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# Survival estimates of adult Sooty Terns *Sterna fuscata* from Bird Island, Seychelles

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Sooty Tern *Sterna fuscata* populations on the Seychelles Islands have been exploited for human consumption of their eggs for at least the last 75 years. This has led to concern about possible declines in these populations. To address these concerns, the Seychelles Government has instituted a research and management plan to ensure the sustainability of the egg harvest. The harvest model, upon which current harvest regulations are based, was constructed with an assumed adult survival rate because there are no published Sooty Tern survival rate estimates. We fill this knowledge gap and address this assumption. We estimated adult Sooty Tern survival to be 0.91 ($\widehat{SE}$ = 0.01), which was close to the estimate used in the model. This estimate is also comparable with other seabird survival estimates. In the future this estimate could be improved with higher recapture rates. In addition, further advances in models for estimating probabilities of age at first breeding, prebreeder survival and population growth should be used to best effect, by making appropriate improvements to the ring search protocol, to provide further feedback to the management programme.

The Sooty Tern *Sterna fuscata* is an important exploited species in the Seychelles Islands with *c.* 750 000 eggs currently being harvested annually for human consumption (Schreiber *et al*. 2002). Eggs have been harvested commercially since at least 1928 (Ridley & Percy 1958) and the possibility of overexploitation was raised by Vesey-Fitzgerald (1941). The desire to ensure the sustainability of this egg harvest has led to the need for a scientifically based management strategy. Feare (1976a) developed a management plan and proposed, on the basis of a 2-year study, that the annual harvest should not exceed 20% of eggs laid annually and that harvest should be limited to two islands. This recommendation was based on a harvest model (Feare 1976a) and a number of assumptions for which there were few or no data.

One of these assumptions was that although most Sooty Terns would be site faithful, there would be sufficient dispersal between islands that the Seychelles/Amirantes colonies could be considered a metapopulation, and exploited colonies could receive recruits from protected colonies. This assumption with respect to breeding dispersal has recently been validated through the study of ringed birds (Feare & Lesperance 2002), and subsequent unpublished observations are demonstrating an as yet unquantified level of natal dispersal.

A second assumption concerned adult survival rates. Earlier studies in Seychelles colonies had been short-term (Ridley & Percy 1958; Feare 1976b) and, although they provided valuable information on some aspects of the birds' biology, they were unable to provide estimates of annual survival. Feare (1976a) assumed that, like many seabirds, the Sooty Tern was a long-lived species with an annual adult survival rate of 0.92–0.93. Survival rates from other tern species have often been estimated to be within this range (Schreiber & Burger 2001). In order to obtain data that would confirm or refute the assumed values of annual adult survival and breeding frequency used by Feare (1976a), a further programme of study was begun in 1993. This involved the ringing of cohorts of Sooty Terns in the major colonies in the Seychelles and Amirantes, followed by searches for these ringed birds in subsequent breeding seasons (Feare & Lesperance 2002).

Population growth rate in long-lived animals is thought to be most sensitive to changes in adult

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survival (Cairns 1992, Pfister 1998) and the results of Feare's model are influenced most by this rate; thus deriving an empirical estimate of Sooty Tern adult survival for this population is imperative. Here, we present such an estimate and discuss this in relation to our management goals, as well as compare this survival rate with that of other seabird species.

## METHODS

### Ringing and re-sighting of ringed birds

In 1993–95, Sooty Terns were ringed at the major colonies in the Seychelles and Amirantes Islands. In practice, data from only one of these colonies, on Bird Island, have been adequate to provide estimates of adult survival because this is the only colony that is sufficiently accessible to permit observers to search for ringed birds each year and to find an adequate sample of marked birds. In 1993 and 1994, 550 and 2250 breeding adult Sooty Terns, respectively, were caught in hand-nets on Bird Island and ringed using numbered metal British Trust for Ornithology rings. Starting in 1995, searches have been made annually for ringed birds in this colony, which currently holds *c.* 700 000 pairs (C. J. Feare unpubl. data). Searches have involved teams of two to four people, each with a hand-net to catch any ringed birds that were detected. These people walked along transects, marked every 50 m by posts erected within the colony. Searches were undertaken in June, during the incubation period, when Sooty Terns are reluctant to leave their nests. At this time of year the southeast trade winds blow, and searchers generally walked slowly down wind, encouraging incubating birds to stand, so rendering rings visible. The response of birds was, of course, variable, and although some behaved in the desired way, others failed to stand or flew off, but this technique appeared to maximize the chances of finding ringed birds. In each year, *c.* 30 person-hours were devoted to searches. Most ringed birds that were caught were incubating eggs. Those that were not incubating were nevertheless at nest-sites and were probably about to lay. When birds were caught, the ring number was recorded. On Bird Island, the only areas where Sooty Terns in adult plumage assembled but did not lay eggs were on beaches around the periphery of the nesting colony. These birds were too wary to be caught. We therefore conclude that the ringed birds that we caught were breeding adults.

