Survival estimates of Antarctic terns *(Sterna vittata bethunei)* on the Snares Islands, New Zealand

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Abstract The survival of adult and fledgling Antarctic terns (*Sterna vittata bethunei*) at the subantarctic Snares Islands was studied from 1976 to 2007. Annual adult survival was 0.91 and that of birds banded as fledglings was 0.42 in the first year and 0.94 in subsequent years. On average, a breeding adult would have a reproductive life-span of 10.2 years while a fledgling that survived the first year would have a life expectancy of 17.4 years. The disparity between the survival of birds banded as breeding adults and fledglings is probably be due to relatively small samples sizes. The estimated survival rates of Antarctic terns are similar to those reported for New Zealand fairy terns (*S. nereis davisae*). No terrestrial predators occur at the Snares Islands, and extensive predator-control is undertaken in the areas where New Zealand fairy terns nest, and so these survival rates may be typical of other breeding terns in the absence of terrestrial predators.

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Keywords Antarctic tern; Sterna vittata; Laridae; mortality; New Zealand; Snares Islands; predator-free

INTRODUCTION

In New Zealand, Antarctic terns (*Sterna vittata bethunei*) breed on southern Stewart Island and outlying islands, and the subantarctic Snares, Antipodes, Bounty, Auckland, and Campbell Islands (Turbott 1990). The total population of this subspecies was estimated at <1000 pairs (Robertson & Bell 1984) and its conservation status is listed as "Range Restricted" by the New Zealand Department of Conservation (Hitchmough *et al.* 2007). However, apart from two breeding season surveys at the Snares Islands during the mid-1980s (Sagar *et al.* 2003), there has been no systematic recording of population size of the Antarctic tern on any other island group.

Tern species around the world are considered to be long-lived, with estimates of annual adult survival often within the range 0.91-0.93 (Schreiber & Burger 2001). Population growth rate in such long-lived species is most sensitive to changes in adult survival rates (Nur & Sydeman 1999), and so, given the relatively small size of the Antarctic tern population within New Zealand, it is important to have an estimate of adult survival in this species. Here, we provide the first empirical estimate of annual adult survival rate in the Antarctic tern and compare this with other tern species.

METHODS

The study was carried out at North East Island, the Snares Islands (48°02'S, 166°36'E), during 31 visits between Nov 1976 and Apr 2007. A long-term study of the population size and distribution, and breeding of Antarctic terns at the Snares Islands was undertaken during the period 1976-1987 and this study determined that a minimum of 65 breeding pairs was present during the 1983/84 and

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1984/85 breeding seasons (Sagar *et al.* 2003). This breeding study involved the banding of adults and chicks, and the subsequent capture and resighting of uniquely marked individuals formed the basis of the survival analyses reported here.

Banding and resighting of birds

Antarctic terns were banded during a study of their breeding biology during Oct-Feb in 1976-77 and each year from 1983 to 1987 (see Sagar et al. 2003 for details). During this time breeding adults of unknown age were captured with a handnet by PMS or CMM. On capture, each bird was fitted with a numbered stainless steel band and a unique combination of up to 3 colour bands. Chicks near fledging were also banded with unique combinations of metal and colour bands. However, in 1987, the final year of the breeding biology study, only one chick was fitted with a unique colour band combination - all other chicks banded that year were fitted only either with a numbered metal band or with a numbered metal band plus a single blue band to denote year of banding. Consequently, chicks not uniquely colour-banded were not included in the band-recapture analysis, but have been used to provide information about longevity.

All birds were banded with uniquely numbered stainless steel bands, and we consider the probability of metal band loss to have been very low or nil. Wrap-around colour bands were fitted to all adults and chicks.

During 1976-77 and 1983-1987, visits to the island were made during the breeding season (September-January), and checks for banded birds were made at the breeding colonies and at roosting sites adjacent to these colonies. Birds banded as breeding adults of unknown age were found to have strong nest site retention from year to year (Sagar *et al.* 2003) and this facilitated identification of these birds. The annual visits made from 1992 to 2007 occurred postbreeding (Feb-Aug), when many birds congregated at a single roost on a bare rock platform. At this roost the birds were confiding and able to be approached so that their legs could be checked for bands. This way, a "capture" history was compiled for each individual and used for survival analysis.

Antarctic terns have few potential predators on the Snares Islands, which lack terrestrial mammals. Remains of three Antarctic terns were found among 3752 prey items recovered from brown skua (*Catharacta lonnbergi*) middens on the Snares Islands (Miskelly *et al.* 2001), but none of these birds was banded.

