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Geolocation Reveals Year-Round at-Sea Distribution and Activity of a Superabundant Tropical Seabird, the Sooty Tern *Onychoprion fuscatus*

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Migration is a fundamental aspect of the ecology and evolutionary history of many animals, driven by seasonal changes in resource availability and habitat structure. Seabird migration has been investigated extensively in highly seasonal temperate and polar environments. By contrast, the relationships between migration and seasonal environmental changes have rarely been studied in tropical marine habitats. The sooty tern *Onychoprion fuscatus* is the most abundant tropical seabirds, and has been ranked as the most important tropical species in terms of its annual estimated consumption of marine resources. We used global location sensing (GLS loggers) to describe for the first time the year-round at-sea distribution and activity patterns of sooty terns from a large breeding colony in the western Indian Ocean (Bird Island, Seychelles). While breeding, they foraged within $1,074 \pm 274$ km of the colony. After breeding, birds undertook an extensive post-breeding migration throughout the Indian Ocean; average distances traveled exceeded 50,000 km per individual. Sooty terns used mainly four distinct core oceanic areas during the non-breeding period; in the Bay of Bengal (A), northeast to an area straddling the Chagos-Laccadive plateau (B), southeast to an area on each side of the 90 East Ridge (C) and southwest to an area around Comoros (D). Individuals exhibited a high degree of fidelity to these core areas in successive years. We also established that they performed an unusual behavior for a non-Procellariiformes seabird; most individuals undertook a 1-month pre-laying exodus, during which they foraged in a specific area c. 2,000 km to the south-east of the colony. Year-round at-sea activity of sooty terns revealed that they spent only 3.72% of their time in contact with seawater, so indicating that they must sleep in flight. Activity parameters exhibited seasonal (breeding vs. non-breeding periods) and daily variations; they notably never land on the water at night. In the Seychelles, breeding sooty terns are threatened by commercial egg harvesting. Our discovery of extremely wide non-breeding at-sea distribution highlights the risk of other threats during their non-breeding period, such as over-fishing, marine pollution and climate change.

Keywords: at-sea distribution, at-sea activity, GLS, non-breeding, pre-laying, sooty tern, Indian Ocean, seabird

INTRODUCTION

Animals from groups as diverse as mammals, birds, fish, and insects migrate across different spatial and temporal scales to cope with cyclic changes in resources and habitats (Wassenaar and Hobson, 1998; Egevang et al., 2010; Block et al., 2011). Animal migration represents a fundamental aspect of their ecology and evolutionary history, and contributes in a major way to ecosystem functioning (Bauer and Hoyer, 2014; Dingle, 2014). Unraveling patterns of migration is thus essential for our understanding of the ecology, life history, and behavior of most animals (Nathan et al., 2008). Studying animal movements, particularly those of small species, is a difficult logistical and engineering challenge. Researchers have recently made considerable technological progress to track the distribution of individual animals (Bridge et al., 2011), but the movements of some species, even keystone species that have central roles in ecosystems, remain little known.

The sooty tern *Onychoprion fuscatus* is the most abundant tropical seabirds, with a global population estimated at 60–80 million birds (Schreiber et al., 2002). It nests in dense colonies, sometimes involving more than 1 million pairs (Feare et al., 2007), on islands scattered throughout the tropical Atlantic, Pacific and Indian Oceans. This species has been ranked fourth in terms of its abundance among world's seabirds, and the first of tropical bird species in terms of its annual estimated consumption of marine resources (Brooke, 2004). Their potential impact on marine resources is thereby likely to be significant. Despite the key role of sooty terns play in tropical marine ecosystems, some fundamental aspects of their ecology, especially their at-sea distribution, remain little known (Schreiber et al., 2002).

In terms of some life history traits, sooty terns share common characteristics with highly pelagic birds, such as albatrosses, shearwaters, and tropicbirds than most other terns (Dinsmore, 1972). This includes a long lifespan (over 30 years), delayed sexual maturity (5–6 years), low reproductive rate (one egg clutch), and long incubation and fledging periods (Schreiber et al., 2002). It is generally assumed that the extreme life history traits of pelagic seabirds, such as slow growth of chicks, low fecundity, and high adult survival, result from the difficulties in finding food in the pelagic environment (Lack, 1968; Weimerskirch, 2001). According to this idea, sooty tern life history traits could be adaptations that facilitate exploitation of pelagic ecosystems (Dinsmore, 1972). Some at-sea surveys (Ballance et al., 1997; Jaquemot et al., 2005) and stable isotope analyses (Cherel et al., 2008; Young et al., 2010) support this hypothesis but the at-sea distribution and behavior of this species remain poorly known during the breeding and non-breeding periods (Schreiber et al., 2002; Soanes et al., 2015).

