

Population viability analysis predicts long-term impacts of commercial Sooty Tern egg harvesting to a large breeding colony on a small oceanic island

THALISSA INCH,¹  MALCOLM A.C. NICOLL,²  CHRIS J. FEARE^{3,4} & CATHARINE HORSWILL^{*2,5} 

¹Division of Biosciences, University College London, Gower Street, London, WC1E 6BT, UK

²Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK

³WildWings Bird Management, Grayswood Common, Haslemere, Surrey, GU27 2DN, UK

⁴School of Biological, Earth and Environmental Sciences, Faculty of Science, University of New South Wales, Sydney, NSW 2052, Australia

⁵Department of Genetics, Evolution and Environment, University College London, Gower Street, London, WC1E 6BT, UK

The over-exploitation of wild birds and the products derived from them can be a key threat driving changes in bird species richness and abundance. However, inadequate information on harvest levels combined with irregular population monitoring often means that the role of harvesting in population decline is difficult to quantify. Historically, the pan-tropical Sooty Tern *Onychoprion fuscatus* has been subjected to extensive egg harvesting, yet the role of sustained harvesting in population change and future population viability remains unclear. In this study, we used published and new estimates of key demographic rates for a large, harvested Sooty Tern population in Seychelles, western Indian Ocean, to run a series of population viability analyses. We retrospectively assess the impact of historical levels of egg harvesting, and also predict how this population may respond under different future harvesting regimes, assuming no additional environmental change. We provide evidence that egg harvesting has played a substantial role in driving the population decline of Sooty Terns to date and demonstrate that continued harvesting will probably lead to further, possibly dramatic, declines in population size. These results indicate that recent levels of egg harvesting in Seychelles are not sustainable. We also show that the life-history strategy of Sooty Terns, including a delayed age of first breeding, means the current 2-year local moratorium on egg harvesting is unlikely to generate an observable population-level response in Seychelles. Instead, we recommend that the current moratorium is extended at least beyond the age of first breeding (i.e. 5 years) to support appropriate evaluation. We additionally show that harvesting Sooty Tern eggs at much lower levels, i.e. 10% of the population size, is unlikely to reverse population decline. Therefore, long-term egg harvesting strategies require careful evaluation to maintain a balance between the social, commercial, cultural and biodiversity significance of Sooty Terns in Seychelles.

Keywords: conservation, harvesting, population viability analysis, Seychelles, tropical seabird.

The exploitation of threatened and near-threatened species is recognized as one of the greatest threats this century to global (Maxwell *et al.* 2016) and avian biodiversity (Lees

et al. 2022). Wild birds and their products – including meat, eggs and guano – are of high economic value as food and fertilizer. However, effective management is often hampered by inadequate information on harvest levels (Lees *et al.* 2022). This is especially true for species that have faced historical harvesting where our frame of reference is also subject to shifting baselines (Papworth

*Corresponding author.
Email: catrsw@gmail.com
Twitter: [CatHorswill](https://twitter.com/CatHorswill)

et al. 2009). These factors obscure the impact of previous harvesting regimes and present major hurdles for regulators and conservation managers (Newsome et al. 2007, Scheele et al. 2017).

One commonly used approach for inferring how populations may respond to anthropogenic pressures, such as harvesting, is to use a population viability analysis (PVA). This approach is based on a simplified model of population dynamics that allows the response to altered demographic processes to be examined (Reed et al. 2002). However, rarely are populations monitored in sufficient detail to resolve the full suite of demographic processes required to parameterize these models (Horswill et al. 2021). Therefore, whilst there is little doubt that harvesting can detrimentally impact bird populations, explicitly linking historical harvesting to population declines remains a challenge (but see Chen et al. 2015, Mondreti et al. 2018, Jakubas et al. 2022).

Seabirds are one of the most threatened groups of birds in the world, with almost half (47%) of all species demonstrating declining population trends (Dias et al. 2019). Commercial and cultural harvesting of seabirds and their eggs occurs in a range of locations, including the Falklands (penguins – Spheniscidae spp., Boersma et al. 2002), Arctic (puffins – *Fratercula* spp., Sua 2020), New Zealand (Sooty Shearwater *Puffinus griseus*, Newman et al. 2008), Madagascar (Crested Tern *Thalasseus bergii*, Le Corre & Bemanaja 2009) and Seychelles (terns – Sternidae spp., Feare & Doherty 2011). High commercial value has promoted large-scale legal and illegal harvesting of some species, especially their eggs (SOM Fig. S1; Feare & Doherty 2011). Understanding the impact of previous harvesting regimes and how populations may respond to continued harvesting pressure is therefore central to developing effective evidence-based conservation actions.

Human colonization of Seychelles began in the late 18th century and substantial harvesting of Sooty Tern *Onychoprion fuscatus* eggs became widespread by the end of the following century (Ridley & Percy 1958). Sooty Tern eggs provided a food resource for people during the south-east trade wind period (May–October) when rough seas prevented fishing and reduced the availability of staple food. Concern that legal and illegal Sooty Tern egg harvesting in Seychelles was impacting the local breeding populations was first raised over 80 years ago (Vesey-Fitzgerald 1941). Subsequently, in the 1950s recommendations were made to (1) limit

annual egg harvests to half of the Sooty Tern colonies in the Amirante and Inner Island groups, Seychelles (Fig. 1), with the largest colony (on Desnoeuvs Island, Fig. 1) and all other smaller colonies (Aride, Bird, African Banks, Recif, Ilot Frégate) being exploited in alternate years, and (2) set an annual egg harvesting period that ended on 7 July each year (Ridley & Percy 1958). In the 1960s, these actions were deemed to have stabilized the trajectories of Sooty Tern colonies in the Amirante and Inner Island groups, and subsequently the egg harvesting season was extended until 14 July each year (Ridley & Percy 1966). However, detailed studies on local Sooty Tern demography indicate that egg harvesting, in addition to habitat change, continues to threaten Sooty Tern colonies in Seychelles (Feare 1976b, Feare et al. 2007, Feare & Doherty 2011, Feare & Larose 2014).

