# FORAGING AREAS OF BREEDING ADULT SOOTY TERNS *ONYCHOPRION FUSCATUS* ON BIRD ISLAND, SEYCHELLES

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**ABSTRACT**

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The foraging areas used by adult Sooty Terns *Onychoprion fuscatus* during incubation and early chick-rearing on Bird Island, Seychelles, were investigated using small GPS loggers. Birds departed the colony mainly during the night and foraged by day. Most foraging trips were completed within 24 hr, but during incubation the longest duration recorded was seven days and 14 hr (during which the bird travelled 2,783 km and reached a maximum of 692 km from the colony). Departures were generally in an arc from south (180°) through westerly to 40°. Sooty Terns foraged frequently in waters over the Seychelles Bank shelf break, but some birds travelled further, including to the area around the Coco-de-Mer Ridge *ca*. 400 km north of Bird Island. In the four days after hatching, adult foraging trips tended to be shorter, within 24 hr, and the small sample of tracks obtained revealed that they potentially foraged over deeper areas. Most of the foraging areas identified were within the Seychelles' Exclusive Economic Zone, with some foraging areas occurring outside the Seychelles marine protected areas.

**Key words:** foraging, foraging range, Indian Ocean, marine protected area, tropical seabird

## INTRODUCTION

Sooty Terns *Onychoprion fuscatus* are the most numerous and among the most pelagic of tropical seabirds (Schreiber et al., 2020), and much is known about their biology when breeding on land (e.g., Ashmole, 1963; Feare, 1976; Feare & Doherty, 2004, 2011; Jaquemet et al., 2008; Reynolds et al., 2019). After breeding, adults from a large colony on Bird Island, Seychelles, disperse widely over the tropical Indian Ocean, ranging over most of the ocean north of *ca*. 25°S (Jaeger et al., 2017).

During the breeding season, however, the need for frequent return to the nesting colony to establish nest territories, incubate eggs, and feed young forces adult Sooty Terns to become central place foragers, with energetic constraints predicted to limit their foraging ranges (Flint, 1991). This raises the possibility of prey depletion within the foraging range, which has been demonstrated in some seabirds (the origin of the concept of "Ashmole's halo"; Birt et al., 1987; Gaston et al., 2007) and could account for the Sooty Terns' extensive post-breeding dispersal (Diamond, 1978; Jaeger et al., 2017). Soanes et al. (2015) and Neumann et al. (2018) investigated the foraging trips of incubating Sooty Terns in the Caribbean and Seychelles, respectively, using GPS loggers. Caribbean Sooty Terns foraged largely within 90 km (Soanes et al., 2015), as did the first tracks of the Seychelles birds (Neumann et al., 2018). However, three later tracks of Seychelles Sooty Terns revealed birds travelling 289, 691, and 895 km from their colony; at the time of these journeys, prolonged incubation shifts, lack of regurgitation during handling of adults, and abandonment by parents of eggs and recently hatched chicks indicated a sudden onset of food shortage (Neumann et al., 2018).

The objective of the current study was to undertake a multi-year (2016–2019) investigation of the foraging behaviour of adult Sooty Terns nesting on Bird Island, Seychelles, mainly during incubation, to identify feeding areas used. We additionally include data from 2014, which included tracks obtained during a period of severe food shortage that resulted in breeding failures (Neumann et al., 2018), and we discuss the relevance of current Seychelles marine protected areas to the breeding season foraging areas identified in this study.

## METHODS

### Study Colony

Bird Island (03°40′S, 055°12′E) is a *ca*. 100 ha (1 km$^2$) coralline sand cay situated on the northern edge of the shallow (< 100 m) Seychelles

Bank (Fig. 1), close to the insular slope dropping to 2,000–4,000 m deep (Feare, 1979; Hill et al., 2002). The Sooty Tern colony, currently comprising < 400,000 pairs, occupies *ca*. 14 ha (0.14 km$^2$) at the northwest corner of the island, on mainly open ground lightly vegetated with the herbs *Portulaca oleracea* and *Boerhavia repens* and several grass species; most of the vegetation dies back as the breeding season progresses, due largely to trampling and guano deposition by the birds. Since 2006, a portion of the colony, which has varied in size 25%–50% in different years, has been protected as a strict nature reserve. Sooty Tern eggs have been harvested in most years from the remainder of the nesting area, the eggs being sold on the main inhabited islands of Seychelles as a traditional delicacy. All our studies were undertaken in the reserve, away from human disturbance.

In Seychelles, Sooty Terns nest during the southeast monsoon season, which reaches peak wind velocities and associated rough seas in July–August. Egg-laying usually begins in late May/early June, and chicks hatch after *ca*. 28 days of incubation (Feare, 1976), thus hatching just before or during the period of strongest winds.