Developments of tracking devices have enhanced our understanding of movements of wide-ranging marine predators during both the breeding and non-breeding periods (e.g., Phillips et al., 2006; González-Solís et al., 2007; Weimerskirch et al., 2015). Until recently, device sizes restricted deployments on large seabirds. Geolocation (Global Location Sensing or GLS logging), using archival light-recording tags, offers considerable potential

for tracking seabird movements even for small species (Egevang et al., 2010), over long time intervals, such as the non-breeding period (Croxall et al., 2005).

Here, we analyzed data collected using GLS deployed on sooty terns from Bird Island (Seychelles, Indian Ocean) to describe for the first time their year-round at-sea distribution and activity, and address the following questions:

- (1) Animal migration is viewed as a biological phenomenon driven by seasonal changes in resource availability and habitat. Accordingly, seabirds perform large migration at polar and temperate latitudes (Croxall et al., 2005; Phillips et al., 2006; Shaffer et al., 2006; González-Solís et al., 2007; Bost et al., 2009; Egevang et al., 2010; Weimerskirch et al., 2015) where environmental conditions show marked seasonality. Seasonality in tropical zones is less marked than at higher latitudes and our study aimed to discover as the extent of migrations undertaken by this tropical species.
- (2) Resources in tropical waters are also believed to be less predictable than those in polar or temperate zones, and consequently tropical seabirds should exhibit a lower foraging site fidelity than seabirds of higher latitudes (Weimerskirch, 2007). In the present study, sooty terns were tracked for 2 years in order to investigate the fidelity to their foraging areas from year to year.
- (3) Based on the absence of sooty terns at their breeding colonies during the non-breeding season and the aversion of this species to landing on the water, Ashmole (1963) suggested that they do not rest on water and must sleep on the wing. We used the salt water sensor capability of the GLS to investigate the at-sea activity pattern of sooty terns in order to examine Ashmole's hypothesis.

MATERIALS AND METHODS

Ethic Statement and Research Permits

Capture, handling and deployment of GLS devices on sooty terns were performed under research programs approved by the Center for Research on Bird Population Biology (Program 616; CRBPO; National Museum of Natural History, Paris). Fieldwork in the Seychelles was performed under the approval of the Seychelles Bureau of Standards (A0347) and the Ministry of Environment, Energy and Climate Change.

Study Site, Species, and Data Collection

The study was carried out at a sooty tern colony of c. 500,000 pairs on Bird Island, Seychelles (3°43'S and 55°12'E). Sooty terns nest on the ground and breed annually during a breeding season, which lasts ~5–6 months. Adults arrive at the colony in April–May, females lay in June and incubation takes 28 days (Feare, 1976). Both parents share chick-rearing duties at the colony until fledging when around 8 weeks after hatching; this is followed by a period of post-fledging care (Feare, 1976). We studied the at-sea distribution and activity of individual sooty terns using GLS loggers (Mk13 and Mk18, British Antarctic Survey, Cambridge). These data loggers measured visible light intensity every minute and tested for saltwater immersion every 3 s. The maximum light

level, and number of positive tests from 0 (continuously dry) to 200 (continuously wet) were stored at the end of each 10 min block. GLS loggers were attached to plastic leg rings using cable ties and deployed on the tarsus of 86 terns during two successive incubation periods (60 loggers in June 2011 and 26 loggers in June 2012). The GLS loggers were attached to birds that had been incubating for about a week to reduce the risk of desertion. The mass of the logger, ring, and cable tie was 2.6 g, below the limit of 3% of adult body mass (~ 190 g) recommended for flying birds (Phillips et al., 2003; Ramírez et al., 2013). GLS loggers were recovered during the 2012 and 2013 breeding seasons (incubation stage) by a team of up to five people walking slowly through the colony and catching marked birds using hand nets (Feare and Doherty, 2004). Three searches were undertaken daily in different parts of the colony such that the entire area of the nesting colony was searched every 2 days. During other studies, repeated recapture of ringed sooty terns during incubation has never led to desertion (Feare, pers. obs.), so we consider that the searches for GLS-tagged birds are unlikely to have adversely impacted the marked birds or their near neighbors. Although some established breeders on Bird Island move within the colony or to other colonies between breeding attempts (Feare and Lesperance, 2002), the majority show some degree of site fidelity and so more search effort was devoted to the areas in which birds were originally marked. We recovered 50% ($N = 43$) of the loggers, but we failed to download data from seven of them. Six GLS loggers were retrieved and successfully downloaded in 2012 (with data recording for 1 year: 2011–2012), 30 in 2013 (17 with data recording for 2 years: 2011–2013, and 13 for 1 year: 2012–2013).

