Foraging ranges of incubating sooty terns onychoprion fuscatus on Bird Island, Seychelles, during a transition from food plenty to scarcity, as revealed by GPS loggers

FORAGING RANGES OF INCUBATING SOOTY TERNS *ONYCHOPRION FUSCATUS* ON BIRD ISLAND, SEYCHELLES, DURING A TRANSITION FROM FOOD PLENTY TO SCARCITY, AS REVEALED BY GPS LOGGERS

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Received 30 May 2017, accepted 25 September 2017

ABSTRACT

NEUMANN, J.L., LAROSE, C.S., BRODIN, G. & FEARE, C.J. 2018. Foraging ranges of incubating Sooty Terns *Onychoprion fuscatus* on Bird Island, Seychelles, during a transition from food plenty to scarcity, as revealed by GPS loggers. *Marine Ornithology* 46: 11–18.

The foraging tracks of incubating Sooty Terns, nesting on Bird Island, Seychelles, were identified using global positioning system (GPS) loggers attached to the central pair of rectrices. By chance, our 2014 study covered a transition from food abundance to shortage. Incubation shifts during food abundance were mainly 1–2 d long but, at the height of food shortage, ranged from 4 d to 13 d, leading to temporary and permanent nest desertion by individuals left caring for the egg. The duration of foraging trips and the distance travelled also increased, from 151 km to 271 km for birds absent for 1–3 d, to 2 142–2 779 km by birds that were away from the colony for 4–10 d. This technique, coupled with spatial analyses that relate track paths and foraging locations to bathymetry, sea surface temperature, and chlorophyll levels, permitted more detailed investigations of the breeding birds' use of their oceanic habitats. It also provided data to support and define areas to be recommended for Marine Protected Area status in Seychelles and elsewhere.

Key words: bathymetry, chlorophyll concentration, food shortage, GPS tracking, *Onychoprion fuscatus*, Sooty Tern, seabird foraging, sea surface temperature, Seychelles

INTRODUCTION

Sooty Tern *Onychoprion fuscatus* is the world's most numerous tropical oceanic avian species (Schreiber *et al.* 2002). As such, these birds could be valuable sentinels for anomalies in their oceanic environment. Knowledge of their feeding areas, and changes to these areas, could be informative at two scales: on a broad oceanic realm when the birds migrate away from their nesting colonies in the non-breeding season, and on a more local scale when they are constrained to the vicinity of the breeding colony to incubate eggs and feed young. The latter will be important for the designation of Marine Protected Areas.

Much is known about Sooty Tern biology within breeding colonies (Ashmole 1963, Harrington 1974, Feare 1976, Schreiber *et al.* 2002, Jaquemet *et al.* 2007, Hughes 2014) but, until recently, little has been known about their life at sea (Jaquemet *et al.* 2008). When nesting, both sexes share incubation of the single egg, and incubating birds can lose 10% of their body mass per day (Feare 1976, Flint 1991). During this phase of the breeding cycle, when adults have to collect food only for their own requirements, we would expect foraging trips to be as short in time and distance as possible. Flint (1991) estimated, based on time and energetic considerations, maximum foraging ranges for adults brooding young (290 km) and adults feeding larger chicks (522 km).

Ashmole (1963), studying Sooty Terns on Ascension Island (South Atlantic), concluded that their long incubation shifts, averaging *ca.* 5.5 d, indicated that they had to travel long distances to procure food. Feare (1976), on the other hand, found that Sooty Terns on Bird Island, Seychelles (3°43′S, 55°12′E) in the Indian Ocean, generally had much shorter incubation shifts, 1–2 d, suggesting that their food sources were closer to the colony.

Miniaturization of tracking devices has allowed the distribution of Sooty Terns at sea to be studied (Soanes *et al*. 2015; Jaeger *et al.* 2017). The advent of very small and light global positioning system (GPS) tracking devices permits identification of feeding areas used by breeding seabirds. This technique also facilitates examination of the relationship between the duration of incubation shifts and distance travelled on foraging trips (Ashmole 1963). Here, we describe the use of GPS loggers to determine, for the first time, where Sooty Terns that nest on Bird Island, Seychelles, forage while their mates are incubating. By chance, this study, conducted in June–July 2014, spanned a transition from 1–2 d foraging trips to exceptionally long ones that lasted <13 d, which we conclude was a response to a period of extreme food shortage.

METHODS

Incubation shift duration

In an area of the colony dominated by *Portulaca oleracea*, the vegetation type preferred by Bird Island's Sooty Terns (Feare *et al.* 1997) and in which their legs can be clearly seen, the locations of 12 nests were marked with numbered plastic garden labels. (Previous experience had shown that birds readily accepted such markers.) Incubating birds were ringed on 18 June 2014 (with British Trust for Ornithology alloy rings) on the right leg. Incubation shift duration was measured by recording, at 07h00 daily, the identity of the incubating birds (both ringed and unmarked). Monitoring of the incubation shift durations of these birds continued until the eggs hatched (8–12 July). When working GPS tags were deployed, beginning 3 July, incubation shifts of these birds and their mates were monitored by daily nest visits to check the identity of the incubating birds; tagged birds were given orange Darvic rings, uniquely engraved with letters, while the untagged birds were unmarked.