### GPS Tags and Attachment

PathTrack nanoFix GEO+ (PathTrack, UK) GPS tags were used. These weighed *ca*. 3 g (*ca*. 1.7% of the mass of an incubating Sooty Tern of *ca*. 180 g, the lowest mass of birds to which we attached tags) and measure 25 mm × 10 mm × 8 mm. Dorsal solar panels recharged the battery, and a posterior 50-mm antenna received GPS signals. Tags were set to record locations every 10 min from 05h30 to 19h30 and hourly overnight. Geographic locations recorded by tags are accurate to *ca*. 20 m (PathTrack to CJF, personal communication, 2014).

Incubating adults were caught using hand nets, a technique that has been widely used in the Bird Island colony over several decades with no recorded nest desertions by the caught birds. Tags were attached to incubating adults in a part of the colony where eggs had been laid *ca*. 10 days before being caught. We attached the tags using a thigh-loop harness (Mallory & Gilbert, 2008). The tag sat on the lower back of the bird, anterior to the uropygial gland. The harness material used was 1.25-mm slip elastic (Preston Innovations, UK), a highly flexible material that allows movement of the bird and easy adjustment for the person fitting the tag. The elastic was secured in front of the anterior attachment loop of the tag by crimping a small aluminium ferrule (1.5 mm, cut in half; S3i Group, UK) and the trimmed ends of the elastic were sealed with a dab of superglue. The slip elastic is biodegradable so that if we were unable to recapture a tagged bird, the tag would fall off after *ca*. 6 mo. (verified with a tagged Brown Noddy *Anous stolidus*). All Sooty Terns we tagged were recaptured.

