AGE AT FIRST BREEDING AND PRE-BREEDING SURVIVAL IN SEYCHELLES SOOTY TERNS *ONYCHOPRION FUSCATUS*

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SUMMARY

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Age at first breeding and annual survival between fledging and first breeding were estimated from band recapture data, taking into account resighting probability, collected in a large colony of Sooty Terns *Onychoprion fuscatus* nesting on Bird Island, Seychelles. The model of age at first attempted breeding probability indicated that most young birds first bred when 5 years old, conforming with earlier estimates from other colonies. Annual survival between fledging and first attempted breeding was estimated for the first time for Sooty Terns, as 0.77, giving a probability of young birds surviving to breed at age 5 of 0.26. Implications of these findings for the exploitation of eggs from Seychelles Sooty Tern colonies are discussed.

Key words: Sooty Terns, *Onychoprion fuscatus*, age at first breeding, survival, egg exploitation, Seychelles

INTRODUCTION

With an estimated breeding population of >6 000 000 pairs, and despite historical declines in numbers and local extinctions of some colonies, the Sooty Tern *Onychoprion fuscatus* is the most numerous oceanic bird in the western Indian Ocean (Feare *et al*. 2007). In Seychelles, there are continuing threats from commercial egg harvesting; illegal poaching of eggs, chicks and adults; continuing habitat change; intensive commercial fishing; and climate change, especially sea level rise (Feare *et al*. 2007). Egg harvesting is regulated by the Seychelles government, following guidelines indicated by research on Sooty Tern population dynamics (Feare 1976a,b, 2002, Feare & Gill 1997, Feare & Lesperance 2002, Feare & Doherty 2004), to ensure sustainability of the annual production. However, owing to the bird's deferred maturity and long life, harvest recommendations have relied on assumptions about some demographic parameters. Feare & Doherty (2004) provided the first estimate of adult annual survival for Seychelles Sooty Terns and, following continued collection of band recapture data in the large breeding colony (300 000–700 000 pairs) on Bird Island (55°12'E, 3°43'S), we here report the first estimates of age at first attempted breeding and pre-breeding survival.

METHODS

Banding and recapture of banded birds

In 1993 a banding programme was begun in most of Seychelles' Sooty Tern breeding colonies, using British Trust for Ornithology numbered incoloy bands, in order to test some of the assumptions made in an earlier harvest model by one of us (Feare 1976a). Because of the island's accessibility and easy visibility of nesting birds, Bird Island has proved the only location where annual searches for banded birds can be undertaken during incubation, when bands can be seen and birds caught for identification. Breeding adults of unknown age were banded in 1993 (550 birds) and 1994 (2250), and three cohorts of well-grown chicks were banded in 1993 (650 banded 16–18 August), 1997 (1000, 4–30 September) and 2002 (1550, 27 August–4 September). In the 1993 and 2002 cohorts, chicks were 30–60 days old (60 days is approximate fledging age) when banded, according to plumage development criteria (Feare 1976a), and in the 1997 cohort, chicks were approaching fledging. Most chick mortality occurs during the first 10 days after hatching (Feare 1976a), and significant mortality of older chicks occurred only in 1994, caused by exceptionally heavy rainfall in late August. The cohorts in this study thus suffered little mortality between banding and fledging.

Each year from 1995 to 2008 searches for banded birds were made as described in our earlier publication (Feare & Doherty 2004). All accessible parts of the colony were searched (dense *Suriana* bush, where nest density is lower than in the main colony, in c. 2 ha of the c. 9 ha colony, is largely impenetrable to humans, and few banded Sooty Terns can be seen or caught there) but effort has varied depending on the time and number of people available. All searches for banded birds have been undertaken during incubation, when most adults remain close to their nests when a human approaches, and their bands can be seen. Once seen, most banded birds can be readily caught using small hand nets in order to record their band numbers. Adults vary in their approachability, however, and a few birds fly off when still out of catching distance. Nests of these birds were marked and revisited, with a careful approach usually permitting the incubating adult to be caught. While Sooty Terns on Bird Island tend to return to the general area of earlier nesting attempts (C.J.F., unpubl. data), annual changes in vegetation cover lead to inter-annual changes in bird distribution (Feare *et al*. 1997), so that birds do not return to the same nest site year after year.