A recent government-organized census indicated that the national Sooty Tern population in Seychelles has declined by approximately 60% since 2015 (Morgan & Cupidon 2021). Selection of 2015 as the baseline date is arbitrary and does not take into account more significant population changes that are known to have occurred previously. For example, early descriptions indicate that the Sooty Tern population on Bird Island (Inner Islands, Seychelles; Fig. 1) is likely to have approached 5 million breeding pairs in the late 19th century (Fryer 1910, Feare 2017). By comparison, the recent census estimate for Bird Island was 334 000 breeding pairs (Morgan & Cupidon

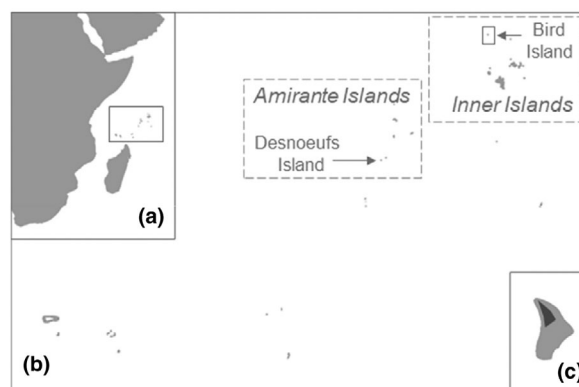


Figure 1. (a) Location of Seychelles (black rectangle) in the Western Indian Ocean. (b) Map of Seychelles showing the location of Bird Island (black rectangle). Amirante Islands including Desnoeuvs Island (the largest Seychelles Sooty Tern colony) and Inner Island groups are also detailed in dashed boxes. (c) Map of Bird Island with study colony shown as a dark grey polygon.

2021). Major habitat change in the early 20th century caused by island-wide guano mining and coconut planting considerably reduced the available nesting area of Sooty Terns on Bird Island (Feare 2017). More recently, clearance of coconut plantations and coastal vegetation in the late 1960s increased the terns' nesting area supporting population growth (Feare 2017). Nevertheless, the Seychelles Sooty Tern census still reported a 47% decline on Bird Island between 2015 and 2021 (Morgan & Cupidon 2021). In response to the reported national decline in Sooty Tern numbers across Seychelles, a national 2-year moratorium on egg harvesting was introduced: 2022–2023. Understanding the likely observable population response to such an intervention is central to being able to assess the efficacy of this approach as a conservation strategy.

In this study, we use a long-term mark recapture dataset (1972–2020) for Sooty Terns on Bird Island, Seychelles, to estimate age-specific rates of apparent survival. We then combine these with published estimates of age at first breeding and breeding success in a series of PVAs. We use the PVAs to (1) assess the impact of historical levels of egg harvesting on the observed population trajectory, and (2) predict how the current Sooty Tern population on Bird Island might respond to future egg harvesting regimes, assuming no additional environmental change occurs.

METHODS

Study system

Sooty Terns are pelagic seabirds that breed on islands throughout most of the tropical oceans (del Hoyo *et al.* 1996). The global population is estimated to be approximately 30 million breeding pairs (Jaeger *et al.* 2017), making them an important marine consumer (Danckwerts *et al.* 2014). In Seychelles, Sooty Terns breed between April and October and colonies are typically large (some contain over a million pairs, Rocamora *et al.* 2003). Breeding colonies occur mainly in sandy areas with low-lying vegetation (Feare *et al.* 1997), although some also occur on rocky islands (i.e. Aride Island).

This study uses population and demographic data collected from Sooty Terns breeding on Bird Island, Seychelles (3.72°S, 55.21°E, Fig. 1). Bird Island is a *c.* 100-ha sand cay that lies on the northern edge of the shallow (< 100 m) Seychelles

bank (Fig. 1b). Its Sooty Tern colony occupies a *c.* 14-ha treeless, herb-dominated sandy plain at the north-west of the island (Fig. 1c). This is the only colony in Seychelles that has been the subject of a long-term study involving extensive ringing and subsequent annual searches for marked birds and is hence the most suitable colony to assess the effects of egg harvesting. Census data estimate that Bird Island supported approximately 700 000 breeding pairs in 1996 (Feare *et al.* 2007), declining to 334 000 breeding pairs in 2021 (Morgan & Cupidon 2021). Mark–recapture monitoring of Sooty Terns on Bird Island began in 1972; however, the rings used varied during the subsequent decades. A subset of rings deployed in 1972 were aluminium and showed signs of severe abrasion and thinning in the 1990s, although unique identification numbers remained clearly legible. From 1973 onwards, most rings deployed were made from an incoloy metal that resisted abrasion. From 1994 to 1996, cohorts of chicks were ringed with Darvic rings (0.5 mm thick and 6 mm wide), and in 1994 and 1997 these were also accompanied by incoloy metal rings on the opposite leg (Feare 2011). The Darvic rings suffered high plastic degradation, breakage and loss, and therefore since 1997 all birds have been ringed using British Trust for Ornithology incoloy rings only.

Chicks and breeding adults selected for ringing were taken from the central areas of the colony to minimize edge effects (Feare 1976b). For chicks, plumage scores (Feare 1976b) were also collected to document age since hatching. Since 1993, chicks selected for ringing were between 30 and 60 days old (Feare & Doherty 2011). Ring re-sighting data were predominantly collected during the beginning of the breeding season by capturing incubating adults, i.e. May to June. The re-sighting interval was 1 year, from the beginning of the breeding season in year t (1 May) to the beginning of the breeding season in year $t + 1$ (30 April). To minimize biases introduced by skewed sampling of the different age classes (chicks and adults, SOM Table S1), we estimated apparent survival separately for fledglings and adults. Sex of individual birds was not determined and therefore not considered in our study.

Apparent adult survival

To estimate rates of apparent adult survival for Sooty Terns, we fitted Cormack–Jolly–Seber (CJS)

models using Program MARK (v. 9, White & Burnham 1999). We included mark–recapture data for years with regular ringing and resighting effort, i.e. 1993–2020 (Table S1), and removed the first release occasion for birds ringed as chicks. The final dataset included 11 954 individuals first captured at age 1 or older. Goodness of fit testing was conducted using Program UCARE (v.2.3.2, Choquet *et al.* 2009) to examine whether our data deviated from the underlying assumptions of the CJS model. We used Test 2.C to assess whether capture heterogeneity was present; for example, if certain individuals were more likely to be seen in subsequent years, possibly reflecting observers returning to the nesting sites of known individuals. We also used Test 3 to assess whether survival heterogeneity was present, whereby individual survival rates vary within each age class. In addition, we calculated the overdispersion parameter, median \hat{c} , in Program MARK (Cooch & White 2019). To estimate median \hat{c} , we used a lower bound of 1.0, an upper bound of 4.0 and 100 replicates. We then used the predicted value as a quasi-likelihood adjustment to account for lack of fit during model selection (Cooch & White 2019). Our initial model (from here on ‘the global model’) was constructed to have the largest number of parameters that provided adequate fit to the data. All candidate models were then nested within the global model and the most parsimonious was selected based on the corrected second-order Akaike Information Criterion (QAICc) value (Cooch & White 2019). Here, a difference of more than two QAICc units was taken to indicate strong support for the model with the lower score (Burnham & Anderson 2002).

