (Seber 1982; Pollock et al. 1990). This assumption is violated in many wildlife populations, leading to negative bias in estimates of apparent survival (Sandercock 2006). In seabirds, heterogeneity in these parameters frequently results from 2 behavioural mechanisms: transience and skipping (or trap-dependence). Transience occurs when birds, often younger adult 'pre-breeders,' are detected at a colony during a breeding season, but do not establish site-fidelity and are never detected again (Bradley et al. 1999; Oro et al. 1999; Dittmann et al. 2007). Inclusion of these individuals, with what is effectively a zero probability of apparent survival after 1st capture (Pradel et al. 1997), with

resident individuals, will lead to underestimates of apparent survival for residents, as we were unable to differentiate between permanent emigration and mortality. Where this effect was suspected, we used a set of models where apparent survival rate of adult birds in the year following 1st capture (S_A^1) differs from that for all subsequent years (S_A^{2+}), based on the approach of Pradel et al. (1997).

It is also common for breeding-age seabirds not to be detected at a colony in one year, but to return and breed in subsequent years (Chastel 1995; Bradley et al. 2000). This 'skipping' or temporary emigration can be incorporated into models as a form of 'trap-dependence' in which the probability of detection in a breeding season is allowed to depend on whether or not an individual was captured in the previous year (Sandland & Kirkwood 1981; Pradel 1993). Where trap-dependence was modelled, we used the form:

$$\text{logit}(p) = a_{(g^*t)} + bx,$$

where, p is the probability of detection and x is a covariate with a value of 1 if a bird was captured, or 0 if it was not encountered, in the previous year (Pradel 1993; Clucas et al. 2008). The subscripts g and t indicate variations due to group (breeding site) and time (between years) are allowed in the model.

Before assessing the relative merits of a candidate set of models we assessed the goodness of fit of a global model, with full time-dependence of parameters and with each colony defined as a separate group, using the programme U-CARE (Choquet et al. 2000). This assessment was based on 2 tests: Test 3 tests the assumption that all birds banded during one capture occasion have the same probability of surviving to the next occasion and thus tests for transience. Test 2 tests whether birds known to be alive in the period between 2 sampling occasions show homogeneity in capture probabilities and thus tests for trap-dependence. The overall goodness-of-fit statistic also provides an estimate of over-dispersion in the data (summarised by the variance inflation factor, $ĉ$) which can be used to adjust the standard error estimates of parameters in fitted models (Lebreton et al. 2003).

We used Akaike's information criterion corrected for over-dispersion ($QAICc$) to rank candidate models. Model ranking results are also expressed using 2 other relative measures: firstly, $\Delta QAICc$, the difference between the $QAICc$ value for the most preferred model and the model of interest. A $\Delta QAICc$ of ≤ 2, suggests that both models are supported equally well by the data; secondly, the $QAICc$ model weight, which provides a measure of the weight of evidence in support of a particular model (Burnham & Anderson 2002). To obtain overall estimates of the demographic parameters

Table 1. Goodness-of-fit statistics for global models in analysis of (a) adult survival, and (b) young survival and age of first return to a colony. Values are output from Program U-CARE for Cormack-Jolly-Seber and multi-state data, respectively. The term 'overall' reports the combined χ^2 statistic for all component tests and summarises the goodness of fit of the 'raw' model. Removal of component tests corresponding to transience (*3.SR* and *3G.SR*) and trap-dependence (*2.CT* and *M.ITEC*) effects improved the fit of both models, as measured by the variance inflation factor, $\hat{c}$, for which values closer to 1.0 indicate a better fit.

	Mauao				Motuotau I				Combined			
	χ^2	df	P	$\hat{c}$	χ^2	df	P	$\hat{c}$	χ^2	df	P	$\hat{c}$
(a) Overall	412.8	137	<0.001	3.0	55.2	35	0.016	1.6	468.0	172	<0.001	2.7
3.SR & *2.CT* removed	164.7	106	<0.001	1.6	28.8	24	0.227	1.2	193.5	130	<0.001	1.5
(b) Overall	178.7	118	<0.001	1.5	45.8	28	0.018	1.6	224.5	146	<0.001	1.5
3G.SR & *M.ITEC* removed	102.8	92	0.207	1.1	36.6	21	0.019	1.7	139.4	113	0.046	1.2

we used the model averaging function in Program MARK (White & Burnham 1999).