Since 2006 eggs have been harvested daily from 50–60% of the colony area. The harvested area is clearly marked, and eggs are collected in the early morning. Sooty Terns lay mainly between

13h00 and 16h00 (Feare 1976a), and searches for banded birds in this area were undertaken daily after 15h30, by which time most birds that intended to lay on a particular day would have done so. However, most birds in the harvested area do not have eggs, and even those that do are much more wary than those in the protected part of the colony, rendering them much more difficult to catch for identification. These variations in the effort to search for, and ability to catch, the birds impose constraints on the analyses to which the recapture data can be subjected.

Statistics and models

We relied upon a capture-mark-recapture model (Cormack 1964, Jolly 1965, Seber 1965) as expanded upon by Clobert *et al*. (1994), Spendelow *et al*. (2002) and Williams *et al*. (2002) to estimate adult and pre-breeder survival as well as the probability of recapture and age-specific probabilities of first-time attempted breeding. Following Williams *et al*. (2002) we defined the following threshold ages:

k — the first age at which an animal can breed

m — the age by which all animals breed

and the following model parameters:

p_i^{k+} — the probability that a marked breeder (denoted as age k+) in the study population at sampling period i is recaptured during period i;

φ_i^{k+} — the probability that a marked animal of age > k survives until period $i + 1$ and remains in the population;

φ_i^0 — the probability that a young animal (age 0) released at sampling period i survives until sampling period $i + k$;

$\alpha_i^{(v)}$ — the probability of breeding for an animal of age v at sampling period i that has not previously bred.

Following Spendelow *et al*. (2002) we made the following assumptions with this modelling parameterization:

1) the age k of first possible breeding is known; we allowed the possibility that birds could breed at age 1, although the youngest banded bird found incubating was a single individual 3 years old.
2) all animals become breeders by age m; we assumed that any individual that had not attempted to breed by age 10 would do so. Harrington (1974) concluded that all Sooty Terns commenced breeding by 10 years old. The number of banded birds from the 1993 and 1997 Bird Island cohorts peaked at 10 and 8 years, respectively; thereafter, banded birds seen in the colony for the first time were likely to have bred earlier but had not been detected because of the low recapture probability.
3) every young animal released at age 0 in sampling period i has the same annual probability φ_i^0 of survival until attempting to breed; most chick mortality occurred in the first 10 days of life, and birds banded at 30–55 days old suffer little mortality before fledging (see above and Feare 1976a). We assume all pre-breeders survive at the same rate.
4) every adult animal aged >k in sampling period i, has the same probability φ_i^{k+} of survival until sampling period $i + 1$; in our earlier (Feare & Doherty 2004) best fit model, survival was constant over time. We assume all adult individuals have the same probability of survival.
5) every marked breeding animal present in the population at sampling period i has the same probability p_i^{k+} of being recaptured; the main determinant of recapture probability was search effort (see below); and banded birds that nested in the main nesting habitat (open sandy substrate with low herb vegetation [Feare *et al*. 1997]) were considered equally detectable and catchable.
6) marked pre-breeding animals of age > 0 are not exposed to sampling efforts and have a probability of 0 of being captured in any sampling period; in 19 years of observation, no pre-breeding banded birds have been found in the Bird Island colony.
7) every marked pre-breeding animal of age v, where $k<v<m$, in sampling period i has the same probability $\alpha_i^{(v)}$ of initiating breeding and becoming a breeder in i; we assume all individuals of the same age that have not bred have the same probability of commencing breeding.
8) every marked animal that attempts to breed for the first time in period i, breeds with probability 1, or with asymptotic adult breeding probability if skipped breeding occurs, at all sampling periods after i; Sooty Terns are not known to skip breeding once they recruit to the breeding population (see Feare & Doherty 2004).
9) marks are not lost; all of the chicks were banded with British Trust for Ornithology incoloy bands; bands on birds marked in the early 1970s still show no signs of wear, suggesting that none have been lost.
10) sampling periods are instantaneous, and recaptured animals are released immediately; our field seasons were short (< 20 days), and birds were recaptured and held for less than 2 min.
11) except for the temporary absences of pre-breeders, all emigration from the sampled area is permanent; band recoveries demonstrate philopatry among birds reared on Bird Island (28% of chicks banded in 1993 have been resighted on Bird Island; C.J.F., unpubl. data); the true extent of this is not currently quantifiable but see Discussion. Only one chick reared on Bird Island has been reported from another Seychelles colony, but other colonies are not subject to the intensive search effort on Bird Island. On the other hand, recoveries of banded adults show that human disturbance (egg harvesting), can stimulate emigration (Feare & Lesperance 2002), but its effect on philopatry is unknown. The initiation of commercial egg harvesting on Bird Island in 2006 would not, however, have influenced the return of first-time breeders by 2008, the last year of data analysed in this paper.
12) the fate of each animal with respect to capture and survival probability is independent of the fate of other animals.