### Statistical methods

We followed the analysis strategies of Lebreton *et al.* (1992) and Burnham and Anderson (2002) in employing Cormack–Jolly–Seber (Cormack 1964, Jolly 1965, Seber 1965) open-population capture–recapture models as available in Program Mark (White & Burnham 1999). We fitted models consisting of probability of survival parameters ($\phi$) and recapture probability parameters ($p$). We modelled these parameters as being constant over time (.) or varying with year ($t$). Therefore, our most general model was one in which survival and recapture probabilities were a function of time ($\phi_t p_t$). We used this model in a bootstrap goodness-of-fit test. The goodness-of-fit test can indicate overdispersion in the data and, if warranted, $\hat{c}$, the variance inflation factor, can be estimated and used to adjust subsequent estimates of variance and model selection criteria (Burnham & Anderson 2002). The $\hat{c}$ value was calculated by dividing the deviance of the general model by the average deviance from the results of bootstrap simulations.

### Model set and model selection

In addition to our most general model ($\phi_t p_t$), we also constructed models in which survival was constant over time while recapture probability varied through time ($\phi_. p_t$), survival varied over time while the recapture rate remained constant ($\phi_t p_.$) and a model in which both rates were constant through time ($\phi_. p_.$).

We used Akaike's Information Criterion (*AIC*) for model selection (Burnham & Anderson 2002). *AIC* balances the overall fit of a particular model with the number of parameters needed to achieve the fit. Models with lower *AIC* values are assumed to explain better the variation in the data. In practice, we used the small-sample, $\hat{c}$-corrected, version of *AIC* denoted as $QAIC_c$. Models with $QAIC_c$ values differing ($\Delta QAIC_c$) by less than 2 were considered equivalent. We also examined model weights in evaluating the models. Unless otherwise noted, we present our data as point estimates with standard errors.

## RESULTS

### Sample size

Table 1 summarizes the capture histories on Bird Island of the 2974 birds that we used for our analysis. Recapture of birds did not begin until 1995. The low

**Table 1.** Capture history summary for Sooty Terns captured, ringed and released on Bird Island, Seychelles, from 1993 to 1994. Recapturing of birds did not start until 1995.

| | | Year of first recapture | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Number released | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | Total |
| 1993 | 526 | 0 | 21 | 28 | 13 | 24 | 24 | 23 | 16 | 24 | 173 |
| 1994 | 2250 | | 116 | 177 | 75 | 162 | 95 | 90 | 90 | 64 | 869 |
| 1995 | 152 | | | 7 | 10 | 10 | 6 | 7 | 10 | 7 | 57 |
| 1996 | 242 | | | | 15 | 31 | 13 | 21 | 15 | 11 | 106 |
| 1997 | 117 | | | | | 18 | 9 | 12 | 8 | 4 | 51 |
| 1998 | 266 | | | | | | 23 | 25 | 23 | 16 | 87 |
| 1999 | 247 | | | | | | | 15 | 14 | 33 | 62 |
| 2000 | 211 | | | | | | | | 24 | 21 | 45 |
| 2001 | 223 | | | | | | | | | 23 | 23 |

**Table 2.** Models of survival ($\phi$) and recapture probability ($p$) either being constant (.) or time ($t$) dependent for Sooty Terns on Bird Island, Seychelles. The $QAIC_c$ is the small-sample size, $\hat{c}$-corrected, version of Akaike's Information Criteria. $\Delta QAIC_c$ is the difference between a particular model and the model with the overall lowest $QAIC_c$. The $QAIC_c$ weights are the weight associated with each model. The model that best explains the data is in **bold**.

| Model | $QAIC_c$ | $\Delta QAIC_c$ | $QAIC_c$ weights | Model likelihood | No. of parameters | Deviance |
|---|---|---|---|---|---|---|
| **$\phi_. p_t$** | **8511.30** | **0.00** | **0.94** | **1.00** | **9.00** | **270.54** |
| $\phi_t p_t$ | 8516.83 | 5.54 | 0.06 | 0.06 | 16.00 | 261.99 |
| $\phi_t p_.$ | 8570.61 | 59.31 | 0.00 | 0.00 | 10.00 | 327.84 |
| $\phi_. p_.$ | 8596.85 | 85.55 | 0.00 | 0.00 | 2.00 | 370.13 |

**Table 3.** Recapture probabilities of Sooty Terns on Bird Island, Seychelles, from 1995 to 2002. No birds were recaptured in 1994. The $\bar{\bar{x}}$ is a weighted average.