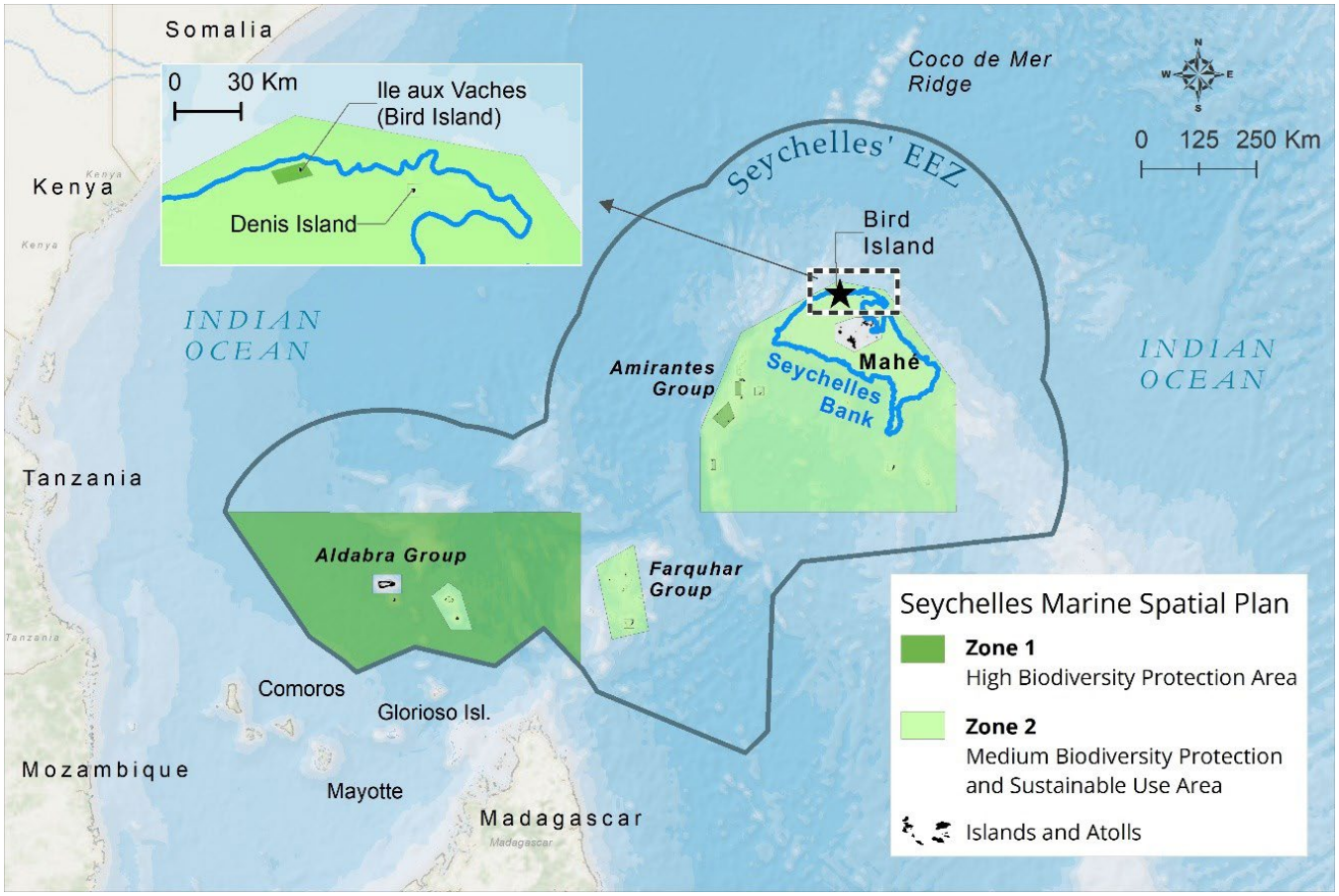


**Fig. 1.** Location of Bird Island on the northern margin of the shallow Seychelles Bank. The Seychelles Exclusive Economic Zone (EEZ) is outlined, along with areas designated as marine protected areas (MPAs) in the Seychelles Marine Spatial Plan. The darker MPA in the southwest is a High Biodiversity Protection area. The paler area in the northeast is a Medium Biodiversity Protection and Sustainable Use area. Bird Island, however, lies in a small, rectangular High Biodiversity Protection area (see inset). Map provided by the Seychelles Marine Spatial Plan Team: Rick Tingey, Helena Simms, Joanna Smith

When a Sooty Tern was captured, it was weighed using a 500-g Pesola balance. If the mass was a minimum of 180 g, the nest was marked with a numbered plastic label (a standard practice in the Bird Island colony, with no nest desertions) and the bird was given an individually engraved orange Darvic leg ring (Ecotone, Poland) before the GPS tag was attached. This coloured ring allowed us to identify the tagged bird when it returned to relieve its mate after a foraging trip. When the bird was recaptured, we removed the tag and downloaded the location data to a computer.

Tags were deployed on incubating Sooty Terns in 2014 (seven tag deployments), 2016 (20), 2017 (16), 2018 (eight), and 2019 (nine). Some deployments provided multiple tracks, indicating that we had failed to detect some individuals when they first returned to the colony. In 2016 and 2017 tags were deployed on some adults whose eggs proved to be on the point of hatching, after which parents become increasingly difficult to catch with hand nets. However, these tagged individuals provided tracks of adults one to four days after their eggs had hatched.

In 2018 both members of five pairs were fitted with GPS tags to discover whether members of mated pairs foraged in the same places or differed in their selection of feeding areas. We visited nest sites daily at *ca*. 09h00 and *ca*. 16h00 to check for returning ringed adults.

Across all years, six tags malfunctioned and yielded either no data or substantially incomplete data; these failed tracks were excluded from our analyses. For unknown reasons, but possibly due to poor solar charging of the batteries, two to four tracks each year recorded gaps in data during flight, usually as a bird returned to its nest on Bird Island. As time and location fixes could be reliably obtained both prior to and after a recorded gap, these tracks were mapped and included in our analyses.

### Data Processing

Location data (latitude and longitude) were downloaded from the tags according to PathTrack protocols (PathTrack Archival GPS logger). Further analyses were conducted in R using RStudio (R Core Team, 2021; R Studio Team, 2021). The ExMove toolkit (Langley et al., 2024) was used to standardise the tracking data and to define a "trip" as any journey by which a Sooty Tern vacated Bird Island and was located over open water for 30 min (and for at least three GPS fixes) before returning to Bird Island. "Short trips" were less than 2 hr long, and the birds remained within a few kilometres of Bird Island; these were birds likely to have undertaken trips to sea to drink and/or wet their feet and body plumage, behaviours that are considered to facilitate maintenance of egg temperature and humidity (Feare, 1976). "Long trips", presumed to represent foraging, were all > 2 hr in duration and were the focus of this study. Some GPS loggers recorded multiple short and long trips; others recorded single trips. For each track, we calculated the trip duration (hr), total distance travelled (km), and the maximum distance travelled (i.e., the foraging range, km). For long trips (assumed to indicate foraging activity), we calculated departure date and time and the direction of departure to the distal point (bearing). Departure times were grouped into 4-hr intervals, and we used linear mixed-effects models to determine whether departure time influenced trip duration, total distance travelled, and foraging range (all log-transformed to improve model fit). We also included year and breeding stage as fixed effects to investigate whether trip duration, total distance travelled, and foraging range varied between years or between egg incubation and early chick-rearing. We ran the models using the *lmer* function in the "lme4" R package (Bates et al., 2015); the term *individual* was included as a random effect in these models to account for pseudo-replication caused by some individuals undertaking multiple trips. Model diagnostics were assessed by plotting residual values against the fitted values and by assessing Q–Q plots. Pairwise comparisons were calculated via the "emmeans" package (Lenth, 2025). Departure angles were grouped into 20° intervals and plotted to allow inter-annual visual comparisons.