Model set

Based on results of previous analyses (Feare & Doherty 2004), and our limited data set, in all models adult survival was constant (φ^{k+}) and the detection probability of breeders varied annually (p_i^{k+}). The annual variation in detection probability would help account for differences in annual search effort. Since young birds are unobservable from the time they fledge until they return to the island to breed, we estimated only a single, constant pre-breeding annual survival parameter (φ^0) in all models. We focused primarily on estimating the probability of first-time attempted breeding ($\alpha^{(v)}$). We modelled this parameter in three ways; 1) as a constant for all ages in the case that the probability of first-time attempted breeding was not dependent on age, 2) as a linear function of age in the case that the probability of first-time attempted breeding was related to age, and 3) as a quadratic function of age in the case that the probability of first-time attempted breeding initially increased with age to some peak, and then dropped off as pre-breeders got older. We set m = 1 (the youngest age at which birds could breed) and k = 10 (the age at which all birds would have attempted to breed). We used Program MARK (White & Burnham 1999) to model all parameters with a logit-link function and to perform a goodness-of-fit test.

We conducted a median $\hat{c}$ goodness-of-fit test (Cooch and White 2011) to test for overdispersion. We used Akaike's Information Criteria corrected for small sample size (AIC_c) to compare and rank models (Burnham & Anderson 2002), and we present model-averaged estimates.

RESULTS

In Program MARK our goodness-of-fit test indicated no overdispersion ($\hat{c}$ = 0.97). Our model selection ranked two of our models highly. All models had the same structure on pre-breeding survival, adult survival and detection probabilities. However, our best model (AIC_c model weight = 0.54) modelled the probability of first-time attempted breeding as a quadratic function of age. The competing model (AIC_c weight = 0.46) modelled the age-specific breeding probability as a linear function of age. Because of the uncertainty in the best model, we chose to model average the parameter estimates across our model set (Burnham & Anderson 2002), and we present these below.

We estimated annual pre-breeder survival at 0.767 (SE = 0.208), and annual adult survival as 0.913 (SE = 0.003). Detection probability was overall low (0.06–0.25) but varied over time (Fig. 1). The age at which pre-breeders chose to first attempt breeding varied, with fewer than 3.5% of the birds attempting to breed before age 4. After age 4, any individuals that had not yet attempted to breed did so at increasing rates, although there is sampling and model selection uncertainty around these rates (Fig. 2). Very few birds had not attempted to breed by age 7 (Fig. 2).