Light Data Analysis

GLS loggers record elapsed time and light level, allowing estimates of geographic position twice per day with an average spatial accuracy of 186 km for birds in flight (Phillips et al., 2004). Latitude was derived from day and night lengths and longitude from the time of local midday and midnight with respect to Greenwich Mean Time (Hill and Braun, 2001). Sooty tern locations were estimated using the “TripEstimation” package in R (Sumner et al., 2009) and following the method of Thiebot and Pinaud (2010). We did not perform the correction with sea-surface temperature because our logger models (Mk13 or Mk18) did not record seawater temperature. The dates of non-breeding, pre-laying and breeding periods were determined by identifying rapid shifts in distance from the colony. Fifty percentage (core area) and 90% (home range) kernel density distributions were used to examine at-sea distribution of sooty terns (Phillips et al., 2006; Weimerskirch et al., 2017). They were calculated with “adehabitat” packages in R (Calenge, 2006).

At-Sea Activity Data Analysis

The GLS loggers also contained a wet/dry sensor that detects immersion in seawater and provides information on foraging/resting activity when birds make contact with the sea (Phalan et al., 2007). We calculated a common activity value derived from the immersion sensors as the percent of time spent in contact with the seawater (Phalan et al., 2007; Mackley et al.,

2010a,b; Pinet et al., 2011a). We also calculated the average number of minutes per day that each bird spent in three activity types (1) “floating” (the GLS logger was continuously in contact with seawater for at least one 10 min period, indicating that the bird was sitting on the water; (2) “flying/roosting” (the GLS logger was continuously dry for at least one 10 min period, as would occur when a bird was flying or roosting on land or on floating debris); and (3) “presumed foraging” (the GLS logger recorded intermittent wet and dry states for at least one 10 min period) (McKnight et al., 2011, 2013). We finally calculated the average duration of flying and foraging bouts (Phalan et al., 2007; Mackley et al., 2010b; McKnight et al., 2011). Each activity parameter was calculated in both darkness and daylight (each 10 min block was categorized as daylight or darkness based on the light data) and for both breeding and non-breeding periods (classified with the migration dates derived from geolocation data).

Statistical Analysis

Inter-annual variations were tested on departure dates from the colony, return dates to the colony, durations, distances traveled and geographical ranges during the pre-laying and non-breeding periods, and on the number of individuals that migrated into the four non-breeding core areas. We used student *t*-tests and χ^2 tests because generalized mixed linear models (GLMM), with individuals as random effect, did not produce a better fit compared to generalized linear models (AIC, Akaike Information Criterion, difference of both models < 2). The fixed effects of several temporal variations (annual, seasonal and daily) on activity parameters (response variables: percentage of time spent in contact with seawater, flying and foraging bout durations, numbers of foraging bout per night/day) were investigated using GLMM with individuals as random effect. All analyses were performed with R version 3.0.1 (R Core Team, 2016). Values are means \pm standard deviations.

RESULTS

Effect of GLS Deployment

All recaptured sooty terns were in good physical condition and no significant difference was detected in their body mass between GLS logger deployment and recovery ($N = 40$, $t = -1.25$, $p = 0.222$, mean \pm SD: 191.3 ± 18.3 and 196.9 ± 25.2 g, respectively) or between equipped birds and control birds randomly chosen and weighed at the same time ($N = 40$, $t = -0.376$, $p = 0.708$, mean \pm SD: 196.9 ± 25.2 g and 199.4 ± 28.3 g, respectively).

At-Sea Distribution

Sooty terns tracked with GLS loggers showed a clear segregation in their core areas during the non-breeding, pre-laying and breeding periods (Figure 1). While breeding, birds were distributed around the colony and their average maximum distance from the island was $1,074 \pm 274$ km per individual. They departed the colony for their post-breeding migration on 30 September ± 19.0 days and remained at sea during their entire non-breeding period that lasted 6.9 ± 0.7 months (average date of return to the colony: 3 May ± 15.5 days). Total distances