Foraging areas were identified as those in which birds spent prolonged periods around a localised area away from Bird Island (i.e., a greater density of points in close spatial proximity). Birds transitioning between foraging areas were identified by showing longer distances between fixes and movement in a sustained direction. We used the *kernelUD* function in the "adehabitatHR" R package (Calenge, 2024) to identify areas where high point concentrations indicated purported foraging zones (50% kernel utilisation distributions—presumed active feeding areas), as well as foraging ranges (95% kernel utilisation distributions—presumed search areas). We extracted US National Oceanic and Atmospheric Administration (NOAA) bathymetric data from within the 50% kernel utilisation distribution areas using the "marmap" and "exactextractr" R packages (Baston, 2023; NOAA, 2022; Pante et al., 2023).

### Ethics Statement

The Seychelles Bureau of Standards approved this GPS tracking project (reference number A0157), with support from what is now the Ministry of Agriculture, Climate Change and Environment.

## RESULTS

### Time, Duration, Distance, and Direction of Departures From the Colony

When engaging in foraging trips (those > 2 hr), Sooty Terns departed from the colony throughout the diurnal cycle (Fig. 2). Trip duration varied with departure time, with those departing in the evening and early night (16h00–20h00 and 20h00–24h00, respectively) being longer than those departing in the late night and morning (00h00–04h00 and 08h00–12h00). Maximum distance travelled also varied with departure time, with birds embarking on longer trips in the evening and early night than in the morning (estimate = −1.24, standard error [SE] = 0.4, $t = -3.01$, $p = .034$; and estimate = −1.11, SE = 0.33, $t = -3.33$, $p = .018$, respectively) that extended to greater ranges (estimate = −1.1, SE = 0.36, $t = -3.08$, $p = .035$ and estimate = −0.92, SE = 0.3, $t = -3.09$, $p = .035$, respectively).

Foraging trips undertaken during egg incubation and chick-rearing were similar in duration (estimate = −0.75, SE = 0.37, $t = -1.2$, $p = .067$), maximum distance travelled (estimate = −0.46, SE = 0.38, $t = -1.2$, $p = .24$), and foraging range (estimate = −0.36, SE = 0.34, $t = -1.06$, $p = .31$), although sample sizes were small (Table 1).

Trip durations, distances travelled, and foraging ranges were similar between years (Table 1), although two longer trips in 2014 (183 and 157 hr) were associated with severe food shortage, as indicated by widespread desertions of eggs towards the end of the incubation phase and widespread deaths of recently hatched chicks (Neumann et al., 2018). Despite recording some tracks > 75 hr (Table 1 in all

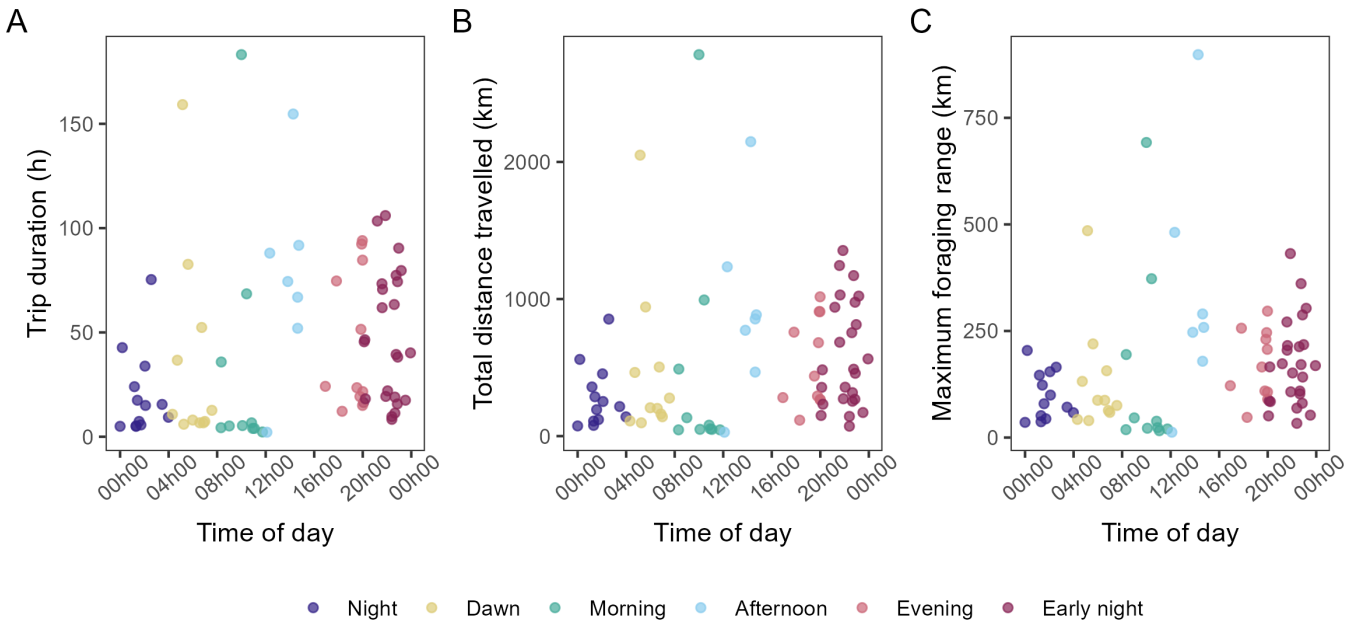


**Fig. 2.** Variation in Sooty Tern *Onychoprion fuscatus* (A) trip duration, (B) total distance travelled, and (C) maximum foraging range from Bird Island based on the time of day of departure for foraging trips of incubating adult GPS-tagged Sooty Terns, divided into 4-hr windows.

years that birds were tagged, 2016 to 2019), we saw no evidence of the nest desertions that were widespread in 2014. Thus, all birds tagged in 2016–2019 were actively breeding throughout the period that tags were deployed.