Identification of food shortage

Breeding Sooty Terns on Bird Island normally alternate incubation duty every 1–2 d (Feare 1976). During incubation, especially during hotter parts of the day, they occasionally leave the egg briefly to fly to the sea immediately offshore to drink, returning after a few minutes. Apart from this, they are highly attentive. Disturbance to incubating birds can stimulate regurgitation of food (Feare 1975, 1976; Soanes *et al.* 2015). Such disturbance can be caused by fighting between adjacent pairs or defense against intruders. Human disturbance, walking through the colony or especially handling birds, also promotes regurgitation. Such disturbances are evidenced by dried regurgitations found on the ground. Prolonged absences of incubating or brooding birds, manifested by large numbers of unattended eggs or dead young, and failure of any bird to regurgitate on disturbance, are thus indicative of food shortage (Ashmole 1963, Feare *et al.* 2015).

GPS tags

The tags selected were PathTrack Nanofix GEO+ (www.pathtrack.co.uk). They weigh *ca.* 3 g (*ca.* 1.7% of the mass of an incubating Sooty Tern of *ca.* 180 g) and measure 25 mm × 10 mm × 8 mm. Dorsal solar panels recharged the battery, and a posterior 50 mm antenna received satellite signals. Tags were set to record locations every 10 min from 05h30 to 19h30 and hourly overnight. (Earlier studies using geolocators showed that Sooty Terns fed little during the night; Jaeger *et al.*, 2017). In practice, there were occasional breaks in location recording when insufficient satellites (four or fewer) could be detected for a reliable fix, and one tag had longer gaps with intermittent recording, suspected to have been caused by water ingress. Geographic locations recorded by tags are accurate to *ca.* 20 m (PathTrack, unpubl. data).

In addition to horizontal locations, the loggers also provide a GPS-derived altitude measurement. However, the altitude recorded by GPS relates to the reference ellipsoid, a smoothed model of global sea level. This is not the same as the true sea level (called the geoid), which is far more irregular, due to the influence of local variations in the earth's gravitational pull. There are different methods of determining the offset between the reference ellipsoid and the geoid; in practice, measurements are taken directly at certain points on the earth's surface, and geodetic heights between these points are estimated by interpolation (Moritz 2011). In the western Indian Ocean, the reference ellipsoid is *ca.* 20–60 m above the geoid or actual mean sea level (NCAOR 2015). Furthermore, actual sea level is variable, under the influence of tides, currents, wind, and atmospheric pressure (Singh & Aung 2005). As a result, GPS measures of altitude of Sooty Terns flying over the sea are subject to spatial variations in the relationship between the reference ellipsoid and the geoid and to temporal effects on actual mean sea level. These influence the confidence for fine-scale variations in apparent altitude of Sooty Terns over the sea surface. Thus, in this paper, we only make general statements about flight altitude.

Tags were attached to the bases of the central pair of rectrices using Tesa tape (Soanes *et al.* 2015, Feare & Larose 2015). The total weight of tag and tape was *ca.* 3.6 g (*ca.* 2% of adult body mass of 180 g, the lightest Sooty Tern on which we put tags).

Between 3 and 18 July, GPS tags were deployed on 14 incubating Sooty Terns. All the birds returned to their nests and were caught as soon as they were seen, but six birds that had been absent for seven or more days returned without their tags. In one bird, one central rectrix was missing and the other was broken off proximal to the attachment site of the tag; in all other birds that returned without tags, both central rectrices were broken in the same position (as found also by Soanes *et al.* 2015). Birds were weighed when tags were fitted and on subsequent recapture.

Mapping tracks to identify foraging areas and their relationship to oceanographic factors

ArcMap 10.1 (ESRI, 2011) was used to map the tracks taken by Sooty Terns, using latitude and longitude coordinates downloaded from the tag records. The tracks were displayed as points (where each point corresponded to a tag fix in sequential date–time order) and then converted to lines. Areas where birds were recorded spending prolonged periods of time and making short "hops" around a localized area (i.e., a greater density of points in close spatial proximity) were considered putative foraging areas. Transition flight between foraging areas was identified by longer distances between fixes, with movement maintained in a certain direction. Point density, illustrating higher concentrations of fixes, was mapped for each track using the Kernel Density function in ArcMap 10.1.

In Seychelles, Sooty Terns breed seasonally, from May to October, when the islands are subject to southeast trade winds (Feare 1976). This seasonality has been linked to an annual decrease in sea surface temperature (SST) and an increase in primary production (indicated by chlorophyll concentration in surface waters) at this time (Jacquemet *et al.* 2007). Surface feeding conditions can also be influenced by underwater structures, such as sea mounts, which can generate upwellings of cooler water (Pitcher *et al*. 2007), and by convergences of different currents, where turbulence can also bring nutrients to the surface.