DISCUSSION

From recaptures of birds banded as chicks on Johnston Atoll, northwest Hawaiian Islands, Harrington (1974) concluded that the youngest age at which Sooty Terns first breed was 4 years old, that most first bred at 6–8 years, and that all had probably started breeding by 10 years old. On the Dry Tortugas, Florida, the youngest birds found breeding were 4 years old (W. & M. Robertson, in Schreiber *et al*. 2002). On Ascension Island, where Sooty Terns breed approximately every 9.5 months (Ashmole 1963, J. Hughes, pers. comm.), ringed chicks have been recorded first breeding after seven breeding seasons, equating to around 5.5 years old (J. Hughes, pers. comm.). On Bird Island, Seychelles, a single 3-year-old Sooty Tern has been found breeding, but most have been first recorded at 6–9 years. However, some birds have been first recorded later than this, and 8 birds from the 1993 cohort of banded chicks were not recorded breeding until 17 years. These apparently late-returning birds had presumably bred previously but not been recorded during searches for marked birds, because of the difficulty in detecting banded birds in large breeding colonies (Fig. 1). This study represents the first attempt at modelling the return of young Sooty Terns in Seychelles, taking into account resighting probability, and indicates that most Seychelles birds first attempt to breed when 5–6 years old (Fig. 2).

Our estimate of annual adult survival for the 1995–2008 dataset did not differ from the earlier estimate using data from 1995–2002 (Feare & Doherty 2004). Our estimate of pre-breeding annual survival (0.767) is the first obtained for Sooty Terns. Like the estimates of adult survival, this is a minimum figure, as some of Bird Island's young are likely to recruit to other colonies, but the extent of this emigration is unknown. The estimate, which indicates that a pre-breeder would only have a 26.5% chance of surviving until age 5, is lower than the assumption (30–50%) used in an sustainable harvest model by one of us (Feare 1976a,b), calling for a re-examination of the recommendations. However, our estimate is an average, based on three cohorts of banded juveniles, and the large standard error around this estimate doubtless reflects variable survival among these cohorts and the generally low resighting probability and its wide variations.

By 2010, 28.0% of chicks banded in 1993 had been recorded breeding in the Bird Island colony, and 7.2% of the chicks banded in 1997 and 14.0% of chicks banded in 2002 had been recorded (birds from this last cohort are still being recorded for the first time). The high return of 1993 chicks (28% exceeds the 26.5% estimated

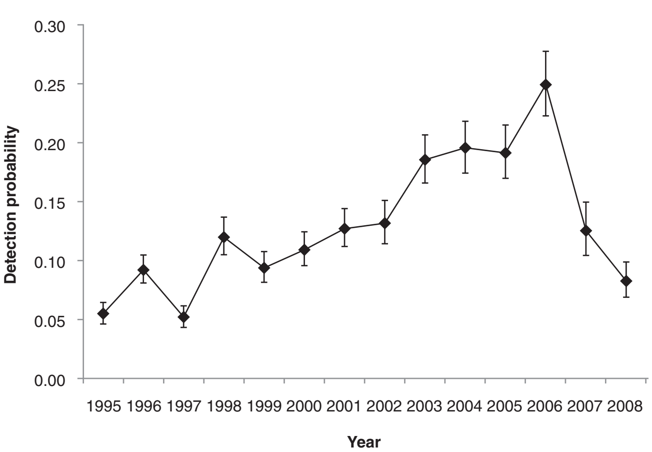

Fig. 1. Detection probability of Sooty Terns on Bird Island, Seychelles, 1994–2008. Error bars are 95% confidence intervals.