Most headings from Bird Island were in an arc from 180° (south) through westerly to 40° (north-northeast) (Fig. 3). These involved tracks over the Seychelles Bank to the south and over deeper water south of the bank to *ca*. 6°S, around the western edge of the Seychelles Bank, as well as tracks north to the southern end of the Coco-de-Mer Ridge at *ca*. 0°40′N (Fig. 1).

### Foraging Areas Used by Bird Island Sooty Terns

During incubation, foraging core areas extended over a range of depths, including the shelf break of the Seychelles Bank to deep water (~2,000 m), predominantly on its northern, western, and southern boundaries (Fig. 4). In 2016, however, one bird travelled to the region of, but not over, the Coco-de-Mer Ridge (Fig. 4).

When feeding young chicks, in 2016 tagged birds foraged over the shallow waters of the Seychelles Bank, with some of their core foraging area extending over deep water (Fig. 4). In 2017, adults feeding chicks showed a greater tendency to forage further from the colony over deep water to the north of Bird Island, with core areas including waters of depths of > 3,000 m (Fig. 4).

### Foraging Tracks of Mated Pairs

Of the five pairs of birds in which both members were fitted with tags in 2018, birds from only three nests provided tracks of both members (one of each of the other two pairs failed to provide any

**TABLE 1**
**Summary of foraging trips undertaken by breeding Sooty Terns *Onychoprion fuscatus* from Bird Island, Seychelles between 2014 and 2019**

| Year | Individuals | Trips | Trip duration (hr)[a] | Total distance travelled (km)[a] | Maximum foraging range (km)[a] |
|---|---|---|---|---|---|
| **Egg incubation** | | | | | |
| 2014 | 7 | 7 | 72.0 ± 0.4 (15.7, 183.2) | 974.8 ± 0.4 (150.3, 2,782.9) | 312.5 ± 0.2 (50.8, 898.3) |
| 2016 | 13 | 26 | 28.2 ± 0.1 (0.8, 103.4) | 346.3 ± 0.1 (10.2, 1,235.0) | 108.8 ± 0.1 (4.4, 481.4) |
| 2017 | 8 | 10 | 39.6 ± 0.3 (0.7, 159.2) | 487.0 ± 0.2 (7.7, 2,049.6) | 146.9 ± 0.1 (3.3, 485.2) |
| 2018 | 8 | 16 | 52.7 ± 0.2 (0.7, 92.3) | 601.5 ± 0.2 (8.2, 1,029.6) | 179.0 ± 0.1 (3.3, 372.6) |
| 2019 | 5 | 7 | 44.8 ± 0.3 (4.0, 77.4) | 635.9 ± 0.3 (53.1, 1,244.3) | 192.1 ± 0.1 (23.3, 361.0) |
| **Chick-rearing** | | | | | |
| 2016 | 1 | 8 | 20.0 ± 0.2 (5.2, 84.7) | 306.8 ± 0.2 (109.6, 1,016.2) | 108.9 ± 0.1 (51.4, 296.6) |
| 2017 | 5 | 9 | 26.2 ± 0.3 (2.2, 106.0) | 368.4 ± 0.2 (28.4, 1,354.0) | 124.5 ± 0.1 (12.5, 431.6) |

[a] Values are means ± standard error, with ranges included in brackets.