| | | | 95% CI | |
|---|---|---|---|---|
| Year | $\bar{x}$ | $\hat{SE}$ | Lower | Upper |
| 1995 | 0.05 | 0.00 | 0.05 | 0.07 |
| 1996 | 0.09 | 0.01 | 0.08 | 0.11 |
| 1997 | 0.05 | 0.01 | 0.04 | 0.06 |
| 1998 | 0.13 | 0.01 | 0.11 | 0.15 |
| 1999 | 0.09 | 0.01 | 0.08 | 0.11 |
| 2000 | 0.11 | 0.01 | 0.09 | 0.13 |
| 2001 | 0.13 | 0.01 | 0.10 | 0.15 |
| 2002 | 0.14 | 0.01 | 0.11 | 0.17 |
| $\bar{\bar{x}}$ | 0.08 | 0.01 | 0.07 | 0.08 |

number found in 1997 was due to abnormal conditions that are discussed further below.

## Model results and estimates

We detected overdispersion in our data with our bootstrap goodness-of-fit test ($P < 0.01$). The $\hat{c}$ value was 1.27, which indicated that this overdispersion was not large, and this value was used in further model selection and estimates of variance. A model in which survival was considered constant through time while recapture rates varied over time was by far the best at describing our data set; the next best model had a $\Delta QAIC_c$ of 5.54 (Table 2). Our best-supported model had a $\Delta QAIC_c$ weight of 94% (Table 2). The survival estimate from this model was 0.91 ($\hat{SE} = 0.01$; 95% CI = 0.89, 0.93). The weighted average recapture rate was 0.08 ($\hat{SE} = 0.01$; 95% CI = 0.07, 0.08) and the annual recapture rates are presented in Table 3.

# DISCUSSION

## Survival rate

We believe that our adult survival estimate of 0.91 is the first for Sooty Terns. Our analysis also suggests that adult survival is relatively constant in this population. This estimate is of apparent or local survival, because it is known that some emigration from Bird Island to other colonies occurs (Feare & Lesperance 2002). Our estimate suggests that the rates (0.92–0.93) used by Feare (1976a) in his harvest model were realistic and do not call for drastic changes to the harvest model.

## Comparisons with other seabirds

Schreiber and Burger (2001) reviewed available data and reported annual survival rates for adult seabirds of between 0.62 and 0.97. Within this range, penguins (Sphenisciformes) tend to have lower annual survival, and petrels and albatrosses (Procellariiformes) higher survival; pelicans, boobies and cormorants (Pelecaniformes) and gulls, terns and skuas (Charadriiformes) are intermediate (Hamer *et al.* 2001).

Our estimate for the Sooty Tern falls at the upper limit of estimates of annual adult survival for other terns (Caspian Tern *Sterna caspia* 0.87–0.91, Cuthbert & Wires 1999; Sandwich Tern *Sterna sandvicensis* 0.65–0.83, Møller 1983; Roseate Tern *Sterna dougallii* 0.74–0.91, Spendelow *et al.* 1995; Common Tern *Sterna hirundo* 0.88–0.92, Nisbet & Cam 2002, Nisbet 2002; Arctic Tern *Sterna paradisea* 0.90, Schreiber & Burger 2001; Least Tern *Sterna antillarum* 0.80–0.93, Massey *et al.* 1992, Renken & Smith 1995; Bridled Tern *Sterna anaethetus* 0.78–0.83, Dunlop & Jenkins 1994; Black Noddy *Anous minutus* 0.75, Tarburton 1987). However, only the estimates by Nisbet and Cam (2002) for Common Terns, Renken and Smith (1995) for Least Terns and Spendelow *et al.* (1995) for Roseate Terns are based on Cormack–Jolly–Seber models and are thus comparable with our estimate for Sooty Terns. In their analysis of annual survival rates of seabirds, Hamer *et al.* (2001) reported that pelagic feeders, among all seabirds, had higher survival rates than inshore feeders. Although Sooty Terns are the most pelagic of all terns (Ashmole & Ashmole 1967, Schreiber *et al.* 2002), their high annual survival could also be associated with other life-history traits, such as their confinement to tropical waters, breeding on remote, largely predator-free islands, and their largely aerial existence (Schreiber *et al.* 2002).

## Probability of detection

Our recapture rates were quite low (Table 3). These low rates can also be seen in the capture summary in Table 1, which shows that many birds were not first recaptured until many years after release. The lowest annual recapture rate (1997, Table 3) was probably due to the late arrival of the birds to breed in that year, and to tall vegetation (following heavy rainfall), which rendered the birds' legs difficult to see. Detection rates will need to be increased before the more precise modelling, necessary to detect differences in survival between years, can be undertaken. From 1998 onwards, the probability of detection has increased to *c.* 0.11 but further increase will raise practical difficulties. Although the time available for searches for ringed birds (the incubation period, 28 days for each pair: Feare 1976b) is relatively long, the Sooty Tern project to date has not had the personnel available to commit to intensive searches throughout the Bird Island colony for this period, and in most years searches have had to be undertaken in 4–5 days.