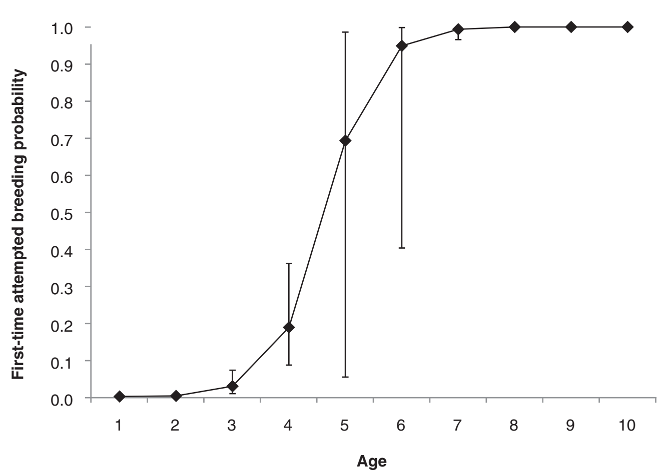

Fig. 2. Age-specific first-time attempted breeding probabilities of Sooty Terns on Bird Island, Seychelles. Error bars are 95% confidence intervals.

survival of chicks from fledging to return at 5 years old) suggests that most chicks reared on Bird Island return there to breed. The low return of 1997 chicks suggests either lower survival of birds from this cohort or high emigration. Lack of observation in other Seychelles colonies prohibits examination of the latter possibility, but 1997 was a poor year for seabirds in Seychelles (Ramos 2001), suggesting widespread food shortage that could have reduced pre-breeder survival of Sooty Terns after leaving the colony. To better model cohort variation in recruitment, more consistent search effort, with higher detection probabilities, will be needed.

Large annual variations in recapture probability (Fig. 1) were due mainly to variation in search effort. Both the time and number of people available for searching varied widely; for the years when search effort was recorded, the number of banded birds found was related to search effort in (Fig. 3). From 2006 onwards, however, the commercial harvesting of eggs from 50–60% of the colony likely introduced further constraints on recapture. In the harvested area, eggs are collected daily shortly after dawn; as a result, the only birds that have eggs during band searches are those that have laid eggs later during that day. All birds in this area, with or without eggs, are very wary and difficult to catch for identification. In addition, because human disturbance is a major cause of inter-colony movement of established breeders (Feare & Lesperance 2002), harvesting could stimulate some breeding birds to leave for other colonies. To further decompose our detection probabilities into the probabilities that individuals are present to be observed (availability) and the probability that available birds are observed additional data will be needed from radio telemetry or a robust design data collection scheme (Kendall *et al*. 1997), for example. Such additional data could help reduce biases and increase precision in our estimates. Further variation in recapture probability can be caused by unusually heavy rainfall in April–June, promoting vegetation growth that can obscure the birds' legs, as happened in 1997.

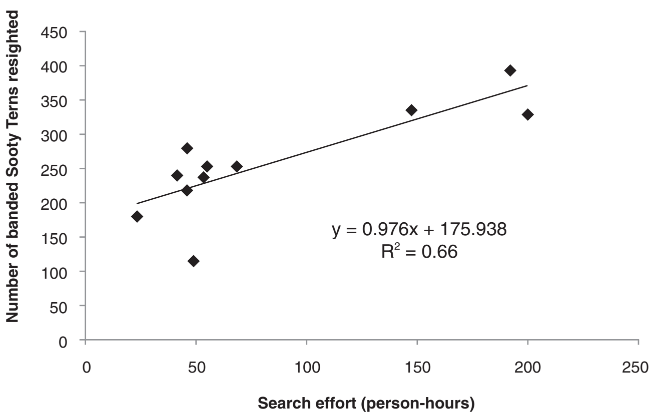

Fig. 3. Number of banded birds recaptured annually on Bird Island in relation to search effort (person-hours), 1995–2006 (no data for 2005, 2007 or 2008, as the search effort was not recorded in those years).