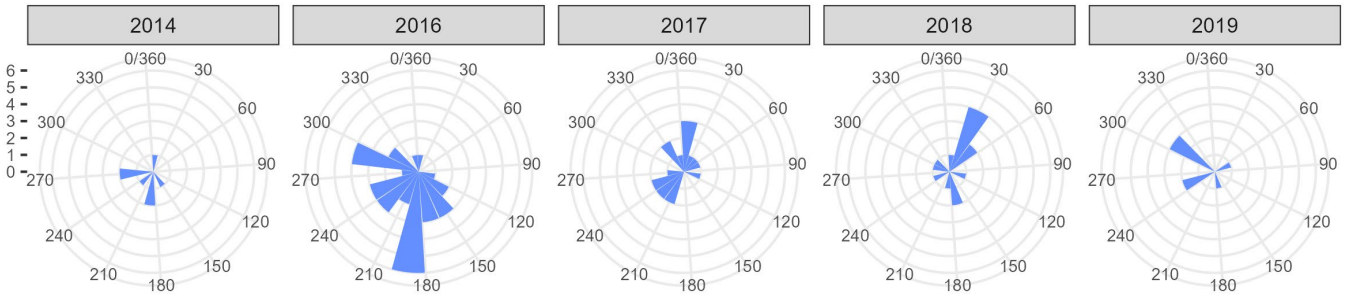


**Fig. 3.** Departure angles of Sooty Terns *Onychoprion fuscatus* to the distal points of their > 2-hr foraging trips from Bird Island, Seychelles during 2014 and between 2016 and 2019. The lengths of the blue wedges indicate the number of trips recorded for each heading in each year (marked as zero to six trips).

location data). In the three successfully tracked pairs, members foraged in different ocean areas (Fig. 5).

### Time of Feeding Bouts

The concentrations of activity indicative of feeding bouts occurred during both daytime and nighttime. However, as we programmed different recording schedules for day and night tracking (see Methods), we cannot quantify the relative frequencies of day and night feeding or compare the durations of diurnal and nocturnal feeding bouts.

## DISCUSSION

While Sooty Terns have been recorded feeding at night (Gould, 1967), possibly targeting potential prey that undertake nocturnal migrations to the surface (Schreiber et al., 2020; Spear et al., 2007), our tracking data indicate that breeding Sooty Terns on Bird Island commonly left the colony during the night. Most spatially concentrated activity was recorded during the day, suggesting that most feeding is diurnal. However, some spatially concentrated activity was also recorded during nighttime, suggesting some nocturnal feeding as well. Jaeger et al. (2017) found that foraging bouts, indicated from water sensors on geolocators deployed on Bird Island Sooty Terns, were significantly more frequent, and of longer duration, during day than at night. An advantage of daytime feeding could be the ability to locate temporary patches of abundant prey, generally small fish and squid driven to the surface by larger sub-surface predators (Maxwell & Morgan, 2013; Schreiber et al., 2020) through "local enhancement" (Bairos-Novak et al., 2015; Boyd et al., 2016). This involves the attraction of prospecting birds to groups already indulging in frenzied and conspicuous feeding over shoals of predators, especially tuna (Thunnini, subgrouping in Scombridae; Au & Pitman, 1986). This technique for locating food sources is visual and presumably most efficient during daytime feeding.