## Management implications/further studies

The object of the Seychelles Sooty Tern study is to provide biological data that can be applied to harvest management to ensure the sustainability of exploitation of Sooty Tern eggs. On average, *c.* 0.75 million eggs are collected for human consumption each year and advice to the Seychelles Government includes estimates of the number of eggs that can safely be harvested, the colonies that should be exploited, and the harvest method that should be applied.

Feare (1976a) proposed that the annual harvest should not exceed 20% of eggs laid annually. This was based on a number of assumptions, including high breeding site fidelity but with some intercolony movements (addressed in Feare & Lesperance 2002) and high constant adult survival (addressed in this paper). The models that best fitted the ring re-sighting data collected from 1995 to 2002 suggest that Feare's (1976a) assumed annual survival was somewhat optimistic. However, our slightly lower estimate of 0.91 does not call for significant changes to the harvest proposals currently in operation, and indeed Feare's assumed survival falls within the 95% confidence limits around our estimate. Other assumptions that might be tested with further data collection concern estimates of prebreeding survival, age of first breeding and natal dispersal (Clobert *et al.* 1994, Spendelow *et al.* 2002, Williams *et al.* 2002, Lebreton *et al.* 2003). Few Sooty Terns are thought to attempt breeding before 4 years of age and they probably do not attempt to breed until 6–10 years of age (Harrington 1974, Schreiber *et al.* 2002, C. J. Feare unpubl. data). To estimate the age-specific probabilities of first breeding and prebreeding survival will require more years of data, especially with our low recapture rates. Models are available to estimate these quantities accurately, especially for seabirds (Clobert *et al.* 1994, Spendelow *et al.* 2002, Williams *et al.* 2002, Lebreton *et al.* 2003). To improve these estimates, more chicks should be ringed, and recapture rates should be increased. Increased ringing and recapture rates may also help alleviate the slight overdispersion we detected in our data. This overdispersion may have resulted from some territories being more exposed to observation than others, or from mated pairs being seen together often. Although the overdispersion that we detected is not uncommon in such studies, increased ringing and recapture (especially if spaced equitably throughout the colony) would probably help in this matter.

We also assume that Sooty Terns attempt to breed every year. Some seabirds, especially larger ones such as King Penguin *Aptenodytes patagonicus* (Weimerskirch *et al.* 1992), Wandering Albatross *Diomedea exulans* (Weimerskirch *et al.* 1986) and some frigatebirds *Fregata* spp. (Diamond 1975), have such long breeding cycles that they are unable to nest annually. Smaller seabirds generally lay annually, some even subannually (Hamer *et al.* 2001), including Sooty Terns on Ascension Island (Ashmole 1963, Ratcliffe *et al.* 1999). However, although some petrels have nesting cycles lasting less than a year they still breed biennially (Chastel 1995). Dry Tortugas Sooty Terns were recorded missing in some years, especially after successful breeding (W.B. and M.J. Robertson, in Schreiber *et al.* 2002), but on Bird Island breeding adults appear most likely to breed annually. The probability of skipping a breeding year could be estimated using a multistate approach (Kendall & Nichols 2002, Lebreton & Pradel 2002). To test the assumption of annual breeding, we used this multistate approach and constructed a model in which there were two states, an observable breeding state and an unobservable non-breeding state. We then estimated the probability that a bird in the breeding state would change to a non-breeding state in the following year. This probability was estimated to be zero, further supporting our assumption that adults attempt to breed annually. Another approach would be to treat the problem as 'temporary emigration'. In general, the skipping of breeding in some years is known as 'temporary emigration' in that some birds are not available for capture in all years. To estimate the probability of temporary emigration in Seychelles colonies (i.e. probability of skipping a breeding year) data will need to be collected using a robust design (Kendall *et al.* 1997). The robust design allows for more efficient estimation as well as the ability to estimate more parameters than might be estimated through a multistate approach. Using the robust design approach will require either the current recapture effort to be split into at least two separate capture occasions or more capture occasions will have to be added. Again, the ringing of more cohorts and increased recapture rates would improve the estimation. We also suggest that the Seychelles situation may be ripe for an active adaptive management plan (Walters & Holling 1990, Kendall 2001) by building upon the current harvest model, incorporating a number of possible management actions (i.e. differing rates of egg harvest), and utilizing an optimal dynamic programming approach. The mark–recapture data being collected could also be used to estimate population growth (Nichols & Hines 2002) as an additional 'currency' in this modelling effort.

Finally, we recognize that Sooty Terns have been the subject of research in a number of locations around the world (i.e. Dry Tortugas, Puerto Rico, Ascension Island, Johnston Atoll, Christmas Island [Pacific Ocean]) and it would be valuable to have estimates of demographic parameters from these studies for comparison.

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