We overlaid the GPS tracks on basemaps showing bathymetry (GEBCO 2014), sea surface temperature (SST; NEO 2017a), and

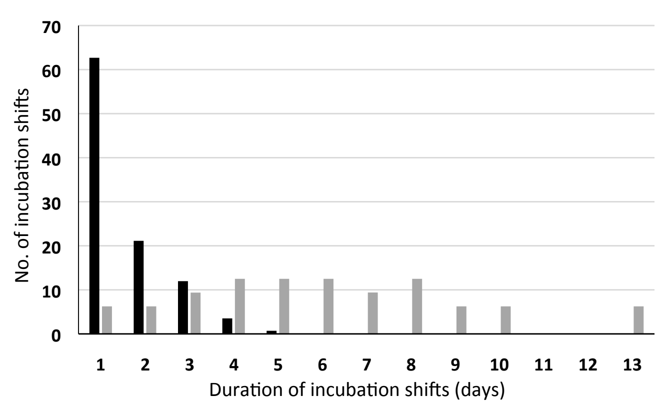

Fig. 1. Frequency distribution of foraging trips lasting 1–13 d during the periods 18 June–8 July (black bars), and 9–23 July (grey bars) 2014 (Mann–Whitney U = 130, P = 0.019).

chlorophyll concentrations (NEO 2017b), to view the relationships between these factors and bird feeding behavior (Jaquemet *et al.* 2007). We also investigated possible effects of wind speed and direction using data for Seychelles from ERA-Interim (Dee *et al.* 2011) and Windfinder (2017).

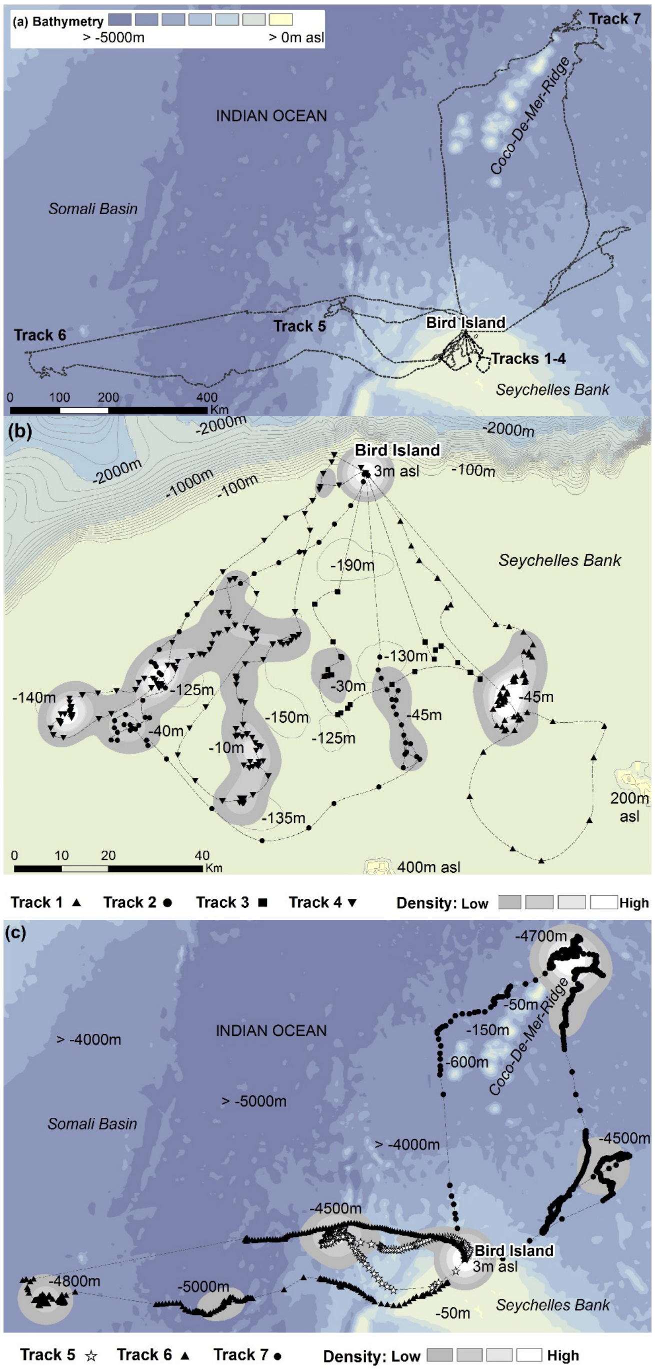

Fig. 2. Tracks obtained from incubating Sooty Terns, with dates of departure given in Table 1. (a) Location of all seven tracks overlaying ocean bathymetry during food abundance (tracks 1–4) and food shortage (tracks 5–7). (b) Kernel density of track fixes for tracks 1–4, showing putative foraging areas during times of food abundance. (c) Kernel density of track fixes for tracks 5–7, showing putative foraging areas during times of food shortage. For track 6, location was recorded only intermittently, probably as a result of water ingress into the logger.