Analysis

Recapture histories were constructed from data collected between 1976 and 2007 (Table 1). An analysis of capture-recapture data was carried

out using the computer program MARK (White & Burnham 1999). The terms "captures" and "recaptures" as used here denote, respectively, those birds caught and banded for the first time and those birds previously banded and resighted at the study site. Because the island was visited at irregular intervals, captures and recaptures were separated into breeding seasons signified by the year in which the summer began. Thus, recaptures in Sep of year (X) and Mar of the following year (X + 1) would be grouped as all being recaptures from year X. Consequently, banding data for trips were combined where they were conducted within the same breeding season. Antarctic terns are rarely recorded from mainland New Zealand and few are thought to disperse from the Snares Islands, as there have been no sightings of banded birds from elsewhere in the subantarctic and they do not appear to disperse permanently to other subantarctic islands (Sagar et al. 2003). Therefore, it seems appropriate to consider apparent survival (Φ) , estimated using Cormack-Jolly-Seber markrecapture analysis, to represent true survival (S) in this population. Either way, we recovered no dead marked birds, and were unable to use the live and dead recovery model of Burnham (1993) to estimate immigration.

A general model that is fully time-dependent for survival (Φ) and re-sighting probability (P) was taken as the starting point, and then used as the basis for all goodness of fit analyses. Age and sex structure was introduced into Φ by distinguishing between birds using a two-age class structure: birds banded as adults of unknown age, and adults banded as fledglings. This structure was selected as terns have been shown to have lower immature survival (Nisbet & Cam 2002). We then examined the influence of time-dependent Φ on both age classes, constant Φ on both age classes, and time-dependent Φ in known-age birds only. The latter model was based on the grounds that for birds banded as fledglings, Φ is lower than adult Φ in terns, and it has been suggested it is more sensitive to annual variation in environmental conditions (Nisbet & Cam 2002). We also assessed the influence of transience on the population using the methodology of Pradel *et al.* (1997). P remained fully time dependent. From the candidate set of age structured Φ models, the most parsimonious one was then selected and age structure introduced into P. We then examined the influence of time-dependent P on both age classes, constant P on both age classes, and time-dependent P in known-age birds only.

Corrected Akaike's information criterion (AICc) produced by MARK (Cooch & White 2001) was used to select the most parsimonious model from a set of candidate models. This procedure was preferred over the use of a likelihood ratio (LRT) to test

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Table 1 M arrays of banding data, by age, for Antarctic terns *Sterna vittata bethunei* captured on North East Island, the Snares Islands. Conventions regarding breeding seasons are defined in the text. Note that observations were made in 1994, 1996, 1997 and annually 2001-2007 inclusive, but no colour-banded terns were seen in those years.

	Number sighted												
		1982	1983	1984	1985	1986	1987	1992	1993	1995	1998	1999	2000
Adults													
1976	14	0	4	1	2	3	3	0	1	0	0	0	0
1983	2			0	1	1	1	2	0	0	1	1	1
1984	4				4	3	2	1	1	0	0	0	0
1985	7					7	6	2	1	1	0	0	0
1986	3						2	0	0	0	0	0	0
1987	4							1	2	1	0	0	0
Fledglings													
1976	5	1	1	0	1	0	0	0	2	0	0	0	0
1983	7			0	0	1	0	0	0	0	0	0	0
1984	21				2	1	2	5	5	0	2	1	1
1985	13					1	1	1	2	0	0	0	0
1986	6						0	1	1	0	0	0	С
1987	1							0	1	0	0	0	0

between two nested models, as some of the analysis was conducted using non-nested models. For one model to be selected above another, Anderson & Burnham (1999) recommended that the difference between their respective Akaike's information criterion (Δ AICc) should be >2. If Δ AICc is between 1 and 2 then these models should be considered nearly tied, and any subsequent inference should be based on the subset of models.

The logit link function, in program MARK, was used throughout the modelling procedure. Goodness of fit (GoF) of the models was evaluated in a series of tests. First, we tested the full parameter Cormack-Jolly-Seber model (time dependent survival and recapture probabilities) using RELEASE TEST2+3 within MARK (White & Burnham 1999) to evaluate assumptions that banded birds had the same recapture and survival probabilities (Burnham et al. 1987; Lebreton et al. 1992). Next we used UCARE (Choquet et al. 2001), which implements the extended form of TEST2+3, derived originally by Burnham et al. (1987), to evaluate recapture heterogeneity with TEST2.Ct (Pradel 1993), which tests for specific behavioural patterns, such as temporary emigration or recapture heterogeneity, which mimic trap dependence. More details of the application of this test were provided in Pradel et al. (1997) and Chaloupka et al. (1999).

The GoF of the best fit model selected by Δ AICc was then assessed in absolute terms using a parametric bootstrap approach available in program MARK. To deal with the issues of validity of the bootstrapped GoF when sampling unequal time

intervals (Gimenez *et al.* 2005) we created a general model in which each year (even those not sampled) was included in the model, but in which P was set at zero in those years in which the island was not visited. Some 100 replicates were run. In addition, both datasets were tested for over-dispersion using the median c-hat procedure in program MARK.