To identify the most parsimonious model for describing rates of apparent adult survival we compared three CJS models (Table 1). In all models, recapture probabilities were time-dependent and set to zero in years without recapture effort (Table S1). The global model was fully time-dependent for survival and recapture probabilities (Table 1, Model 2) and it was possible to estimate annual rates of apparent survival, even in years with zero recapture effort, due to birds being recaptured later in the study. The second candidate model considered a constant rate of adult survival (Table 1, Model 3), and the final candidate model considered a constant rate of adult survival with a second value for 2011 (Table 1, Model 1).

Anomalously low survival was identified for 2011 by the global (i.e. fully time-dependent) model (SOM Fig. S2). We report rates of adult survival for the most parsimonious model.

Apparent juvenile survival

To estimate rates of apparent juvenile survival we included only birds ringed as fledglings (7777 individuals) and all subsequent recaptures for these individuals (955 events). We define juvenile survival as survival from fledging to age 1 year. Seabird rates of survival typically increase from age 1 onwards (Horswill & Robinson 2015); therefore we employed a two-age class structure to describe rates of survival, i.e. juveniles (0–1 year) and adults (> 1 year). To account for a paucity in recaptures ($n = 955$), we set juvenile survival as constant and adult survival (i.e. from age 1 onwards) was either time-dependent (Table 2, Model 2) or constant (Table 2, Model 1). We removed the last five cohorts of fledglings to minimize biases introduced by delayed individual recruitment and return to the colony (i.e. the age of first breeding for Sooty Terns is 5 years, Feare & Doherty 2011). We also used a two-age class structure in recapture rates to account for differences associated with age. Recapture probabilities for both age classes were time dependent to reflect annual variation in recapture effort, and years without survey effort were set to zero (see Table S1). Goodness of fit testing, estimation of median \hat{c} and model comparison followed the same approach as described for estimating apparent adult survival. We also report rates of juvenile survival for the most parsimonious model.

Population viability analysis

We ran a series of PVAs to retrospectively characterize historical harvesting levels of Sooty Tern eggs on Bird Island and predict how future harvesting regimes may influence local population dynamics. We constructed all PVAs using the Natural England PVA tool for seabird species (v.2, Searle *et al.* 2019, available online: https://github.com/naturalengland/Seabird_PVA_Tool). This tool is based on a Leslie matrix model and we specified the model structure as stochastic to incorporate annual fluctuations in demographic rates. We ran all models for 1000 simulations to generate a confidence interval for the estimated population

Table 1. Model selection for the CJS models used to estimate rates of apparent adult survival for Sooty Terns breeding on Bird Island, Seychelles, 1993–2021.

Model no.	Model structure	QAICc	Delta QAICc	Model likelihood	Number of parameters
1	$\varphi_{\cdot,2011} p_t$	15 386.66	0.00	1.00	29
2	$\varphi_t p_t$	15 408.45	21.79	0.00	54
3	$\varphi_{\cdot} p_t$	15 442.86	56.20	0.00	28

In these models, survival (φ) was either fully time-dependent ($(_t)$), constant ((\cdot)) or constant with a second value for 2011 ($(\cdot,2011)$). In all models, recapture rates (p) were fully time-dependent.

Table 2. Model selection for the CJS models used to estimate rates of apparent juvenile survival for Sooty Terns fledging from Bird Island, Seychelles, 1972–2021.

Model no.	Model structure	QAICc	QAICc weight	Model likelihood	Number of parameters
1	$\varphi_{2a: \dots} p_{2a: t,t}$	2389.11	0.00	1.00	43
2	$\varphi_{2a: \dots,t} p_{2a: t,t}$	2461.91	72.80	0.00	89

Two age-classes were included for survival (φ_{2a}) and recapture (p_{2a}). For survival, both age-classes were modelled as constant ((\dots)), or constant in the first age-class and fully time-dependent in the second ((\dots,t)). In all models, recapture rates (p) were fully time-dependent in both age classes ((t,t)).

trajectory. To describe the survival process, we used the age-specific mean estimates produced by the best fitting CJS models. To assign annual variation for adult rates of survival, we used the standard deviation of annual estimates from the global CJS model excluding 2011 ($sd = 0.06$). However, because it was not possible to estimate annual survival estimates for juveniles (i.e. individual values for each year of the study) and thereby derive a measure of temporal standard deviation (as described for adults), we applied a published estimate of temporal variation in juvenile survival from Arctic Terns *Sterna paradisaea* ($sd = 0.03$; Mallory *et al.* 2018). Using an alternative value for temporal variation in juvenile survival from other species of tern, i.e. Common Tern *Sterna hirundo* ($sd = 0.09$, Szostek & Becker 2012), did not qualitatively influence PVA results (SOM Fig. S5).

To describe Sooty Tern breeding success (fledglings per breeding pair), we used the published mean value for Sooty Terns breeding on Bird Island from 1972 to 1973 (i.e. 0.58; Feare 1976a). Annual variation in breeding success has not been recorded for this population and therefore we applied the standard deviation of annual estimates of breeding success recorded for Sooty Terns breeding on Ascension Island ($sd = 0.13$, Hughes *et al.* 2017). Finally, because it was not possible to

derive recruitment from the fledgling mark–recapture data, we set the mean age of first breeding at 5 years to reflect local estimates for Sooty Terns (Feare & Doherty 2011). Using a surrogate value derived from independent data to define age of first breeding is a common approach in PVA of seabirds (i.e. Searle *et al.* 2019, Horswill *et al.* 2022b, Horswill *et al.* 2023). For the PVA, we assumed that replacement laying does not occur. Experimental egg removal demonstrates that the proportion of birds that relay declines over the course of the breeding period, and that breeding success associated with these later-laid eggs is low (Feare 1976a). The contribution that replacement eggs make to future generations is unclear but assumed to be small. Therefore, by excluding relaying from the PVAs, we provide a precautionary assessment that omits any potential compensatory effect from relaying. The demographic profile used to parameterize the PVA is detailed in Table S2.

Population viability analysis validation

In the first set of PVAs, we ran validation analyses for the period with observed start and end population counts (1996–2021). The aim of this analysis was to characterize historical harvesting

levels of Sooty Tern eggs on Bird Island. We compared the observed population trend with that predicted by three PVA scenarios: (1) no egg harvesting, i.e. the baseline demographic profile described above; (2) annual egg harvesting since 2006 at 50% of the population, i.e. breeding success reduced by 50%; and (3) annual egg harvesting since 2006 at 60% of the population, i.e. breeding success reduced by 60%. Although historical harvesting occurred pre-2006, commercial harvesting rates are only known and described in the literature starting from 2006, with 50–60% of the colony being harvested (Feare & Doherty 2011). We therefore use 2006 as our starting point for the PVAs, while recognizing that historical harvesting may be an underlying factor influencing long-term population dynamics.