The work was undertaken under Seychelles Bureau of Standards permit A0157.

RESULTS

Incubation shifts

Incubation shift durations increased during the investigation from 1–2 d (median 1 d, $n = 86$) during 18 June–8 July, to 4–13 d (median 7 d, $n = 16$) during 9–23 July (Fig. 1).

GPS tracks

Seven foraging-trip tracks were obtained from tagged birds. Four birds were tagged before departure on a foraging trip between 3 and 5 July, and three birds were tagged before departure between 9 and 12 July (Table 1). These two groups of birds undertook journeys that differed greatly in duration and distance (Fig. 2). The four birds that departed 3–5 July all foraged over the shallow waters of the Seychelles Bank, to the south of Bird Island (water depth: 30–140 m; Fig. 2b). The bird in track 5 left the Seychelles Bank, foraging over deep water (<4 500 m) to the west. Tracks 6 and 7, in which birds were absent for *ca.* 7 and *ca.* 10 days, followed entirely different routes: one to the west, the other a rectangular pattern to the north and northeast that also involved back-tracking. Distances travelled per foraging trip ranged from 151 km to 2 779 km (Table 1), and the duration of the foraging trips was clearly related to the total distance travelled ($r^2 = 0.94$, $P < 0.001$) and to the maximum distance from Bird Island ($r^2 = 0.94$, $P < 0.001$).

According to track fixes, all seven birds, regardless of the length of their journey, spent at least one full day at the start and at the end of their trip on Bird Island, presumably incubating most of that time but probably also flying briefly to nearby sea to drink (Feare 1976). This indicates that birds were caught partway through their incubation shifts, awaiting the return of their partners. The four birds that foraged locally over the Seychelles Bank spent 30%–60% of their time over land (Table 1) and departed to forage at a similar time in the early morning; the first fix over water was recorded at around 01h00 in all cases. For tracks 1 and 2, both birds departed the island in the early hours on July 4 and returned between 14h00 and 15h00 the same day. The bird in track 3 departed a day later, on 5 July, and was back over land by

TABLE 1
The date of tagging, trip duration, distance travelled, and percent time spent on Bird Island by the seven incubating Sooty Terns in 2014

Track no.	Date of departure	Trip duration	Total trip distance (km)	Max. distance from island (km)	Time spent on island (%)
1	3 July	1 d, 21 h, 50 min	263	91	49
2	3 July	1 d, 23 h, 56 min	271	81	59
3	4 July	1 d, 4 h, 38 min	151	52	60
4	5 July	2 d, 23 h, 30 min	358	87	30
5	9 July	4 d, 1 h, 53 min	853	289	24
6	9 July	7 d, 0 h, 52 min	2 142	895	15
7	12 July	9 d, 23 h, 59 min	2 779	691	16

09h00. The track 4 bird departed just after 01h00 on 6 July, returning at 15h00 on 7 July. The birds in tracks 5–7 spent proportionately less time on land after tagging (15%–24%; Table 1) and had no consistent departure time. They did not return to Bird Island until the end of their journey, suggesting that we caught them soon after their return.

The seven tracks involved 1 892 fixes. Most (94.8%) of the altitudinal records were below the reference ellipsoid, with 97.1% of them >20 m below it. With the reference ellipsoid being 20–60 m above mean sea level in this part of the western Indian Ocean (see Methods), this suggests that foraging Sooty Terns fly low over the water, probably below 40 m, but we cannot be more precise. Of the 92 fixes above the reference ellipsoid, 33 involved records of two to four consecutive fixes, possibly representing sustained flights up to *ca.* 200 m above mean sea level.

The birds provided with GPS tags had a wide range of change in body mass between tagging and recapture, from a loss of 48 g to a