To estimate longevity and expectation of further life we used our estimates of survival from MARK and the calculations in Seber (1982). Expectation of further life was calculated using the formula -1/ln(0.91).

RESULTS

From 1976 to 1987 we fitted 34 breeding adult and 53 fledgling Antarctic terns with unique colour band combinations. The numbers of birds captured and sighted each year are summarised in Table 1. An additional 26 fledglings were banded with a metal band or a metal band plus a single blue colour band during Nov-Dec 1987. Several of these birds were seen during each period of observation, the last in Apr 2006, when it was in its 19th year.

Model fitting

The bootstrap goodness of fit tests indicated that for the observed deviance in the full parameter model, the probability of a deviance as large as or greater than the observed value, was approximately 0.85. Thus, we can assume an adequate goodness of fit. The logistic regression estimates of median c-hat (1.12) indicated that these models do not

Table 2 Comparison of the top six models for factors affecting survival in Antarctic terns *Sterna vittata bethunei* captured on NE Island, the Snares Islands. The factors considered in survival models (Φ) were age (g) and year (t). Models were selected based on Akaike's information criterion (AICc), the lowest AICc indicating the most parsimonious model. K is the number of parameters in the model, Δ AICc is the difference in AICc between the current model and the best model. Those models with Δ AICc > 6 have negligible support and are not considered further.

Model	AICc	∆AICc	AICc weights	Model likelihood	K	Deviance
Φ (<i>g</i>) with separate transience parameter for known-age birds <i>p</i> (<i>t</i>)	470.60	0	0.51159	1	25	223.886
Φ (<i>g</i>) with separate transience parameters for adults banded as fledglings and adults of unknown age <i>p</i> (<i>t</i>)	470.69	0.09	0.48810	0.9541	26	221.212
Φ (g) with same transience parameter for known-age birds and adults of unknown	404.00	1(00	0.00015	0.0000	05	0 40 100
age $p(t)$	486.90	16.30	0.00015	0.0003	25	240.190
$\{Phi(t) \ p(t)\}$	487.26	16.66	0.00012	0.0002	29	229.248
$\{Phi(g) \ p(t)\}$	489.67	19.07	0.00004	0.0001	24	245.687

suffer from a significant degree of over-dispersion. When the RELEASE goodness of fit tests were run on the full parameter Cormack-Jolly-Seber model (time-dependent Φ and P) using UCARE for the dataset, the models passed TEST2 and TEST2. Ct (trap dependence statistic). The dataset failed TEST3, TEST3.Sm (indicating that transience was a significant problem) and TEST3.SR (indicating that survival probabilities were cohort-dependent), and indeed this is what the model selection determined (see below).

The results of model fitting of survival rates and survival probabilities (Table 2) indicated strong support for the model Φ (groups + transience model for birds banded as fledglings in first year of life) P(time). A second model where a separate parameter was estimated for both known-age birds in first year of life and adults following their first year of banding also received good support, but the parameter for the survival of adults of unknown age in the first year after banding could not be estimated. This may account for the low AICc, and so this model is not considered further here. Annual survival probabilities derived from this model were markedly different for survival in the first year of a bird's life (0.42 ± 0.08) and its subsequent survival (0.94 ± 0.03) . Also, AICc values (Table 2) supported a model that had separate survival parameters for fledglings after their first year of life and birds banded as adults of unknown age. In this model survival was greater for fledglings after their first year of life (0.94 ± 0.03) than for birds banded as adults of unknown age (0.91 ± 0.02) . Models incorporating annual survival estimation variation among years had little support (Table 2). In other words, recapture probabilities varied with age of the birds, but did not vary between years.

Survival and longevity

With an annual adult survival rate of 0.91, a breeding Antarctic tern would have, on average, a reproductive life-span of 10.2 years. Similarly, a fledgling, having survived the first year of life and with a subsequent survival rate of 0.94 would have an average life-span of 17.4 years, with the oldest birds surviving over 30 years.

DISCUSSION

Our estimated survival rates for Antarctic terns indicate that they are long-lived, with a potential life expectancy after fledging of over 17 years. The results also indicate that several years elapse between fledging and age of first breeding, providing support for the observations of Sagar et al. (2003) who reported 3 years as the youngest age at which this species bred. An unexpected result of this study was the higher estimated survival of birds banded as fledglings after their first year compared to breeding adults. Potential sources of age-related variation in our survival estimates include band loss, senescence and age-specific emigration. In this study we used numbered stainless steel bands and in our experience with the use of these in several studies of a variety of species over many years, band loss is highly unlikely. In contrast, loss of colour bands has been documented in some banding studies (e.g., Sagar et al. 2002) and such loss could result in under-reporting of birds that were still alive, and so result in biased estimates of apparent survival. However, given that Antarctic tern adults and fledglings were fitted with wrap-around bands of the same size and material we would expect the rate of any band loss to be similar in both age classes. Some fledglings were also fitted with an end-butted colour band above the metal, resulting in a different

potential rate of loss, and so potentially affecting the estimation of survival rate in this age-class.