We knew that sampling effort varied between sites and years, so we only considered models with both time- and site-dependent effects on capture probabilities, in order to reduce the number of models in our candidate set. This also included models with both time- and site- dependent effects on adult survival. For occasions in which no fieldwork was carried out, capture probabilities were fixed at zero.

Apparent survival and *AFR* of juveniles
For this analysis we constructed capture histories from banding records of chicks and of adults returning to the colonies during the Apr-May prospecting period. We estimated *AFR* and apparent annual survival of juvenile birds using a multi-state mark-recapture model, also implemented in Program MARK (Lebreton & Pradel 2002; White *et al.* 2006). These models can estimate survival and capture probabilities for each demographic state and also the probability of transition between 2 states. Our approach followed that used previously to estimate similar parameters in other seabirds that delay their post-fledging return to a breeding colony by 1 or more years (Spendelow *et al.* 2002). This allowed estimation of the probability of first return to the colony at different ages.

In our models for these data, we defined 2 states: 'adult,' which is a bird that has returned to the colony at least once after fledging, and 'young,' which is a bird that has fledged, but not yet returned to the colony. Note that the adult category does not imply breeding status and therefore includes established breeders and pre-breeding individuals. Because young birds are never recaptured in the same state (*i.e.*, they are assumed to be adults on their return to the colony), recapture probabilities were fixed at zero for this state. Similarly, adults cannot become young

birds, so the probability of this transition was also fixed at zero. In addition, it was necessary to set 2 thresholds for the estimation of *AFR*. These were a minimum age at which a returning bird could be encountered (k) and an age by which all individuals that return to the colony have done so (m). We set the minimum *AFR* threshold at 2 years, based on the minimum observed *AFR* in our raw data and on the earliest previously reported return at age 3 years-plus (G. Taylor, *pers. comm.*). For the upper threshold, a natural choice might be the maximum observed age at first return (11 years). However, only 5 of the 132 individuals that were observed to return did so after they were 8 years old, *i.e.*, there was almost no information on the probability of 1st return after this age. We therefore set the upper threshold to be 8 years. Because information was available on all individuals banded as chicks, we knew their age in subsequent years and we were therefore able to model the probability of first return ($\alpha^{(v)}$) as a function of age (v) over the range k to $m-1$. We set $\alpha^{(v)}$ to 0 for $v < k$ and to 1 for $v \geq m$, corresponding to the assumption that individuals will not return to the colony before age k and will all have returned by age m. We assumed that $\alpha^{(v)}$ does not vary over time.

Following Spendelow *et al.* (2002), for this modelling approach, it was necessary to assume:

(1) the age of 1st possible return to the colony (k) is known;
(2) of those that will return, all return to the colony by age m;
(3) every bird released as a chick has the same probability of survival until age k, and this probability does not vary between years;
(4) every marked bird of age $\geq k$ in a given year has the same probability of survival to the following year;
(5) every marked young bird in a given year has a capture probability of zero;

Table 2. Comparison of the 4 best-fitting models, as ranked by *AICc* values and using *ĉ* = 1.5, for estimating survival of adult grey-faced petrels at Mauao and Motuotau, Bay of Plenty, New Zealand, from 1991 to 2008. For defining models, S_A = apparent survival of adults, *TR* = transience, *P* = probability of capture, *TD* = trap-dependence, (.) indicates a constant parameter, *g* = parameter varies by group (site), *t* = parameter varies through time, * indicates full interaction between terms is allowed. Models including time-dependence were included in the initial candidate set, but weights for these models were all ≪ 0.001 so the models were excluded from further consideration.

Model	*DQAICc*	Weight	Number parameters
$S_A(.)\ TR(g)\ P^{TD}(g*t)$	0.0	0.665	30
$S_A(g)\ TR(g)\ P^{TD}(g*t)$	1.4	0.335	31
$S_A(.)\ TR(.)\ P^{TD}(g*t)$	14.7	0.000	29
$S_A(g)\ TR(.)\ P^{TD}(g*t)$	15.3	0.000	30

(6) every marked young bird of age *v* ($k \leq v < m$) has the same probability of returning to the colony in a given year;
(7) every marked adult has the same probability of returning to the colony in a given year;
(8) every unmarked adult has the same probability of returning to the colony the following year.