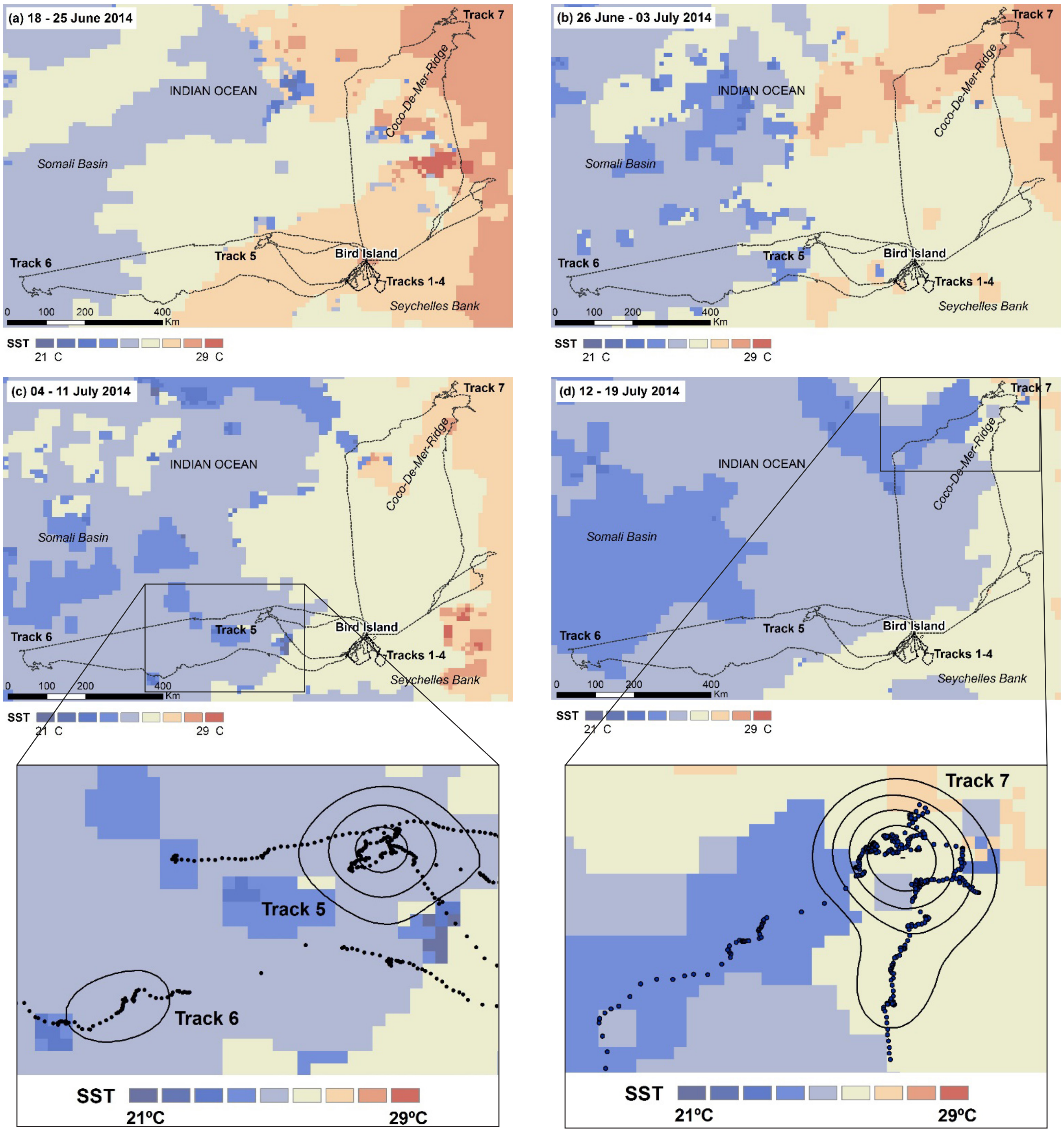

Fig. 3. (a–d) Tracks obtained from incubating Sooty Terns overlaying the 8 d average SST for four periods between 18 June and 19 July 2014. Inset maps for (c) and (d) illustrate the relationship between high-density areas for tracks 5–7 and small pockets of cooler and variable SST during the week of departure.

gain of 23 g, with an average of 7.9 g lost. There was no significant relationship between weight change and the duration of the interval between tagging and recapture (ANOVA $F_1 = 0.04$, $P = 0.84$).

Foraging patterns

The Seychelles Bank appeared to offer at least three locally important foraging areas between 4 and 7 July (Fig. 2b). Birds did not fly the same routes, nor did they appear to feed concurrently at the same locations, suggesting multiple sites of food abundance at this time. Track 4 was the first bird to depart the island for more than 24 h; the circuitous route taken displays a number of sites of higher-density fixes, suggesting that it took longer to procure food as availability decreased. Tagged birds departing from 10 July onwards largely avoided the Seychelles Bank, opting to feed over deeper ocean waters (Fig. 2c). Upon departure, birds in tracks 5 and 6 initially passed over the western bank, where fixes from tracks 2 and 4 had indicated foraging in previous days. However, density analysis reveals that they did not stop here. The bird with track 7 flew directly to the north side of the Coco-De-Mer Ridge, where it spent more than 72 h over deep water (Fig. 2c).

Between 18 June and 19 July, SST decreased over the Seychelles Bank and in the wider ocean; this trend was not linear (Figs. 3–5). Cooling was most pronounced in the western ocean (Fig. 3). For birds foraging over the Seychelles Bank, inspection of SST maps (Fig. 4) shows that the bird with track 1 foraged southeast of Bird Island, close to where SST was markedly cooler, in the week before departure (26 June–3 July; Fig. 4b). For tracks 2–4, the greatest density of fixes was to the southwest, where SST ranged from 25.9 °C to 26.8 °C, equaling the minimum and maximum SST values for 4–11 July (Fig. 5). For birds departing after 10 July, tracks 5–7 also suggest that birds travelled toward and foraged near areas with small pockets of cooler water and variable SST (see inset maps on Fig. 3).

Over the Seychelles Bank, chlorophyll concentrations were higher in July than in June (Fig. 6), and in July a corridor of higher concentration extended from Seychelles to the west, along which birds 5 and 6 appear to have flown. Bird 7 tracked northwest toward the leading edge of a band of increased chlorophyll concentration in the Indian Ocean (Fig. 6), but fed closer to the Coco-De-Mer Ridge, where the concentration was lower.