A factor that could have influenced the survival estimates was the relatively small number of birds banded, and so the resighting probability of each bird has a proportionately higher influence on the calculation of survival rate. Consequently, any ageor sex-related influences on the survival of just one bird could have decreased or increased the survival estimate. However, in a test for age-specificity in the survival of common terns (S. hirundo), Nisbet & Cam (2002) found no evidence that survival depended on either age or sex, except that survival was lower amongst the youngest birds (ages 2-3 years). Despite the large number of birds included in their study, Nisbet & Cam (2002) concluded that confidence limits on estimates of survival were wide, especially for the oldest age-classes, and a slight decline in survival late in life could not have been detected.

Likewise, emigration could have affected the estimates of survival. The nearest other breeding site of Antarctic terns to the Snares Islands are islands off the southern tip of Stewart Island, a distance of c.100 km. No banded terns were noted among 20 seen there on 25-26 November 1985, but few birds were seen close enough to be confident that they were not banded (C.M. Miskelly unpub. data). As far as we are aware, no one has banded Antarctic terns elsewhere or checked for banded Antarctic terns at other breeding sites in the New Zealand region. However, any emigration is expected to be greater in younger birds, and adult Antarctic terns at the Snares Islands appear to have strong nest site retention from year to year, although one bird did move 500 m between breeding attempts in one season (Sagar et al. 2003). If the emigration rate of fledglings was higher than that of adults, then survival estimates of birds banded as fledglings would be expected to be lower than those of birds banded as breeders because of the lower resighting rate.

Our survival estimates appear to be the first for Antarctic terns. In the New Zealand region, the only other estimate of survival of a tern species is for the endangered New Zealand fairy tern (S. nereis davisae), which has one small population of c.30 individuals in Northland (Ferreira et al. 2005). In this species, an estimated 63% of fledglings survived until adulthood (at age 2), while 0.95 of adults survived each year (Ferreira et al. 2005), compared to our estimates of 0.42 for fledglings to age 1 and 0.91-0.94 for adults and fledglings (from age 1). The lower estimated survival rate of Antarctic tern fledglings in their first year compared to fairy terns in their first 2 years after fledging could be the result of higher mortality or emigration in the first year of life for Antarctic terns. Statistical methods to

estimate survival rate are constantly being refined, resulting in an overall increase in the estimates of survival rates within a species as the underlying statistical models improve (Clobert & Lebreton 1991; Prévot-Julliard et al. 1998). Consequently, survival estimates are often difficult to compare unless the same methods have been used (Weimerskirch 2002). However, our study and that of Ferreira *et al.* (2005) used the same statistical programme (MARK) to obtain the estimates of survival. Analyses for both studies were based on similar sample sizes (adults: 33 Antarctic terns, 30 fairy tern; fledglings: 53 Antarctic tern, 55 fairy tern). In addition, both species have similar life history characteristics in that they are non-migratory, feed close to shore, and breed in an environment with few predators although for the fairy tern this is through predator control around nesting areas (Ferreira et al. 2005, Sagar & Sagar 1989, Sagar *et al.* 2003).

Adult survival rates of other tern species obtained by the Cormack-Jolly-Seber models within the programme MARK, and comparable to our estimates, are 0.88-0.92 for common terns (Nisbet & Cam 2002), 0.74-0.91 for roseate terns (S. dougalli; Spendelow et al. 2002), 0.80-0.93 for least tern (S. antillarum; Massev et al. 1992), 0.91 for sooty tern (S. fuscata; Feare & Doherty 2004), and 0.90 for little tern (S. albifrons; Tavecchia et al. 2006). Consequently, our estimate of 0.91 is in the upper range of survival estimates for terns. With the exception of sooty tern, all species are migratory and exposed to a range of predation pressures (Feare & Doherty 2004). The lack of extended migration and terrestrial predators may contribute to the higher survival rate of adult Antarctic terns at the Snares Islands.

All 5 species of terns that breed in New Zealand (Antarctic, fairy, black-fronted *S. albosignata*, Caspian *S. caspia*, and white-fronted *S. striata*) feed inshore and are non-migratory (Higgins & Davies 1996). Therefore, in the absence of native mammalian predators we would expect all to have similarly high survival rates to Antarctic terns and New Zealand fairy terns, at least historically. If this is the case, then their population size would be most sensitive to changes in adult survival rates.

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