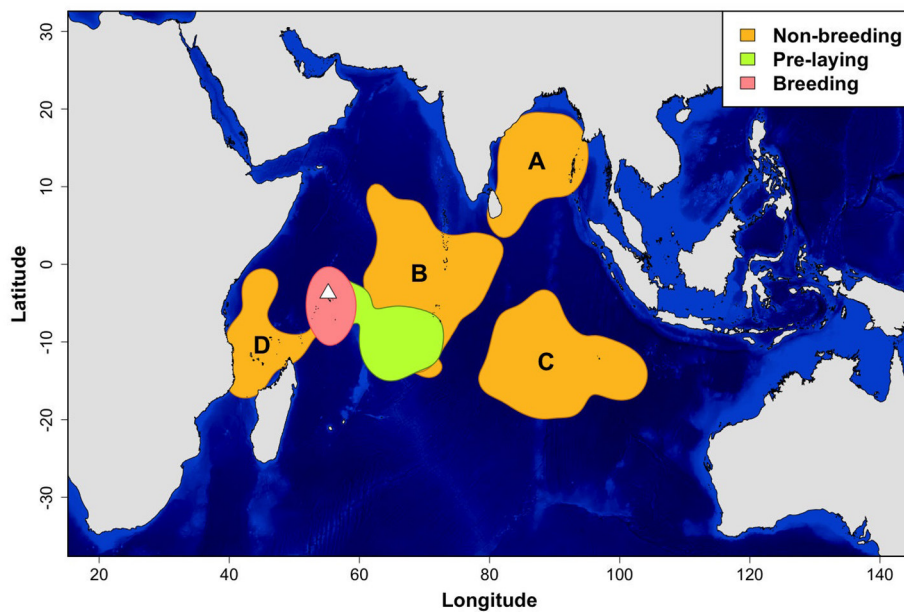


FIGURE 1 | Density distributions of sooty terns ($N = 36$ birds and 53 annual tracks) from Bird Island (white triangle) during the non-breeding, pre-laying and breeding periods. Density contours encompass core areas (50% kernel). For the non-breeding period, locations were concentrated in four main areas: in the Bay of Bengal (A), on each side of the Chagos-Laccadive plateau (B), on each side of the 90 East Ridge (C), and around Comoros (D). Units are in degrees.

covered during the non-breeding period averaged $52,503 \pm 6,546$ km per individual. Maximum distances from the colony ranged from 2,058 to 8,681 km ($4,423 \pm 1,190$ km). Although the non-breeding home range (90% kernel) covered a wide part of the Indian Ocean (**Supplementary Figure 1**), four non-breeding core areas (50% kernel) were identified (**Figure 1**). Eighty percentage of tracked sooty terns visited only one core area during the non-breeding period. Birds that utilized several core areas were categorized in the area in which they spent most of their time. Most birds migrated to the Bay of Bengal (A) or northeast to an area straddling the Chagos-Laccadive plateau (B) (45.2 and 35.9% of birds, respectively). Others traveled southeast to an area on each side of the 90 East Ridge (C) southwest to an area around Comoros (D) (13.2 and 5.7% of birds, respectively).

Sooty terns returned to the colony in April/May but only laid eggs in June/July. During the period between first arrival in the Seychelles and egg-laying, 92.5% of individuals traveled east or south-east to forage at an average maximum distance from the colony of 2182 ± 477 km (**Figure 1**). They performed one or two foraging trips (55.1 and 44.9% of these birds, respectively). The distance traveled was $10,972 \pm 3,376$ km and took place between 10 May and 6 June, and lasted 31.9 ± 12.1 days.

Seventeen individuals were tracked in 2 years. There was no significant difference in the date, duration, mean distance traveled and maximum distance from the colony during the non-breeding and pre-laying periods between the 2 years of the study (t -tests, all $p > 0.367$, **Table 1**). During the first year, birds spent more time in the area on either side of the Chagos-Laccadive

plateau (B) (**Table 2**, $\chi^2 = 5.010$, $p = 0.025$). During the second year, they migrated further east to the 90 East Ridge (C) and to the Bay of Bengal (A), but these differences were not statistically significant (**Table 2**, χ^2 tests: $\chi^2 = 2.355$, $p = 0.125$ and $\chi^2 = 0.915$, $p = 0.339$, respectively). Despite this apparent inter-annual difference in overall distribution, most individuals showed a high degree of site fidelity to their non-breeding grounds between the 2 years (64.7% of birds, see examples on **Figure 2**).