We initiated the PVA with the number of breeding pairs observed at Bird Island in 1996, i.e. 700 000 breeding pairs (Feare *et al.* 2007). We then simulated the population trajectory until the next year with available count data for the whole colony, i.e. 2021 (334 000 breeding pairs; Morgan & Cupidon 2021). These point estimates reflect a similar, albeit slightly slower rate of Sooty Tern decline (~47%) compared with the wider Seychelles (~60%; Morgan & Cupidon 2021), such that biases introduced by erroneous counts are considered minimal.

Population viability analysis projection

In the second set of PVAs, we ran projection analyses between 2021 and 2100 to examine how six different egg-harvesting regimes may influence the future population dynamics of Sooty Terns on Bird Island. We ran these management strategies from the observed population size in 2021 ($n = 334\,000$; Morgan & Cupidon 2021). We also adjusted the baseline rate of fecundity to include egg harvesting at 60% of the population to account for historical harvesting influencing recruitment during the first 5 years of the projection analysis. Thus, the six management strategies all started with egg harvesting conducted at 60% of the population. Then, after 2021 egg harvest was either: (1) terminated, (2) conducted at 10% of the population, (3) conducted at 20% of the population, (4) conducted at 30% of the population, (5) conducted at 40% of the population or (6) conducted at 60% of the population (i.e. 'business as usual'). In these scenarios we assume no additional habitat

modification or environmental change. We also provide the full input log for setting up these PVA scenarios in the SOM Appendix S1. Running the same set of scenarios with a 50% harvest up to 2021 produced comparable results (SOM Fig. S6) and therefore we only present the results for the 60% scenario in the main text. The 60% scenario provides a larger estimate of relative impact and thereby offers a more precautionary approach to assessment.

Sensitivity analysis

In the third set of PVAs, we ran projection analyses between 2021 and 2100 to examine how changes in adult survival associated with conservation measures (i.e. by reducing predation or bycatch risk) may influence the population dynamics of Sooty Terns experiencing differing levels of egg harvesting. Like the previous set of projection scenarios, we ran PVA models from the observed population size in 2021 and incorporated historical egg harvesting at 60% of the population ($n = 334\,000$; Morgan & Cupidon 2021). In all scenarios, adult survival was increased by 1% to 0.920, and from 2021, the egg harvest was either: (1) terminated, (2) conducted at 10% of the population or (3) conducted at 20% of the population.

Extinction

To quantify the long-term impacts associated with harvesting Sooty Tern eggs, we estimated the extinction risk associated with the highest harvesting rate, i.e. 60% of the population. We looked at extinction risk using the 60% harvesting scenario (as opposed to the 50% scenario) because it provides the larger estimate of relative impact and thereby quantifies the worst-case scenario. To quantify extinction risk, we calculated the percentage of PVA simulations where the final population size was lower than a quasi-extinction threshold by the year 2100. We set the quasi-extinction threshold to 100 breeding pairs to reflect a catastrophic decline in population size.

RESULTS

Apparent adult survival and recapture

Goodness of fit testing indicated that the global model for estimating adult survival contained

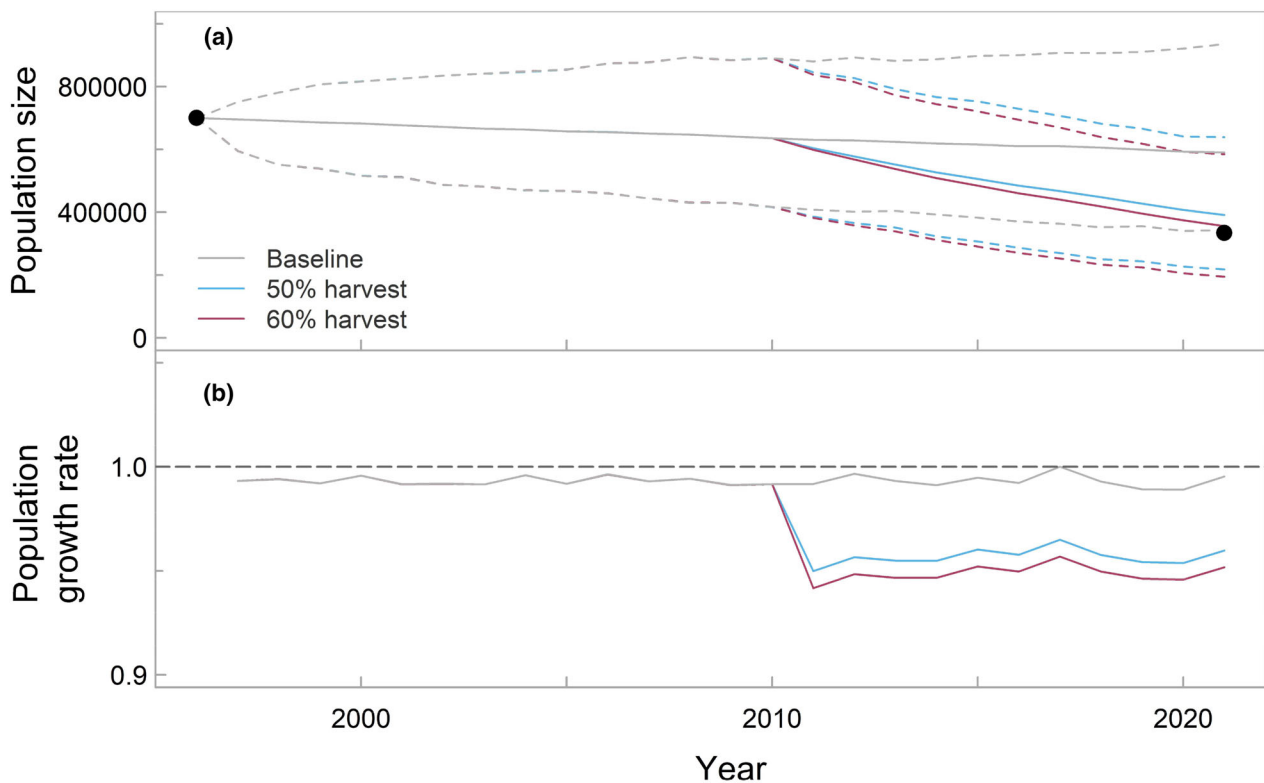


Figure 2. (a) The PVA validation analyses demonstrated that including egg harvesting at 50% of the population (blue) and 60% of the population (red) greatly improved the ability to recreate the observed population decline in Sooty Terns on Bird Island between 1996 and 2021, compared with a baseline model without egg harvesting (grey). Solid lines show the mean population trajectory and dashed lines show the 95% confidence interval. Black points show the observed population sizes in 1996 and 2021. (b) The population growth rate under all scenarios was below zero, indicating a simulated decline in population size. The step change in the simulated population growth rate reflects egg harvesting being introduced in 2006 and the effect being visible 5 years later (i.e. after the first cohort recruits following a delayed reproduction of 5 years).