We direct the reader to the Spendelow *et al.*'s (2002) original publication for a detailed discussion of these assumptions.

As with the estimation of adult survival, we first constructed a global model which we tested for goodness of fit using the multi-state procedures in U-CARE (Choquet *et al.* 2000). This also provided an estimate of over-dispersion in the data, which was incorporated in subsequent model fitting using *QAICc* (Burnham & Anderson 2002). In this case, taking into account the assumptions above and limitations in our data, our global model contained: group effects on survival of young (S_y), group and time effects on survival of adults (S_A), group effects on *AFR*, and both group and time effects on capture probabilities. Where the U-CARE analyses suggested transience or trap-dependence, we modelled these as outlined above.

RESULTS

For the estimation of adult survival we used capture histories of 5844 birds over the 17 years of sampling and for estimating *AFR* we used the histories of 928 chicks, of which 132 were observed to have returned, along with that subset of adults encountered during the Apr-May prospecting periods.

Adult survival

Goodness-of-fit testing of the global model for adult survival showed evidence of trap-dependence (Test

Table 3. Model-averaged estimates of apparent adult survival (and standard errors) and the proportion of transient birds in each annual sample for grey-faced petrels at Mauao and Motuotau I, Bay of Plenty, New Zealand. Models allowing for transience produce estimates for birds in the year following their first encounter (S_A^1) and in all subsequent years (S_A^{2+}).

	S_A^{2+}	S_A^1	Transience
Mauao	0.886 (0.009)	0.723 (0.025)	0.184 (0.007)
Motuotau I	0.890 (0.015)	0.844 (0.033)	0.052 (0.002)

2) and transience (Test 3) effects at both sites (Table 1). When combining data from both sites, the overall χ^2 statistic was significant at both sites leading to a variance inflation factor of *ĉ* = 2.7, indicating lack-of-fit. Removing the *3.SR* and *2.CT* components of the tests, corresponding to transience and trap-dependence, respectively, led to the χ^2 statistic no longer showing any evidence of lack-of-fit at Motuotau, whereas at Mauao there appeared to be some residual lack-of-fit. Removal of these components gave an estimate of *ĉ* = 1.5 for the 2 sites combined. This value was used to correct for over-dispersion in subsequent models that incorporated trap-dependence and transience.

Model fitting showed negligible support for temporal variation in adult survival at both sites, but indicated a site-specific transience effect (Table 2). Model-averaged estimates of key parameters are given in Table 3. We estimated the apparent adult annual survival rate to be 0.89 for resident birds. Apparent survival in the year following 1st capture differed between sites, being lower at the mainland site, Mauao, where the proportion of transient birds was 18%, than on the island, Motuotau (5% transience).

Probability of capture

We calculated model-averaged estimates of annual capture probabilities separately for birds seen and not seen in the previous year. At Mauao, these ranged from 0.12 to 0.52 (mean = 0.40) for a bird seen in the previous year and from 0.06 to 0.35 (mean = 0.25) for a bird not seen in the previous year. At Motuotau, they ranged from 0.15 to 0.45 (mean = 0.30) for a bird seen in the previous year and from 0.12 to 0.39 (mean = 0.25) for a bird not seen in the previous year. Thus both trap-dependence and transience were greater at Mauao than on the nearby island.

Age of first return and survival of young birds

For the global multi-state model, the overall χ^2 statistic was significant at both sites. Removing the *3G.SR* and *M.ITEC* components (which test for transience and trap-dependence, respectively) led to the χ^2 statistic no longer showing any evidence of lack-of-fit at Mauao, whereas at Motuotau there appeared to be some residual lack-of-fit.

Table 4. Comparison of the best-fitting models, as ranked by *AICc* values and using $\hat{c}$ = 1.2, for estimating survival of young grey-faced petrels (S_Y) and age of 1st return (*AFR*) at 2 sites in the Bay of Plenty, New Zealand, from 1991 to 2008. For defining models, S_A = apparent survival of adults, *TR* = transience, *P* = probability of capture, *TD* = trap-dependence, (.) indicates a constant parameter, *g* = parameter varies by group (site), *t* = parameter varies through time, * indicates full interaction between terms is allowed. Models including time-dependence were included in the initial candidate set, but weights for these models were all << 0.001 so the models were excluded from further consideration.