At-Sea Activity

Overall, sooty terns spent a low percentage of time in contact with seawater ($3.72 \pm 1.93\%$), and consequently a short amount of time foraging (3.59 ± 1.66 h.d⁻¹) or floating (0.38 ± 0.20 h.d⁻¹). Most of their time was devoted to flying (20.72 ± 1.36 h.d⁻¹). The percent of time in contact with seawater exhibited marked daily and seasonal variations (see statistics below) but no inter-annual differences (GLMM, F -value = 0.80, $p = 0.372$). Firstly, on a daily basis (**Figure 3**), birds spent a higher percentage of time in contact with the seawater during daylight hours ($6.97 \pm 3.51\%$) than during the night ($0.03 \pm 0.06\%$; GLMM, F -value = 666.14, $p < 0.0001$). Accordingly, sooty terns spent 11.51 ± 0.35 h in flight, none floating and 2.23 ± 0.07 h foraging at night. The corresponding times during the day were 9.21 ± 0.96 , 0.38 ± 0.17 , and 3.36 ± 0.66 h, respectively. Secondly, the percentage of time spent in contact with seawater was lower during the breeding period ($1.97 \pm 2.15\%$) compared to the non-breeding period ($5.03 \pm 5.22\%$, GLMM, F -value = 129.30, $p < 0.0001$). This difference was significant only during the daylight period

TABLE 1 | Details of the non-breeding and pre-laying at-sea movements performed by sooty terns tracked for 2 years (YEAR1: 2011–2012 and YEAR2: 2012–2013) from Bird Island, Seychelles, Indian Ocean.

		Departure date	Return date	Duration (month)	Distance traveled (km)	Range (km)
Non-breeding	YEAR 1	6 October \pm 13.7 days	3 May \pm 15.7 days	6.8 \pm 0.7	51864.2 \pm 6418.3	4221.1 \pm 1396.0
	YEAR 2	27 September \pm 21.7 days	2 May \pm 15.6 days	7.0 \pm 0.7	52992.3 \pm 6708.3	4578.2 \pm 1001.8
Pre-laying	YEAR 1	10 May \pm 14.2 days	10 June \pm 13.0 days	1.3 \pm 0.4	11433.2 \pm 3010.3	2127.8 \pm 382.2
	YEAR 2	12 May \pm 10.6 days	4 June \pm 11.2 days	1.2 \pm 0.4	10556.1 \pm 2850.3	2230.4 \pm 553.4

The range represents the maximum distance between the breeding ground and the non-breeding location. There was no significant difference of parameters between the 2 years (*t*-tests, all *p* > 0.367).

TABLE 2 | Percentage of birds that migrated to the four distinct non-breeding grounds during the entire study period, and split between the two studied years (YEAR1: 2011–2012 and YEAR2: 2012–2013).

Core non-breeding areas	Entire tracked period ^a (N = 53) (%)	YEAR 1 (N = 23) (%)	YEAR 2 (N = 30) (%)
Bay of Bengal (A)	45.2	34.8	53.3
Chagos-Laccadive Plateau (B)	35.9	56.5*	20.0*
Ninety East Ridge (C)	13.2	4.3	20.0
Comoros (D)	5.7	4.3	6.7

*Indicates a significant difference in this percentage between the two years of the study (χ^2 tests, see Results). Upper case letters (A–D) are used in the Figure 1.

^a36 bird tracks split into 53 annual tracks, 17 birds were equipped during two years and 19 birds during 1 year (6 during the first year and 13 during the second year).

(Table 3, *t*-test, *t* = 18.43 and *p* < 0.0001). During the non-breeding period, birds spent more time floating and foraging during daylight (Table 3, *t*-tests, both *p* < 0.0001), and less time flying during both day and night (Table 3, *t*-tests, both *p* < 0.0001).

The average duration of all foraging bouts was 0.28 ± 0.10 h (16.81 ± 6.12 min). This parameter was significantly higher during the day than at night (0.37 ± 0.06 and 0.19 ± 0.04 h, respectively; GLMM, *F*-value = 910.89, *p* < 0.0001). It was also higher during the non-breeding period for day-time values than during the breeding period (Table 3). The average duration of flying bouts was 5.65 ± 4.67 h, it was significantly shorter during day-time than night-time (1.07 ± 0.28 and 10.24 ± 1.20 h, respectively; GLMM, *F*-value = 10,701.30, *p* < 0.0001) and significantly longer during the non-breeding period (Table 3, GLMM, *F*-value = 73.88, *p* < 0.0001). The number of foraging bouts per day was 2.32 ± 2.46 ; there were more foraging bouts during the day than at night (4.50 ± 1.59 and 0.14 ± 0.09 , respectively; GLMM, *F*-value = 1403.81, *p* < 0.0001). Further, there were more foraging bouts during the non-breeding period than during the breeding period (Table 3, GLMM, *F*-value = 159.19, *p* < 0.0001).