survival and capture heterogeneity (SOM Table S3); therefore we applied the predicted median \hat{c} (1.78, $se < 0.01$) as a quasi-likelihood adjustment during model selection (Cooch & White 2019). The global model with time-dependent rates of adult survival provided a better fit to our data than the model with constant survival (Table 1, Model 2 vs. Model 3). However, the model with constant survival and a separate estimate for 2011 was identified as the most parsimonious model (Table 1, Model 1). Using this model, the mean rate of apparent adult survival for Sooty Terns between 1994 and 2020 was estimated at 0.907 (95% confidence interval, CI, 0.900–0.913), with a lower value in 2011 estimated to be 0.482 (95% CI 0.383–0.582). Recapture rates of adult Sooty Terns varied from year to year, probably reflecting variation in survey effort over the duration of the study period (SOM Fig. S3).

Apparent juvenile survival and recapture

Goodness of fit testing indicated that the global model for estimating juvenile survival contained survival and capture heterogeneity (SOM Table S4), and therefore we applied the predicted median \hat{c} (4.17, $se < 0.01$) as a quasi-likelihood adjustment during model selection (Cooch & White 2019). The most parsimonious model (Table 2, Model 1) indicated that juvenile survival was constant from year to year at 0.419 (95% CI 0.368–0.472). Similar to the analysis with adult-only data, the juvenile analysis also showed that the recapture rates of juvenile and adult Sooty Terns varied from year to year (SOM Figs S3 and S4).

Population viability analysis validation

To characterize historical harvesting levels of Sooty Tern eggs on Bird Island, Seychelles, we ran

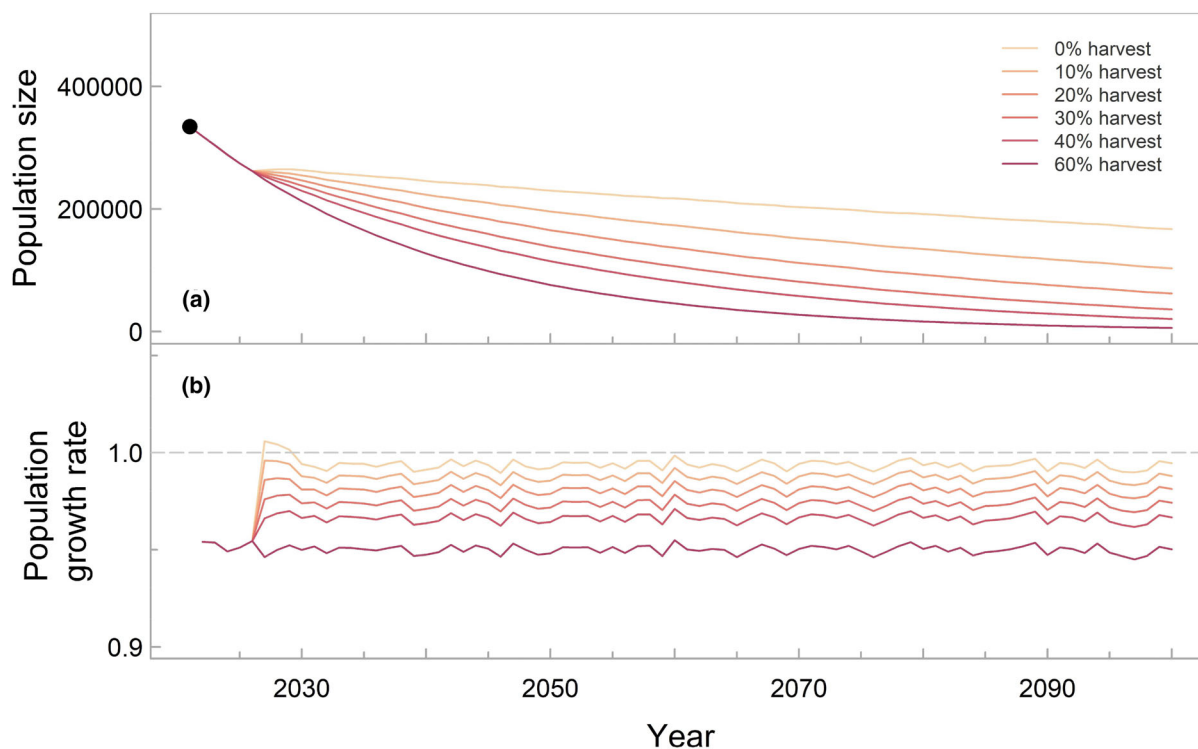


Figure 3. The PVA projection analyses demonstrated that (a) the Sooty Tern population on Bird Island, Seychelles, is likely to decline under all scenarios of egg harvesting, with (b) population growth rates remaining below one, reflecting continued population decline. In all scenarios, egg harvesting occurred at 60% of the population until 2021 and at 0%, 10%, 20%, 30%, 40% or 60% thereafter. Colour ramp reflects harvesting level (yellow = 0% and red = 60%). Projection analyses were run from the observed population size in 2021, $n = 334\,000$ breeding pairs. For 95% confidence intervals around the simulated population trajectories see SOM Figure S7.

PVA validation analyses for the time-period with observed start and end population counts (i.e. 1996–2021). The observed population size of Sooty Terns at Bird Island in 2021 was 334 000 breeding pairs (Morgan & Cupidon 2021). This value fell within the 95% confidence intervals of the 50% and 60% egg-harvesting PVA scenarios (Fig. 2a). Under the 50% scenario, the mean predicted population size for 2021 was 391 003 breeding pairs (95% CI 217 756–638 772), i.e. 15.72% higher than the observed population size (Fig. 2a). Under the 60% egg-harvesting PVA scenario, the mean predicted population size for 2021 was 356 021 breeding pairs (95% CI 194 736–584 575), i.e. 6.38% higher than the observed population size (Fig. 2a). The population trajectory simulated using the baseline demographic profile also potentially declined from the original population size in 1996 of 700 000 breeding pairs (Fig. 2b, Feare *et al.* 2007). The

baseline scenario predicted 590 188 breeding pairs in 2021 (95% CI 342 499–935 120, Fig. 2a).