Model	$\Delta QAICc$	Weight	No. parameters
$S_Y(.) S_A(.) TR(.) AFR(g) P^{TD}(g*t)$	0.0	0.219	31
$S_Y(.) S_A(.) TR(g) AFR(g) P^{TD}(g*t)$	1.1	0.128	32
$S_Y(.) S_A(g) TR(.) AFR(g) P^{TD}(g*t)$	1.4	0.108	32
$S_Y(g) S_A(.) TR(.) AFR(g) P^{TD}(g*t)$	1.4	0.108	32
$S_Y(g) S_A(.) TR(g) AFR(g) P^{TD}(g*t)$	2.1	0.078	33
$S_Y(g) S_A(g) TR(.) AFR(g) P^{TD}(g*t)$	2.5	0.063	33
$S_Y(.) S_A(g) TR(g) AFR(g) P^{TD}(g*t)$	2.7	0.057	33
$S_Y(g) S_A(.) TR(.) AFR(.) P^{TD}(g*t)$	2.8	0.053	31
$S_Y(g) S_A(g) TR(g) AFR(g) P^{TD}(g*t)$	3.4	0.041	34
$S_Y(g) S_A(.) TR(g) AFR(.) P^{TD}(g*t)$	3.7	0.035	32
$S_Y(.) S_A(.) TR(.) AFR(.) P^{TD}(g*t)$	3.8	0.032	30
$S_Y(g) S_A(g) TR(.) AFR(.) P^{TD}(g*t)$	4.2	0.027	32
$S_Y(g) S_A(g) TR(g) AFR(.) P^{TD}(g*t)$	5.2	0.016	33
$S_Y(.) S_A(.) TR(g) AFR(.) P^{TD}(g*t)$	5.3	0.015	31
$S_Y(.) S_A(g) TR(.) AFR(.) P^{TD}(g*t)$	5.7	0.013	31
$S_Y(.) S_A(g) TR(g) AFR(.) P^{TD}(g*t)$	7.3	0.006	32

Removing the *3G.SR* and *M.ITEC* components led to an improvement in $\hat{c}$ from 1.5 to 1.2 for the 2 sites combined (Table 1). We fitted a range of models that included both transience and trap-dependence using this value for $\hat{c}$.

Model fitting indicated support for a range of models (Table 4). Within these, 4 models accounted for most of the *QAICc* weighting. These models indicated that survival of young birds was not site-dependent, but that *AFR* differed between sites. The model-averaged, annualised estimates for S_Y in the first 2 years of life are 0.844 (*SE* = 0.023) for Mauao and 0.865 (*SE* = 0.032) for Motuotau.

Although the best-fitting models all suggest that *AFR* varies between the 2 sites, age-specific estimates for Motuotau were unreliable, with wide confidence intervals, which may be a result of the relatively short-term data set and lesser sampling effort at this site. Given these concerns, we report the variation in the probability of *AFR* for Mauao only in Fig. 1. This shows that around 50% of fledglings that will return to the natal colony do so by 4 years of age, and that by age 6, the probability of a fledgling returning is approximately 1.0. We tested these estimates by varying *m* (the maximum presumed *AFR*) between 6 and 9 years but this altered neither the shape of the resulting probability distribution, nor the asymptote and did not improve the model fit.

DISCUSSION

Our best-fitting models for estimating the apparent annual survival rate of adult birds made allowance for a transience effect. This led to separate estimates of S_A for birds in the year following their first encounter (S_A^1) compared with all subsequent years (S_A^{2+}). Estimates of S_A^1 were lower than S_A^{2+} at both sites with a greater disparity between the 2 at Mauao, the mainland site, where the adult population also contained a greater proportion of transients. This effect has been demonstrated in other similar analyses in which transient behaviour is taken into account. It appears to be common in seabird populations where immature birds may visit a number of potential breeding sites before establishing site fidelity at 1 of them (Prévot-Julliard *et al.* 1998; Clucas *et al.* 2008; Ratcliffe *et al.* 2008). Site-specific variation in levels of transience has also been shown in procellariids. For example, Tavecchia *et al.* (2008) found intraspecific variation in the proportions of transients in both European storm petrel (*Hydrobates pelagicus*) and Balearic shearwater (*Puffinus mauretanicus*) populations at 2 adjacent colonies in the western Mediterranean.