DISCUSSION

This study is the first to describe the non-breeding movements and behavior of sooty terns, a seabird species considered to be the world's most abundant with a correspondingly high consumption of marine resources (Brooke, 2004; Danckwerts et al., 2014). Our data revealed that Bird Island sooty terns dispersed widely over

the Indian Ocean north of c. 25°S, although individuals appeared to migrate to similar geographical areas in consecutive non-breeding seasons. We also describe for the first time that sooty terns undertake a pre-breeding exodus and are among the most aerial of seabirds.

At-Sea Distribution

Our data show that sooty terns undertake extensive post-breeding migrations, the average distances traveled exceeded 50,000 km per individual. In comparison, wandering albatrosses *Diomedea exulans* perform several circumnavigations around Antarctica, covering more than 120,000 km during a year (Weimerskirch et al., 2015), arctic terns *Sterna paradisaea* travel more than 80,000 km between Arctic breeding grounds and Antarctic non-breeding areas (Egevang et al., 2010), and sooty shearwaters *Ardenna grisea* fly 60,000 km (Shaffer et al., 2006). Many seabirds perform latitudinal migrations (Shaffer et al., 2006; González-Solís et al., 2007; Egevang et al., 2010; Kopp et al., 2011) despite some exceptions (Croxxall et al., 2005; Bost et al., 2009; Gaston et al., 2015; Weimerskirch et al., 2015). In the present study, most sooty terns migrated eastward, as do several other seabird species breeding in the western Indian Ocean (Catry et al., 2009; Pinet et al., 2011b; Le Corre et al., 2012). These longitudinal migrations are constrained partly by the Eurasian landmass to the north but also by cold water to the south (Kostianoy et al., 2004), acting as physical/environmental barriers for tropical Indian Ocean seabirds.

The area of the Indian Ocean frequented by non-breeding sooty terns from Bird Island is remarkably large. The four main areas identified in this study represent core areas of high density use (50% kernel contours), whilst location estimates that fell outside these core areas covered most of the Indian Ocean north of c. 25°S. Two birds, one ringed when breeding on Bird Island, the other while breeding on Juan de nova, in the Mozambique Channel, were recovered during a die-off of sooty terns on Sri Lanka in February 2011 (Tharaka Prasad, pers. comm.). This suggests that non-breeding areas are shared by birds from different breeding colonies in the western Indian Ocean. Here, sooty terns are extremely abundant with more than 6 million pairs breeding each year in widely spaced colonies, with some exceeding 1 million pairs (Feare et al., 2007). Tropical waters are less productive than in polar or temperate regions (Weimerskirch, 2007). The division of sooty tern non-breeding at-sea distribution into four core areas could be a way for them

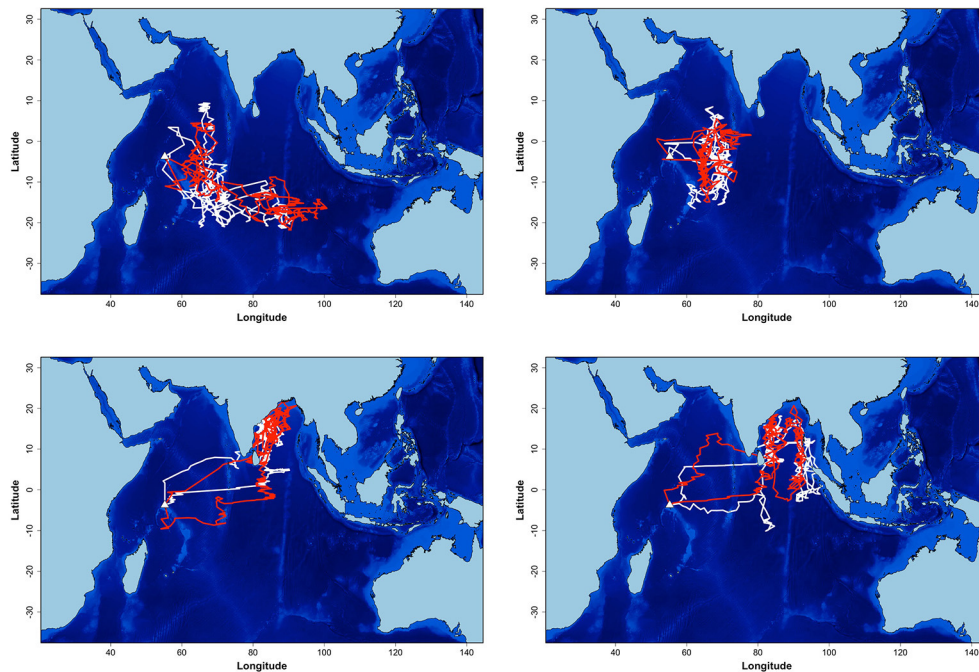


FIGURE 2 | Example of non-breeding at-sea distribution estimation of four sooty terns from Bird Island equipped for 2 years (2011–2012 and 2012–2013). In white: the first year tracks, in red: the second year tracks. Units are in degrees.