Unpaired *t*-tests performed on daily 10 m wind component records (Dee *et al.* 2011) showed no significant change in wind speed between the dates of departure and for the duration of each trip: tracks 1–4 mean 6.82 m/s, standard deviation (SD) 2.56; tracks 5–7 mean 7.23 m/s, SD 2.57, $t_{132} = 1.43$, $P > 0.1$. Dominant wind direction was consistent (southeast) during this period, and wind speed and direction were usual for the time of year in Seychelles (Windfinder 2017).

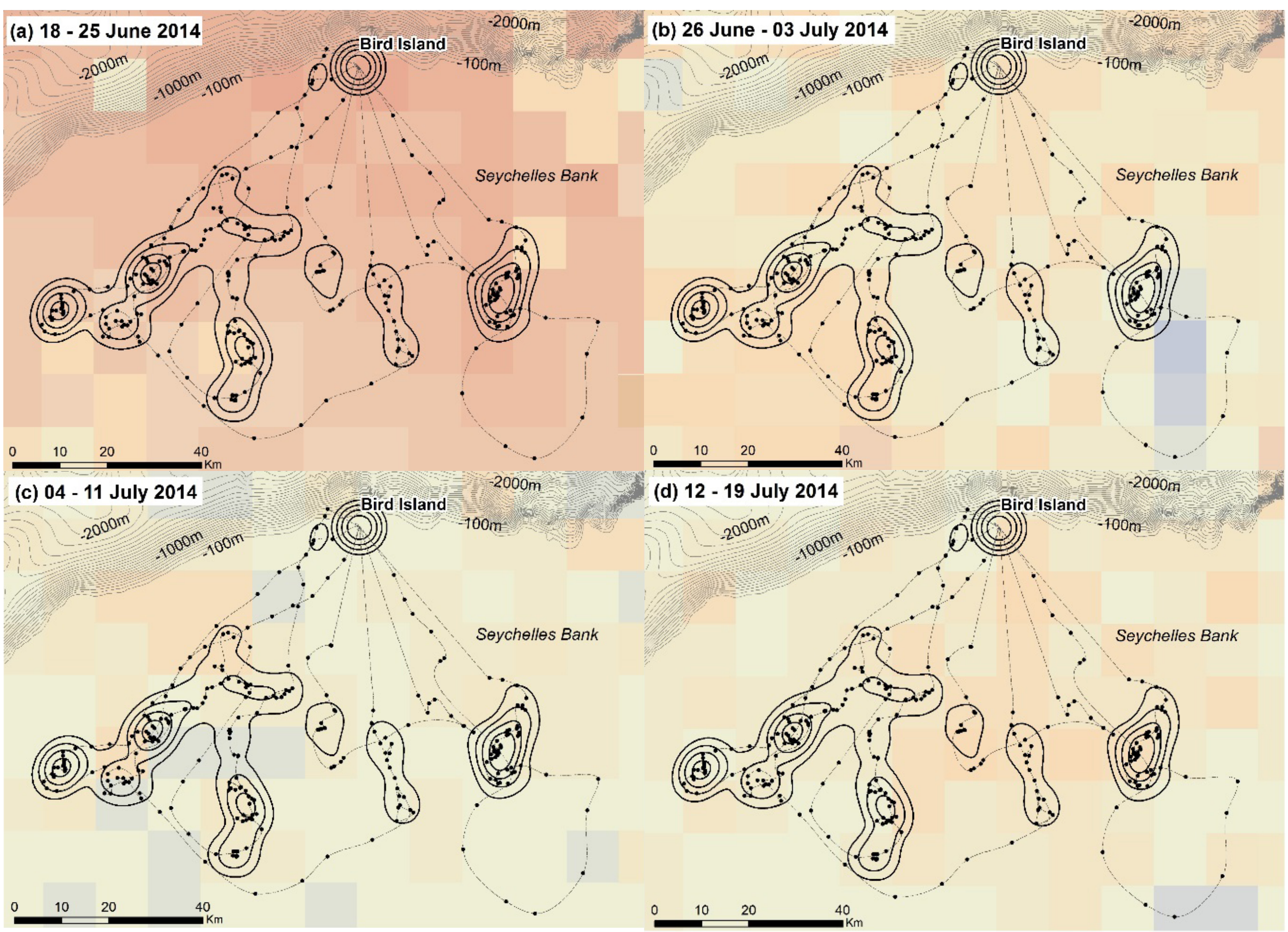

Fig. 4. Tracks obtained from incubating Sooty Terns foraging over the Seychelles Bank during food abundance (tracks 1–4), overlaying the 8–d average SST for four periods (a–d) between 18 June and 19 July 2014.