Population viability analysis projection

We ran PVA projection analyses to examine how six future egg harvesting regimes may influence the long-term population dynamics of Sooty Terns on Bird Island, Seychelles. If harvesting is allowed to continue at 60%, we estimated that the mean population size would decline to 76 093 breeding pairs (95% CI 37 948–133 293) by 2050, and 5867 breeding pairs (95% CI 1747–14 170) by 2100 (Fig. 3a). By contrast, if egg harvesting were terminated in 2021, we estimated that the Sooty Tern population would still decline, but at a much slower rate; the mean Sooty Tern population size would be 229 802 breeding pairs (95% CI 126 801–372 903) by 2050 and 167 256 breeding

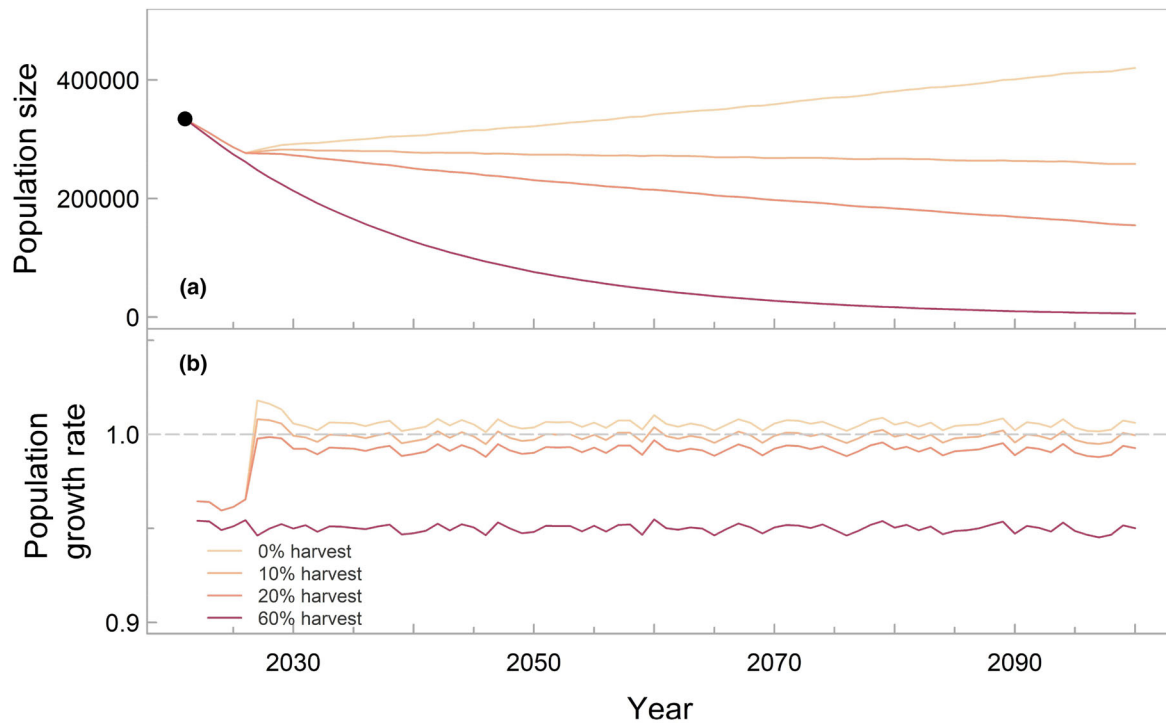


Figure 4. The PVA sensitivity analyses demonstrated that (a) to allow the Sooty Tern population on Bird Island, Seychelles, to increase, egg harvesting needs to be terminated and conservation efforts need to be targeted at increasing rates of adult survival by 1% (i.e. to 0.92). (b) This would support population growth rates > 1 . By contrast, increasing adult survival but maintaining a 20% egg harvesting regime is likely to support continued population decline. Scenarios with egg harvesting at 0%, 10% and 20% included elevated rates of adult survival (0.92). We also show the population trajectory under 60% egg harvesting with baseline survival (0.91) for reference (red). Colour ramp reflects harvesting level (yellow = 0% and red = 60%). Projection analyses were run from the observed population size in 2021, $n = 334\ 000$ breeding pairs. For 95% confidence intervals around the simulated population trajectories see SOM Figure S8.

pairs (95% CI 61 781–353 014) by 2100 (Fig. 3a). Continued harvesting of Sooty Tern eggs at any level (10–60%) reduced the final mean predicted population size (Fig. 3a) and population growth rate (Fig. 3b), compared with the scenario that terminated harvesting in 2021.

Sensitivity analysis

The only projection scenario that resulted in an increasing mean population trajectory for Sooty Terns at Bird Island included termination of egg harvesting combined with targeted conservation actions aimed at increasing adult survival rate by 1%, from 0.910 to 0.920 (Fig. 4a-b). Combining conservation actions that increase adult survival with a 10% egg harvesting rate potentially allows the population to stabilize, but higher levels of egg harvesting (i.e. $\geq 20\%$) are likely to support continued population decline (Fig. 4a-b).

Extinction

Continued harvesting of Sooty Tern eggs at 60% of the population resulted in a 10.2% chance of population extinction by 2100.

DISCUSSION

We used a long-term mark–recapture dataset to estimate age-specific rates of survival for Sooty Terns breeding on Bird Island, Seychelles. We then ran a series of population viability analyses to characterize historical egg harvesting levels and predict how future harvesting regimes may influence local population dynamics assuming no additional environmental change. We provide evidence that egg harvesting has played a substantial role in driving the population decline of Sooty Terns on Bird Island. We also demonstrate that continued harvesting is likely to lead to sustained, possibly

dramatic declines in population size. These results indicate that, under current environmental conditions, recent levels of egg harvesting in Seychelles are not sustainable.

We provide updated estimates of apparent survival for juvenile and adult Sooty Terns. As expected in seabirds (Horswill & Robinson 2015), we found that rates of juvenile survival were considerably lower than rates of adult survival. This contrast probably reflects the different pressures experienced by each age-class. In seabirds, juveniles are more susceptible to top-down pressures, such as pre-fledging predation by other seabirds (Horswill *et al.* 2014), mice (Oppel *et al.* 2022), rats and cats (Hughes *et al.* 2008), as well as post-fledging predation by predatory fish (Honeyborne & Brownlow 2017). Juvenile seabirds are also less proficient at foraging compared with older birds (Porter & Sealy 1982) and potentially more vulnerable to environmental fluctuations (Afán *et al.* 2019). The estimated mean rate of adult survival reported in our study was identical to the value previously reported for this population, i.e. 0.91 (Feare & Doherty 2004). This is despite using a time-series that includes an additional 18 years of mark-recapture data. However, we also identified that adult survival was abnormally low in 2011. This may reflect the El Niño event that occurred between 2009 and 2010 (Kim *et al.* 2011). Previous studies on seabirds in the Southern Hemisphere, also outside of the Pacific Ocean, have linked lower rates of adult survival with environmental changes associated with El Niño (Horswill *et al.* 2014). In agreement, the onset of Sooty Tern egg-laying was unusually late in 2011 (C. Feare pers. obs.), possibly reflecting a change in local environmental conditions (e.g. Frederiksen *et al.* 2004, Schroeder *et al.* 2009).