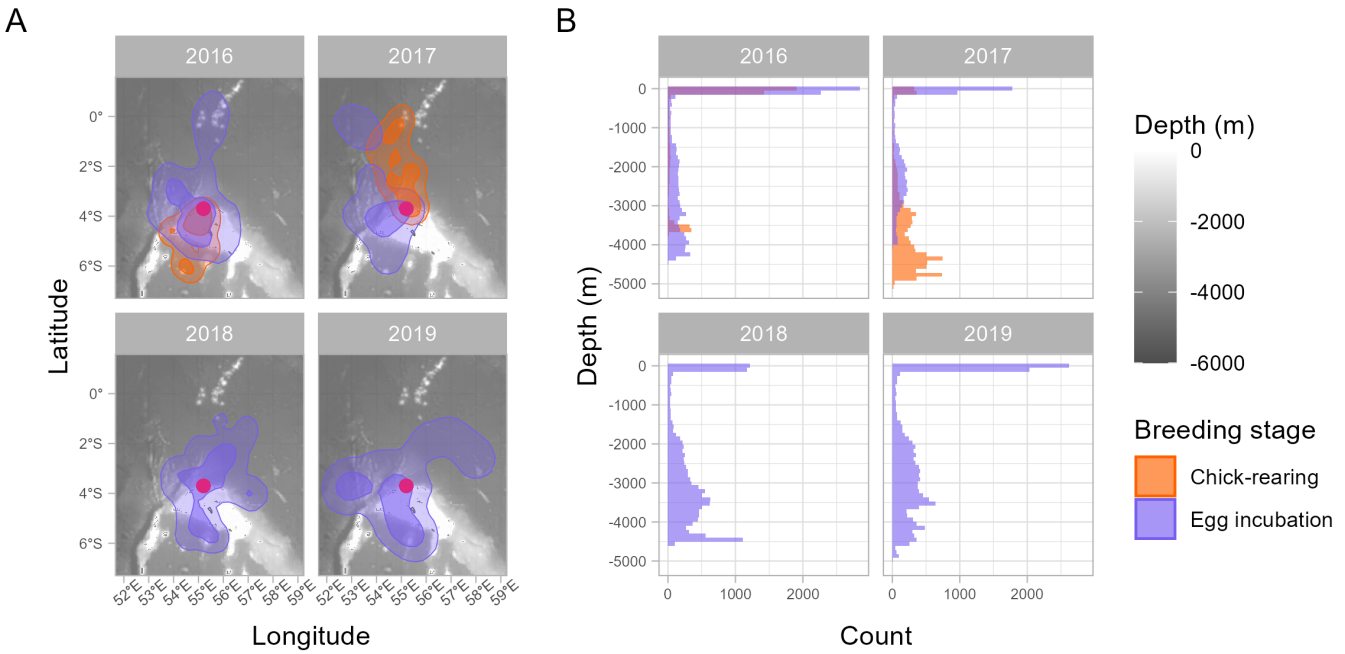


**Fig. 4.** Foraging areas and depths used by Sooty Terns *Onychoprion fuscatus* breeding on Bird Island, Seychelles during the egg incubation and early chick-rearing stages (1- to 4-day-old chicks) of the breeding season in four years (2016–2019). (A) 50% foraging areas (presumed active feeding; darker colouring) and 95% home range (search) areas of the birds (more translucent colouring), with Bird Island illustrated as a pink circle. (B) Histograms of the depths of sea that the birds foraged over (50% utilisation distributions). For sample sizes, see Table 1.

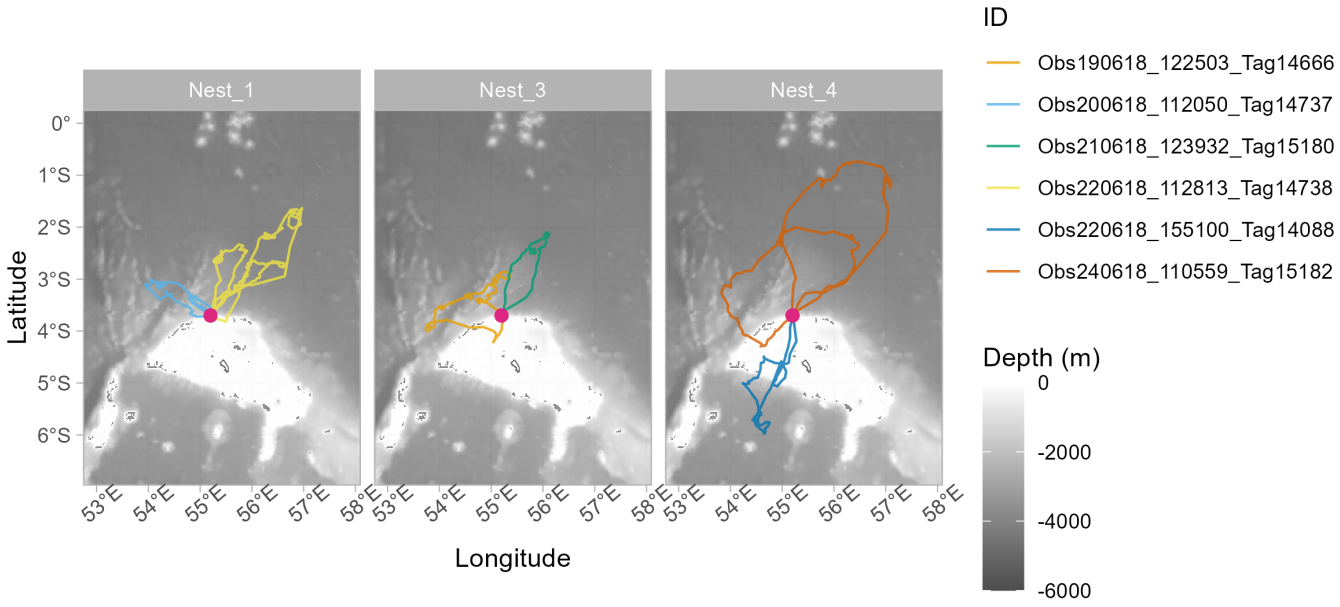


**Fig. 5.** Tracks of three pairs of incubating adult Sooty Terns *Onychoprion fuscatus* from Bird Island, Seychelles (pink dot), of which both members were fitted with GPS tags in 2018.

After leaving the colony, GPS-tagged birds undertook directional flights that were interspersed with more localised movements. The latter likely represented feeding bouts, including locally restricted searches and active feeding.

Most localised searching/feeding sites were around the northwestern, western, and southern edges of the shallow (< 100 m) Seychelles Bank where it drops to ~2,000 m depth. Most of these feeding/prospecting sites were within *ca*. 200 km of Bird Island. In 2016 and 2017 (and in our previous study in 2014; Neumann et al., 2018) we recorded longer tracks, largely to the north towards the Coco-de-Mer Ridge, a submarine range of seamounts, *ca*. 1°N and *ca*. 400 km from Bird Island (Fig. 4). This raises the possibility that Bird Island Sooty Terns, like some other pelagic birds, employ a dual foraging strategy, targeting prey of differing availability or nutrient values from different marine habitats (Clay et al., 2019; Shoji et al., 2015). However, our samples of tracks are too small to confirm this. In our earlier study (Neumann et al., 2018), we attributed long foraging trips to food shortage, but the present study shows that this is not necessarily the case. In 2014, the long-duration trips were accompanied by widespread desertions of eggs and young chicks in the colony and widespread chick deaths, but there was no widespread mortality in 2016–2019. The possibility that Sooty Terns normally undertake long trips to distant feeding areas periodically in the absence of food shortage suggests that adults may be familiar with distant food hotspots and use them to diversify diet in "good" food years—and also use them as emergency destinations during times of food scarcity.