Table 5. Published estimates of apparent survival and average adult body mass for adult procellariids; * indicates a range of estimates depending on age since first observed breeding.

Species	Body mass (g)	S_A	Reference
Westland petrel (*Procellaria westlandica*)	1100	0.965	Waugh *et al*. (2006)
Sooty shearwater (*Puffinus griseus*)	850	0.952	Clucas *et al*. (2008)
Cory's shearwater (*Calonectris diomedea*)	600	0.89	Jenouvrier *et al*. (2008)
Short-tailed shearwater (*Puffinus tenuirostris*)	550	0.882–0.918*	Bradley *et al*. (1989)
Grey-faced petrel (*Pterodroma macroptera gouldi*)	550	0.89	This study
Balearic shearwater (*Puffinus mauretanicus*)	500	0.78	D'Oro *et al*. (2004)
Snow petrel (*Pagodroma nivea*)	400	0.913	Chastel *et al*. (1993)
Hutton's shearwater (*Puffinus huttoni*)	350	0.931	Cuthbert & Davis (2002)

There are at least 2 interpretations of the biological implications of transience. The 1st considers the effect as an index of prospecting behaviour by immature birds, which infers that a colony with a higher level of transience may be more attractive, as failure to establish may be linked to density-dependent processes (Clucas *et al*. 2008). This is unlikely to be the case at Mauao because breeding space is not a limiting factor. On the other hand, it may suggest that some characteristics of the site, perhaps local predation or other disturbances such as light and noise pollution, prevent prospecting birds from settling there. These factors may, in some cases, be sufficient to induce marked local variation in demographic processes within a species (Tavecchia *et al*. 2008).

The apparent annual survival rate of more established adults was estimated at 0.89 at both of our study colonies. Reliable estimates of similar rates for petrel species with which to compare ours are rare because of the requirement for long-term data sets and because of extended post-fledging absences from breeding sites and non-attendance by some breeding-age adults in some years. Assuming that adult survival rate within a taxonomic group scales with body mass (McCarthy *et al*. 2008), our estimate for grey-faced petrels appears to be reasonable, but possibly somewhat low compared with similar estimates for other procellariids (summarised in Table 5).

A range of factors may have contributed to our estimated values. Some individuals captured post-fledging will be immature birds that are yet to breed. If similar demographic trends occur in grey-faced petrels as in short-tailed shearwaters, where adult apparent survival increased with breeding age (Bradley *et al*. 1989), this may have caused an underestimate. It is also possible that birds may show transient behaviour after more than the 1 year accounted for in our models, or that permanent emigration from colonies contributes to lower apparent survival estimates. The close proximity of both colonies to an area of high human recreational use and, in the past decade, intensive coastal redevelopment may have contributed to this. The higher rate of transience at the mainland site could also be an indicator of disturbance.

We must also acknowledge the potential for our sampling procedures, including our dependence on volunteer effort, to have reduced the likelihood of encountering individual birds. For example, we banded birds found on the surface, so those birds that entered burrows soon after landing were less likely to have been encountered. If these birds were established breeders, as is likely, this would serve to under-estimate our estimates of survival through inducing intrinsic heterogeneity in recapture probabilities (Crespin *et al*. 2008; Oppel *et al*. 2011). Some birds may also have deserted the colonies after being handled, especially around the incubation period. Imber (1976) observed that ~10% of grey-faced petrels respond in this way. One approach to dealing with some of this uncertainty would be to restructure the banding programme so that, rather than attempting to cover all of a site with limited personnel, banding effort is concentrated in a consistent and defined sample of plots in every season. This would increase the likelihood of encountering individual birds and accordingly increase confidence that any subsequent estimates of apparent survival rates are driven by biological factors rather than some indeterminate mix of biological and sampling effects (Sainz-Aguilar *et al*. 2010). Also, if grey-faced petrels show similar patterns of colony attendance with respect to breeding status as short-tailed shearwaters, with younger, 'pre-breeding,' adults arriving at the colony later than established breeders (Serventy 1967), further concentration of effort in the Apr-May prospecting phase of the breeding season may give more reliable data with which to estimate S_A^{2+}.