Our estimate of juvenile survival (0.41, $se = 0.03$) was considerably lower than the value previously reported for Sooty Terns on Bird Island (0.76, $se = 0.21$; Feare & Doherty 2011). Possible explanations for this discrepancy include differences in the data collection periods. The previously reported value was based on 3 years of data, whereas we have included all mark-recapture data collected between 1973 and 2021 (Table S1). The extended time series considered in our study may therefore include additional pressures that lower the overall mean rate of apparent juvenile survival, such as environmental fluctuations. We found an abnormally low rate of adult survival in 2011, and

previous work on seabirds suggests that age-specific rates of survival vary additively across age classes, i.e. fluctuate synchronously (Cam *et al.* 2005, Horswill *et al.* 2014). Further work would benefit from examining how the low adult survival event in 2011 may have also impacted the estimated mean rate of juvenile survival. It was not possible to empirically separate annual estimates of juvenile survival due to data paucity. However, it may be possible to hypothetically explore the population response using PVA scenario testing. Juvenile survival has a low demographic impact in long-lived species, although temporal variation can increase its demographic impact on population size (Gaillard *et al.* 2000).

We conducted a PVA validation analysis to characterize harvesting levels of Sooty Tern eggs on Bird Island between 2006 and 2021. Our baseline validation model (i.e. without egg harvesting) estimated the population to be 76.7% greater than the 334 000 breeding pairs recorded in 2021. By contrast, both of our models that included egg harvesting produced mean population estimates that were more in line with the 2021 count. The estimated mean population sizes including 50% and 60% egg harvesting regimes were 15.72% and 6.38% higher than the observed value in 2021, respectively. Differences between the observed and predicted population sizes could reflect variables that were not included in our PVA model, such as on-island (i.e. habitat management, under-represented harvesting pre-2006, immigration) and at-sea drivers of change (i.e. environmental conditions, reduction in fish stocks both during and outside of the breeding season). Further studies may benefit from incorporating these variables into population models and assessing their relative importance to population dynamics (i.e. Horswill *et al.* 2016).

The validation PVA identified that the population trajectory between 1996 and 2021 might still have declined even without egg harvesting, albeit at a considerably slower rate than with harvesting incorporated. This may reflect historical egg harvesting, i.e. prior to 2006, such that the rate of breeding success applied in the PVA includes associated disturbances. Levels of illegal Sooty Tern egg harvesting are currently unknown but are suspected to be high (Mondreti *et al.* 2018). Consequently, the impact of egg harvesting could be greater than anticipated. Alternatively, rates of survival and breeding success may include effects of local habitat change. Previous studies have linked habitat modification in Seychelles,

associated with agriculture (i.e. coconut plantations) and the growth of introduced plants, to local changes in Sooty Tern colony size (Feare 1976b, Feare *et al.* 1997). This may also extend to other nearby islands where disturbance through habitat change could alter recruitment to Bird Island (i.e. through dispersal from Aride; Feare & Lesperance 2002). Another factor that could be causing the baseline population to decline is local environmental change. Sooty Terns are almost near-obligate commensals of tuna, cetaceans and other sub-surface predators (Au & Pitman 1986, Le Corre & Jaquemet 2005). Increasing sea surface temperatures could be forcing bait fish to become inaccessible by causing them to move outside of the foraging range of Sooty Terns during the breeding season (Lan *et al.* 2013). Additionally, extensive overfishing of tuna and other sub-surface predators could be reducing the availability of bait fish near the water surface, within the foraging depth of Sooty Terns. The total catch of tropical tunas, such as Skipjack Tuna *Katsuwonus pelamis*, Yellowfin Tuna *Thunnus albacares* and Big-eye Tuna *Thunnus obesus*, has dramatically increased in the Western Indian Ocean since the 1970s (Fiorelato *et al.* 2020).

We do not account for future environmental change in the projection PVAs. Additional environmental factors that are negatively contributing to population dynamics should be incorporated in PVA impact assessments to evaluate potential 'worst case' scenarios (Horswill *et al.* 2022a). For Sooty Terns, habitat modification associated with agricultural development and climate change are highly likely to exacerbate future rates of population decline. Agricultural development alters the available breeding habitat of Sooty Terns (Feare *et al.* 2007) and increasing sea surface temperatures may impact prey abundance or availability (Thayer *et al.* 2008). Seabirds respond to short-term fluctuations in prey abundance by extending foraging ranges and trip durations, with consequent impacts to chick-provisioning rates and fledging masses (Horswill *et al.* 2017, Campbell *et al.* 2019). Longer foraging ranges also have the potential to result in lower and more variable rates of adult survival in seabirds (Horswill *et al.* 2023). Studies of individual movement and breeding performance across years with different environmental conditions, for example during El Niño events, may help clarify the additional reproductive costs experienced by Sooty Terns during adverse conditions, as well as the likely demographic and population consequences of future climate change.

Our predictions of future Sooty Tern population viability do not account for any potential compensatory effects from egg relaying or negative density dependence. We adopted this approach to provide a maximum estimate of relative impact associated with egg harvesting and thus deliver a precautionary assessment. Breeding success in long-lived species, such as seabirds, typically has a low demographic impact, such that we do not expect compensatory changes in breeding success to generate a large population response (Horswill *et al.* 2021). However, density-independent PVA can also lead to underestimates of the impact in populations where positive density-dependence is present (Horswill *et al.* 2017). Lower nesting densities of Sooty Terns in harvested areas could leave birds more vulnerable to egg predation by chickens and land crabs (C. Feare pers. obs.), generating positive density-dependent regulation. Consequently, future PVA work on Sooty Terns may benefit from integrating density-dependent mechanisms and evaluating their relative influence on population growth.