There are very few estimates of pre-breeding survival in seabirds (Hamer *et al*. 2002) and only five for terns (Sterninae; Table 1). These published estimates have been obtained using different methodologies, limiting their comparability. While our estimate of annual pre-breeding survival for Sooty Terns is higher than that for temperate breeding Roseate Terns *Sterna dougallii*, our estimate equates to survival to a first breeding age of 5 years of 0.265, which is broadly comparable with the lower estimate of survival to recruitment for Brown Noddy *Anous stolidus*, but lower than that obtained for Bridled Tern *Onychoprion anathaetus*. The data from Western Australia were, however, from tropical species during range expansion to the south (Dunlop 2009) and from continental shelf islands rather than their more typical oceanic islands, as in Seychelles. Colony demographic characteristics are likely to be influenced by geographic location and proximity to sources of food and predators, and may vary between establishing and stable colonies. Morris & Chardine (1995) reported Brown Noddies first breeding at 3–6 years in an established Caribbean colony. Further variation in estimated pre-breeding survival may be introduced by the age at which chicks were banded in different studies: chicks banded close to fledging provide a better estimate of survival to recruitment than chicks banded soon after hatching, since the latter estimates will include some pre-fledging mortality, which may differ between terrestrial and free-flying individuals (Feare 2002). Finally, the values

TABLE 1
Estimates of age at first breeding and survival between fledging and recruitment to the breeding population in terns

Species	Location	Age at first breeding	Survival	Measure of survival	Recapture probability estimated	Study
Temperate						
Least Tern *Sterna antillarum*	California, US	3	0.16	FF[a]	No	Massey *et al*. 1992
Common Tern *Sterna hirundo*	Germany	3	0.35	FF	No	Becker *et al*. 2001
Roseate Tern	Connecticut, US	<5	0.53–0.68	A[b]	Yes	Spendelow *et al*. 2002
Tropical						
Brown Noddy	Western Australia	3	0.26–0.33	FF	No	Dunlop 2005
Bridled Tern	Western Australia	4	0.368	FF	No	Dunlop & Jenkins 1992, 1994
Sooty Tern	Seychelles	5–6	0.767	A	Yes	This study

[a] FF = fledging to first breeding.
[b] A = annual.

in Table 1 are apparent survival, as they do not take into account natal emigration, the extent of which is often unknown.

Little is known about the life of juvenile Sooty Terns after fledging. Flying young can receive food from a parent in flight (Feare 1975), and adults accompany young at sea after leaving the colony, but the accompaniment period is unknown. Robertson (1969) reported that the geographical ranges of adults and young in the Atlantic separated after 2–3 months. Thereafter, young birds are believed to spend all of their time at sea, in a predominantly aerial existence (Schreiber *et al*. 2002), until they begin breeding. Juvenile survival during this phase of life appears unrelated to fledging date or body mass, factors which are important before fledging (Feare 2002). The aim of this long-term demographic study of Sooty Terns has been to provide data to establish an egg-harvest level that can be guaranteed to be sustainable, but these data can also be of value in interpreting the birds' responses to changes in their oceanic environment. However, this study has provided only average values of annual adult survival (Feare & Doherty 2004) and pre-breeding survival (this paper), rather than year-, age- or cohort-specific estimates. To ensure sustainability of the egg harvest, a more detailed adaptive management policy is needed. Such a policy requires better and more comprehensive data than are currently available.

Acquisition of such data would necessitate annual banding of adults (in June) and chicks (in August–September), intensive annual searches for banded birds (throughout June into early July), assessment of breeding success (in early July and late August) and annual censuses of all Seychelles colonies (in June). Additionally, vegetation in each colony needs to be managed before laying to maximise the space available for nesting birds (Feare *et al*. 1997). To collect the information described above, teams need to visit the main colonies for approximately four months each year. Transport to and from the remote islands and basic living arrangements on these islands must be provided. Feare & Gill (1997) proposed a levy on the income from egg harvests to support monitoring and thereby make the egg industry self-sustaining. A 15% levy on the egg harvesters is now collected, but this is insufficient to meet the cost of adequate monitoring. This throws into question the capacity of the Government of the Republic of Seychelles Division of Environment to undertake sufficient monitoring, and therefore to manage egg harvesting to reflect any changes in population size, productivity or survival of the Sooty Terns. A further obstacle to sustainable harvest is the difficulty in policing colonies to prevent illegal harvest of eggs, chicks and adults.

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