The tropical Indian Ocean circulation is driven by seasonally reversing wind directions and resulting seasonally reversing surface currents (Schott & McCreary, 2001). During the southeast monsoon season, approximately May–September, southeasterly winds generate a westerly flowing Equatorial Current. This is forced northwards at the African coast, generating the northerly flowing East African Coastal Current and the northeasterly flowing Somali Current. The Somali Current and associated coastal gyres generate coastal upwelling of cool water and primary productivity that, at the peak of the season in July–August, extends eastwards towards the Seychelles Bank (Phillips et al., 2021). Additionally, the Seychelles Bank forms part of the Seychelles-Chagos Thermocline Ridge, where upwelling of nutrient-rich cool waters peaks in July–August (Castillo-Trujillo et al., 2021), leading to a seasonal increase in chlorophyll *a* concentration in surface waters (George et al., 2018). This seasonal productivity doubtless underlies the breeding of Seychelles' Sooty Terns during this season (Jaquemet et al., 2007). Even short-term variations in sea surface temperature (SST) have been shown to influence Sooty Tern foraging success, with enhanced provisioning of chicks during periods of cooler SST (Erwin & Congdon, 2007).

Further concerns emanate from the potential impacts of commercial fishing. Feeding Sooty Terns do not dive but commonly rely on large predatory fish to drive potential prey to the ocean surface; this makes them accessible to the foraging birds that take prey at or above the surface when small fish leap out of the water when attempting to avoid the predatory fish. Seychelles' artisanal fish catches, concentrated largely in shallower waters of the Seychelles Bank and the shelves into deeper ocean, are declining (Christ et al., 2020). These catches include sub-surface predators (e.g., tuna and mackerel [Scombridae] as well as jacks [Carangidae]), important to seabirds in driving prey fish and squid to or above the surface. Possibly of greater significance to Sooty Terns during their breeding season, while foraging in more distant ocean to the north of the Seychelles Bank, is the international commercial fishery that targets especially Yellowfin *Thunnus albacares*, Bigeye *T. obesus*, and Skipjack *Katsuwonus pelamis* Tuna and is concentrated in the western Indian Ocean (Pillai & Satheeshkumar, 2012). This fishery is considered to be overfished (Andriamahefazafy et al., 2020), but the impact of this on Seychelles' Sooty Terns remains to be determined. In the tropical Atlantic Ocean, however, overfishing of tuna is thought to underlie a decline in Sooty Tern breeding populations on Ascension Island and changes in their prey (Reynolds et al., 2019).

Overfishing of tuna by commercial fisheries impacts Sooty Terns indirectly, through the depletion of populations of large fish predators that drive their smaller fish prey to the ocean surface, rendering these small fish available to Sooty Terns. This differs from the direct effects of overfishing of smaller shoaling fish (e.g., Small Sandeels *Ammodytes tobianus* and Great Sandeels *Hyperoplus lanceolatus* taken by diving seabirds in the northeast Atlantic [Furness, 2007], Anchoveta *Engraulis ringens* in the Peru Current [Gozzer-Wuest et al., 2021], and Pacific Sardines *Sardinops sagax* in the Benguela Current [Grémillet et al., 2010]). Depletion of formerly abundant large predatory fish through overfishing might theoretically release populations of smaller fish from predation, leading to increases in their populations; however, decreases in their availability to Sooty Terns if they remain too deep could counter any such benefits.

Most of the foraging areas that we identified fell within the Seychelles Exclusive Economic Zone (EEZ), which extends north of Bird Island to the southern end of the Coco-de-Mer Ridge (Ronconi et al., 2023; Fig. 1). Individuals that travelled > 370 km from Bird Island to northern parts of the Coco-de-Mer Ridge (Fig. 4A)—and one individual that flew west into the Somali Basin in 2014—left areas under Seychelles' jurisdiction during the breeding season. However, while birds that forage over the Seychelles Bank do so within Zone 2 of the marine protected area (MPA; Zone 2 allows sustainable use), defined in the Seychelles Marine Spatial Plan (Ronconi et al., 2023; Fig. 1), most of the birds that foraged to the north and west of Bird Island do so outside the MPA. All the foraging locations detected during the GPS tag deployments fell outside the small Zone 1 ("High Biodiversity Protection Area") rectangle centred on Bird Island (inset on Fig. 1), and foraging Sooty Terns would, therefore, derive no benefit from this protected area.

## ACKNOWLEDGEMENTS

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