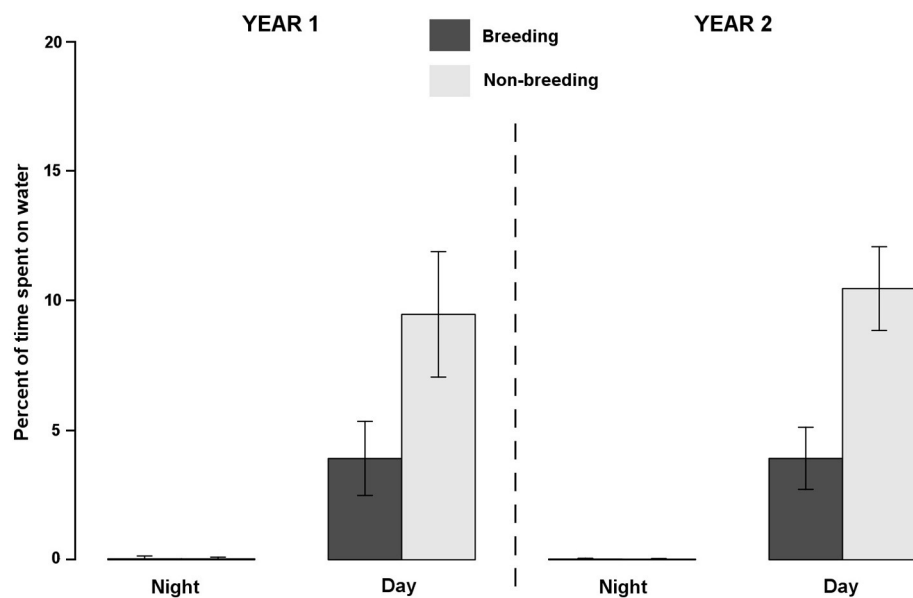


FIGURE 3 | Inter-annual (YEAR1: 2011–2012 and YEAR2: 2012–2013), seasonal (breeding and non-breeding) and diel variations of average \pm standard deviation of time spent in contact with the seawater by sooty terns from Bird Island.

to reduce competition for scarce resources between numerous conspecifics in the Indian Ocean.

In the present study, the fidelity of individuals to a core area in successive years could imply that individual migration patterns are fixed. Several other studies have already reported this behavior (Bradshaw et al., 2004; Broderick et al., 2007;

Phillips et al., 2007; Yamamoto et al., 2014; Ramírez et al., 2016), suggesting that the individual fidelity to a specific non-breeding site is a relatively common characteristic among migratory marine animals. Further data from other breeding colonies are needed to understand how birds select their non-breeding foraging areas, whether they are selected when young through

TABLE 3 | Comparisons between darkness and daylight activity parameter values (mean \pm SD) during the breeding and non-breeding seasons for sooty terns from Bird Island ($N = 36$).

	Darkness				Daylight			
	Breeding	Non-breeding	<i>t</i>	<i>P</i>	Breeding	Non-breeding	<i>t</i>	<i>P</i>
Percentage of time spent in contact with seawater	0.02 \pm 0.05	0.03 \pm 0.05	−0.31	0.760	3.91 \pm 1.30	10.03 \pm 2.05	18.43	***
Floating time per day (hour)	0	0	–	–	0.28 \pm 0.08	0.47 \pm 0.08	13.07	***
Foraging time per day (hour)	0.23 \pm 0.07	0.24 \pm 0.07	0.25	0.803	2.90 \pm 0.58	3.82 \pm 0.73	7.21	***
Flying time per day (hour)	11.65 \pm 0.31	11.47 \pm 0.28	−4.29	***	9.87 \pm 0.63	8.54 \pm 0.76	−9.81	***
Flying bout duration (hour)	9.66 \pm 1.02	10.82 \pm 1.08	−5.68	***	0.89 \pm 0.17	1.25 \pm 0.24	−9.00	***
Foraging bout duration (hour)	0.15 \pm 0.05	0.19 \pm 0.03	−0.173	0.863	0.32 \pm 0.03	0.41 \pm 0.04	12.05	***
Numbers of foraging bouts per night/day	0.09 \pm 0.04	0.18 \pm 0.10	6.19	***	3.08 \pm 0.56	5.93 \pm 0.79	21.39	***

***indicates a *P* value of *t*-test < 0.0001.

individual long-term selection processes (Péron and Grémillet, 2013), and how the movements to multiple non-breeding feeding areas by birds from a single colony evolved. A study of the distributions and habitats of young sooty terns during the 5–6 years prior to their first breeding attempt will be needed to ascertain at what age distant foraging sites are selected. Longer-term data with tracking in years with different oceanic conditions will be also necessary to confirm site fidelity to non-breeding grounds.