DISCUSSION

Although we obtained GPS tracks from only seven foraging Sooty Terns in 2014, these tracks revealed an apparently abrupt change in foraging behavior. This involved a switch from feeding within 100 km to the south of the Bird Island colony over the shallow waters (10–150 m depth) of the Seychelles Bank, to much longer trips, in both time and distance, when they fed over deeper water (4500–5000 m) of the western Indian Ocean, to the north and west of the breeding colony (Fig. 2). The longer absences of incubating adults after the switch (Fig. 1) resulted in abandonment of eggs and recently hatched chicks, signifying that the change in foraging behavior imposed a high cost on parental care. These longer incubation shifts, together with the failure of adults to regurgitate food when handled by us or disturbed during intraspecific interactions within the colony, pointed strongly to a food shortage beginning around 7 July and suggested that food availability over the Seychelles Bank had collapsed.

At about the time of the switch, the SST index for the western tropical Indian Ocean fell sharply by *ca.* 0.8 °C, but recovered within three weeks (The state of the ocean climate 2014). This is apparent in the SST records in Fig. 5, which indicated a decline in SST on the Seychelles Bank but a decline with some recovery over the wider western Indian Ocean. However, although Fig. 4 confirms a general cooling of SST over the Seychelles Bank over the period of study, there is nothing in the finer-scale SST records in Figs. 4 and 5 to account for a sudden collapse in food supplies over the Seychelles Bank. The June and July chlorophyll concentration distribution (Fig. 6) likewise gave no indication of an anomaly on the Seychelles Bank during this period. However, tracks 5 and 6 showed birds travelling over and feeding in areas of higher chlorophyll to the west of Seychelles, while track 7 passed through an area of higher chlorophyll concentration before feeding to the north of the Coco-De-Mer sea mounts, where chlorophyll concentrations were lower. The more distant journeys to the north and west by birds in tracks 5 to 7 take them closer to the Somali upwelling region, the surface outflow from which produces lower SST and higher chlorophyll concentrations, spreading into the northwest Indian Ocean (deCastro *et al.* 2016).

When food was plentiful, departure of birds to the south in the mornings (readily visible from the island's west coast) and arrival from the south in the evenings were conspicuous features of Sooty Tern behavior on Bird Island, as they have been most years since CJF began studying them in 1972. During the food shortage, this southerly commuting ceased; movements were less coordinated and were to the north and west. In 2008, northerly departures were also observed; in that year, 62 incubation shifts of ringed birds ranged from 1 d to 12 d, median 5 (CJF and Naomi Doak, unpubl. data), much longer than the 234 shifts that ranged from 1 d to 5 d, median 1, in 1973 (Feare 1976). Departure and arrival directions on Bird Island might thus be indicative of periods of relative food abundance (over the Seychelles Bank) or shortage and could be used as a quick assessment of feeding conditions each breeding season.

We do not know whether the reduction in food availability was mediated through (1) a change in the abundance, behavior, or distribution of potential prey that put them out of reach for surface-feeding Sooty Terns (Ashmole & Ashmole 1967, Schreiber *et al.* 2002), or (2) a change in the distribution of predatory fishes that drive smaller fish to the surface, only then making them available to Sooty Terns (Au & Pitman 1986, Le Corre & Jaquemet 2005).

The 2014 food shortage event that affected Sooty Terns was short-term and did not appear to have affected Brown *Anous stolidus* or Lesser Noddies *A. tenuirostris*, both of which continued to

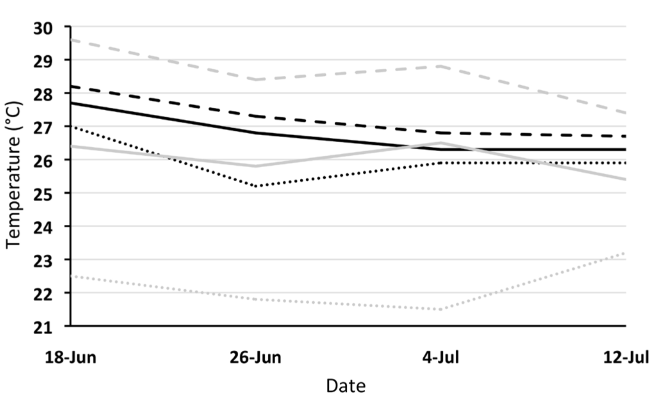

Fig. 5. Maximum (dashed line), minimum (dotted line), and mode (solid line) 8 d SST recorded over four weeks. Black lines represent SST values from the Seychelles Bank (in vicinity of tracks 1–4). Grey lines represent SST values from the wider ocean (in vicinity of tracks 5–7).