To predict how future Sooty Tern dynamics may respond to different levels of continued harvesting, we ran a series of projection PVAs. This analysis demonstrated that a continued moratorium on harvesting Sooty Tern eggs is needed to reduce rates of population decline. There is a visible 5-year lag between initiating the moratorium in 2021 and the change in population trajectory in 2026. This can be explained by age of first breeding. Most Sooty Terns breed for the first time at age 5 years (Feare & Doherty 2011) and therefore a positive effect on breeding success and subsequent recruitment is not observable using PVA until, at least, 5 years later. This result highlights the importance of understanding the life history strategy and breeding ecology of Sooty Terns when developing and evaluating conservation strategies, such as terminating egg harvesting.

We were unable to identify a sustainable level of egg harvesting for Sooty Terns on Bird Island, Seychelles. Furthermore, if egg harvesting is allowed to continue at 60% of the population, there is a possibility that the local population could experience catastrophic collapse by 2100. We also found evidence that to reverse the population decline of Sooty Terns in Seychelles, conservation actions aimed at increasing rates of adult survival, as well as breeding success, would be required. Such actions could include the removal

of land predators and the protection of at-sea resources.

Juvenile and adult dispersal were not included in the PVA analyses. Empirically estimating dispersal is challenging in seabirds. Mark–recapture studies are needed over a large area with large sample sizes if rates of dispersal are low (Coulson 2016). In Seychelles, extensive ringing, accompanied by widespread searches for ringed birds, was undertaken in the 1990s. This revealed both natal and adult dispersal among colonies in the Amirante and Inner Islands. It also suggested that human disturbance associated with egg harvest (commercial and illegal) might stimulate inter-colony dispersal (Feare & Lesperance 2002). Major habitat change and extensive illegal harvesting of Sooty Tern eggs occurred on Aride Island between 2002 and 2021, preceding a 93% decline in the Sooty Tern colony (Bowler *et al.* 2002). Increased dispersal in response to large-scale breeding failure has also been reported in other species of seabird (Boulinier *et al.* 2008).

Changes in immigration can dramatically influence population viability in seabirds (Horswill *et al.* 2022b). The large-scale decline of Sooty Terns across the Seychelles (Morgan & Cupidon 2021) indicates that island-specific rates of population decline cannot be solely attributed to a local redistribution of breeding birds. However, population decline on Bird Island could reflect rates of dispersal from potential source populations, such as Aride Island, declining through time. Alternatively, if disturbance on Aride Island has increased emigration of Sooty Terns to Bird Island, this could mask the true rate of local population decline associated with egg harvesting. Likewise, other large Sooty Tern colonies in the Western Indian Ocean that are not impacted by egg harvesting, such as Europa, Juan de Nova and Glorieuses, could act as source populations buffering population decline on Bird Island.

CONCLUSIONS

In this study, we provide updated estimates of apparent survival for juvenile and adult Sooty Terns breeding on Bird Island, Seychelles. We then used these estimates, alongside published demographic rates, in a PVA to demonstrate that large-scale egg harvesting probably contributed to rapid decline in the Sooty Tern population on Bird Island, Seychelles, between 2006 and 2021. We also show that commercial harvesting poses a serious threat to

Sooty Terns, such that continuation of this practice could lead to further, possibly dramatic, declines in population size. The life-history strategy of Sooty Terns, including delayed reproduction, means that the current 2-year moratorium on harvesting Sooty Tern eggs is highly unlikely to provide an observable, positive population-level response. Effects from a moratorium could become observable after 5 years, as these cohorts of fledglings reach maturity and start to breed. Consequently, an extension of the moratorium at least beyond the age of first breeding (i.e. 5 years) is necessary to support appropriate evaluation. We also demonstrate that continued harvesting, even at much lower levels, i.e. 10% of the population size, is unlikely to reverse population decline, such that long-term harvesting practices require careful consideration to balance the social, commercial, cultural and biodiversity values of Sooty Terns in Seychelles.

On Bird Island, we thank the numerous people who have searched for ringed birds and assisted with bird ringing. Intensive ringing of Sooty Terns between 1972 and 1974 was assisted by the late Marie France Savy and Christine Feare. In 1976, the late Count Maurice Coreth, his wife Ginny and daughter Sophie all contributed to fieldwork. The revitalization of Sooty Tern monitoring in 1993 was stimulated by the then Director of Conservation, Nirmal Jivan Shah, and his successors John Collie, John Nevill, Selby Remie and Ronley Fanchette continued that support. The project was concentrated mainly on Bird Island and Guy and Marie France Savy, Georges and Margaret Norah, and Serge Robert were instrumental in its success. More recently, annual visits have been self-funded by C.J.F. but Bird Island has continued to provide essential logistical support. We are also grateful to the British Trust for Ornithology for permission for C.J.F. to use their rings throughout this project.

AUTHOR CONTRIBUTIONS

Thalissa Inch: Writing – original draft; methodology; validation; visualization; software; conceptualization; writing – review and editing; investigation. **Malcolm A.C. Nicoll:** Writing – review and editing; methodology; validation; visualization; software; conceptualization; supervision; investigation. **Chris J. Feare:** Writing – review and editing; data curation; conceptualization; resources; investigation. **Catharine Horswill:** Writing – review and editing; methodology; validation; visualization; software; conceptualization; supervision; investigation.

ETHICAL NOTE

The research involved long-term ringing and recapturing of Sooty Terns on Bird Island, Seychelles. Recent studies have been approved by Seychelles Bureau of Standards. All handling and ringing of birds were conducted by trained staff under licence to C.J.F. from the British Trust for Ornithology (BTO).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Number of Sooty Tern chicks and adults ringed on Bird Island, Seychelles, between 1972 and 2021.

Table S2. Demographic profile of Sooty Terns at Bird Island used to parameterize the PVA.

Table S3. Goodness of fit test results of apparent survival for adult Sooty Tern at Bird Island, 1993–2021.

Table S4. Goodness of fit test results of apparent survival for juvenile Sooty Tern at Bird Island, 1993–2021.

Figure S1. Tractor containing boxes of Sooty Tern eggs on Bird island, Seychelles (photo taken in 2013). Photo taken by C. Feare.

Figure S2. Survival rates of adult Sooty Tern at Bird Island, Seychelles (1973–2019).

Figure S3. Recapture rates of adult Sooty Tern at Bird Island, Seychelles (1973–2019).

Figure S4. Recapture rates of juvenile Sooty Tern at Bird Island, Seychelles (1973–2019).

Figure S5. PVA validation model using juvenile temporal variation of Common Tern *Sterna hirundo*.

Figure S6. PVA projection analyses including 50% harvest scenario instead of 60%.

Figure S7. PVA projection analyses under the six different harvesting scenarios shown with 95% confidence intervals.

Figure S8. PVA sensitivity analyses under four harvesting scenarios shown with 95% confidence intervals.

Appendix S1. Population viability analysis parameter log.