It was necessary for us to define sampling occasions strategically to make the best use of the available data. These occasions risked violating the
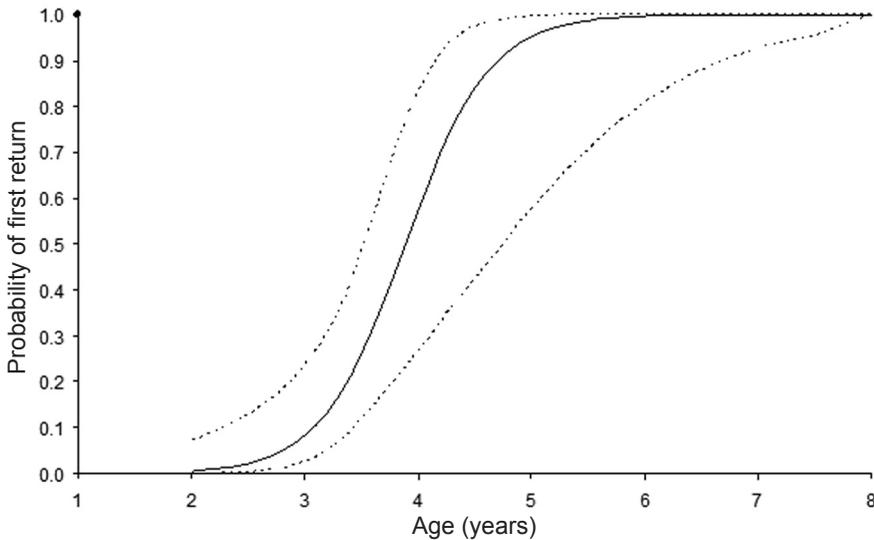
Fig. 1. Estimated probability of 1st return to natal breeding colony at Mauao, Bay of Plenty, New Zealand with age of juvenile grey-faced petrels. Dotted lines are 95% confidence intervals.

assumption of capture periods being of negligible duration compared to the period between them. Any resulting bias is likely to be small if recapture probabilities are greater than 0.2 and capture effort is similar between years (Smith and Anderson, 1987; O'Brien *et al.*, 2005). Our data met these requirements.

The probability of encountering birds was lower if they had not been encountered during the previous breeding season and this effect was more marked at the mainland site than on the island. Although this appears as a 'trap-dependent' effect, it is important to note that this does not necessarily infer a true behavioural response to capture, but more a change in encounter probability subsequent to capture, which can result from other factors (Lebreton *et al.* 1992; Pradel 1993). Our estimates of capture probabilities showed a similar temporal pattern to those reported for other seabird species, which is commonly interpreted as temporary emigration, possibly linked to breeding performance in previous seasons (Barbraud & Weimerskirch 2001; Grosbois & Thompson 2005; Clucas *et al.* 2008). It is probable that more subtle effects related to sex, age and breeding status may be operating, but detection of these would require much more detailed information on individual birds than was available for this study.

Survival of young birds between fledging and 1st return was estimated as being very similar at both sites and also very similar to that of adult birds. This is surprising as survival rates of young birds are commonly reported as being markedly lower than those of adults (Weimerskirch *et al.* 1997; Waugh *et al.* 1999). Although common, this relative difference in survival is not universal. Sandvik *et al.* (2008) reported survival of immature Atlantic puffins

(*Fratercula arctica*) as almost identical to that of adult birds. The similarity in our estimates may result from apparent adult survival being underestimated for the reasons outlined above, but also from relatively high encounter rates from juveniles on their return to their natal colonies if they spend more time on the surface than established breeders, who spend much of their time in burrows. This is clearly an area in need of further study.

The age at which pre-breeding juvenile birds 1st attend a colony varies between individuals (Bradley *et al.* 1999). We estimated that the probability of return is 0.5 at 4 years of age, rising to around 1.0 by age 6. This trend mirrors that reported for other long-lived seabirds, but our estimates of *AFR* also account for the incompleteness of detection of some returning individuals. This method would seem to be a very useful approach to adopt in the many cases where limited resources and large population sizes mean that it is impossible to identify all individuals attending a colony in all breeding seasons. The use of an estimate of the probability of a juvenile bird returning to a colony, with its associated estimate of variance, should prove to be useful in demographic models aimed at the management of bird populations where complete knowledge of population processes is an exception.

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