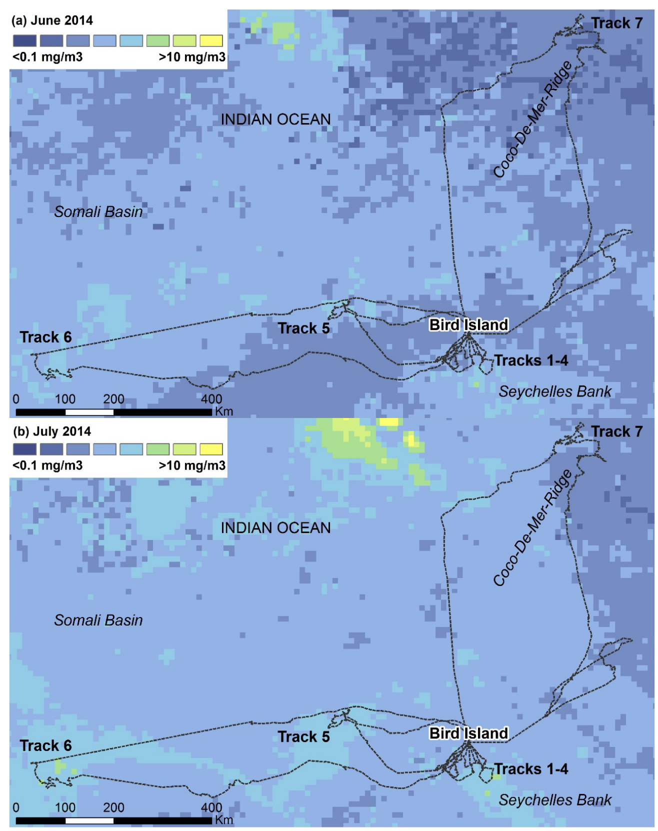

Fig. 6. Tracks obtained from incubating Sooty Terns overlaying the monthly average chlorophyll concentration for (a) June 2014 and (b) July 2014. Missing data (9% for June and 7% for July 2014 datasets) were calculated using an average for that month from the previous five years.

regurgitate food when handled for another investigation (C. Lebarbenchon, pers. comm. and CJF & CSL, pers. obs.) during the Sooty Tern food shortage. During the 1973 breeding season on Bird Island, Feare (1976) recorded two brief periods of weight loss of large chicks, which he attributed to food shortage, and also recorded periodic sharp changes in the species and size of prey being brought to the chicks, suggesting that brief food shortages are not exceptional. Catry *et al.* (2013) documented two kinds of food shortage experienced by the seabird community in Seychelles: (1) short-term events affecting just a few seabird species, for which the cause was unclear, and (2) longer-term events affecting all species, related to large-scale events such as El Niño–Southern Oscillation and swings in the Indian Ocean Dipole. The food shortage that was associated with tracks 5–7 in this study was an example of former.

Due to the uncertainties inherent in the altitude records, we cannot determine precisely how high Sooty Terns fly above the sea surface during their foraging flights. Our data suggest that they generally fly low, probably <40 m, and that sustained flights at higher altitude are rare. This suggests that, on long foraging trips, they do not take advantage of thermals to rest while soaring; in fact, the only evidence of this was one bird whose last four fixes were 50–100 m above the reference ellipsoid just before returning to the breeding colony. Here, towers of circling Sooty Terns often circle off the northwest coast of the island, which is downwind of the colony, and these birds are likely taking advantage of thermals generated by the island. At sea, Sooty Terns might be able to reduce energy expenditure by dynamic soaring, taking advantage of variations in wind shear above the ocean surface, as described by Richardson (2015) for albatrosses. In the Eastern Tropical Pacific, however, D. Ainley (pers. comm.) recorded Sooty Terns soaring in thermals higher than our data suggest and also reported them circling in flapping flight over schools of predatory fish, suggesting that flight behavior can be flexible according to local conditions and stage of the life cycle.

The distances travelled by foraging birds during food abundance were within the theoretical limits derived by Flint (1991) for adults with chicks, but, during the food shortage, the distances covered greatly exceeded these limits. If adult Sooty Terns are able to minimize energy expenditure on long flights by dynamic soaring, this could account for the lack of a significant mass loss in relation to the duration of foraging trips. However, prolonged foraging trips undoubtedly compromised the efficiency of parental care. Eggs and chicks that were unprotected by adults were left exposed to direct sun in the hotter parts of the day, and young chicks received inadequate food.

Despite the small number of tracks obtained to date, this study has demonstrated the potential for accurate tracking devices to improve our knowledge of Sooty Terns' lives at sea and the factors that influence their behavior and survival. Furthermore, information on preferred foraging locations at all stages of the breeding season, and alternatives in times of food shortage, for all of the seabird species breeding in Seychelles (Cecere *et al.* 2013) will provide pointers to areas that should be recommended as Marine Protected Areas within the archipelago. However, our data from tracks 6 and 7 showed that, during food shortage, these birds fed in areas beyond the limits of the Seychelles Exclusive Economic Zone and thus not under Seychelles jurisdiction.

ACKNOWLEDGEMENTS

This work was made possible by the generous financial support of the British High Commission (Seychelles, though Commissioner Lindsay Skoll), James Cadbury, the Percy Sladen Memorial Fund and U3A Haslemere, UK. Excellent logistical support was provided by the owners of Bird Island, Guy and Marie France Savy, in the planning and practical phases of the project. We are also grateful to Camille Lebarbenchon and Muriel Dietrich for assistance in the field and discussion, and to two anonymous reviewers and the editor for helpful suggestions. Gary Brodin is a Director of PathTrack Ltd.

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