In addition to the wide at-sea distribution of sooty terns revealed in this investigation, the study is the first to demonstrate that sooty terns undertake a pre-laying exodus between the arrival at the colony in May and egg laying in June. This behavior is common in petrels and shearwaters (Warham, 1964) but has not previously been observed in terns, and has been recorded in few other non-procellariid seabirds (Phillips et al., 2007). The pre-laying exodus is considered as a strategy available to Procellariiformes because they are able to carry out long-distance foraging trips (Warham, 1964). Having re-established their nest sites and pair bonds at the start of the breeding season, the females, and in some species also the males, desert the breeding area for a period of days or weeks immediately before egg laying (Phillips et al., 2006, 2007). This behavior provides a period of uninterrupted foraging, during which birds build the reserves required to produce eggs (for females) and to prepare for their food deprivation periods during long shifts of incubation (Warham, 1964).

The core area used during the pre-laying exodus of Bird Island sooty terns included the Saya de Malha Bank, a submarine plateau c. 850–1,100 km south-east of Bird Island, and the Chagos Bank, a large plateau at the south of the Chagos-Laccadive Ridge (Figure 1). These are areas of high primary productivity (Burnett et al., 2001; Sheppard et al., 2012) and presumably offers good feeding opportunities. Nonetheless, birds that undertook a pre-laying exodus traveled on average around 10,000 km. This additional energetic cost immediately following the long-distant return migration suggests that the area used is predictably productive. The relative proximity of high productivity areas may facilitate the establishment of large sooty colonies on nearby islands, as in the western Indian Ocean. Some birds were recorded making two trips to the pre-laying core area, possibly

arising from birds losing their first egg and preparing to lay a replacement.

At-Sea Activity

Overall, sooty terns spent 3.72% of their time in contact with the seawater. This is very low compared to other seabirds (Mackley et al., 2010a,b; Pinet et al., 2011a), including tern species (Nisbet et al., 2011). Arctic terns *S. paradisaea* also exhibited low values of time spent floating; the authors suggested that this behavior was virtually absent because they rest on logs, basking turtles or floating ice (McKnight et al., 2013). In fact, a low percent of time spent on water (i.e., a dry sensor) should imply that birds, (1) rest on floating debris or on land, (2) withdraw one leg and/or foot into the plumage while resting at sea (Linnebjerg et al., 2014), or (3) fly with few resting periods on water. In the present study, the estimated locations and the core areas of distribution were mainly over ocean instead of land, indicating that sooty terns do not rest on land. Moreover, the average movement speed measures, from estimated locations during non-breeding nights and days, were 10.03 ± 6.45 and 10.02 ± 6.36 km.h^{−1}, respectively. These results indicate that birds were moving and thus did not rest on floating debris or on water.

Sooty terns experience difficulty in taking off from the surface of the water (Mahoney, 1984) and become waterlogged after resting on water (Watson and Lashley, 1915). Their uropygial gland produces preen oil with less lipid content than in terns that frequently land on the water (Johnston, 1979). These results have led to speculation that sooty terns have poor feather waterproofing and do not rest on water (Ashmole, 1963; Dinsmore, 1972). In this study, we recorded extended non-stop flights at night (more than 10 h per night) and almost no resting time on the water during the day (<30 min per day). This seems to confirm the long-held belief that sooty terns are among the most aerial of birds, and sleep in flight (Ashmole, 1963; Schreiber et al., 2002). Some other seabird species, such as frigatebirds, are also suspected of sleeping in flight (Rattenborg, 2006).

Sooty tern diet during the breeding season comprises small epipelagic fish, fish larvae and flying squid. The proportions of these main dietary constituents vary between colonies (Jaquemet et al., 2008), within breeding seasons (Feare, 1976) and between years (Feare, unpublished data), suggesting

opportunistic foraging. Prey are obtained at or above the sea surface through association with schools of predatory fish, especially tuna. These drive their prey to the surface, making them available to sooty terns. The diet of sooty terns during migration is unknown.

In this study, we showed that most of the time spent in contact with seawater is foraging behavior (89.9%) with almost no floating on the sea surface (10.1%). Foraging bouts occurred mainly during daytime, suggesting sooty terns mainly fed during the day. At-sea observations revealed that sooty terns normally feed on the wing by “air dipping” or “contact dipping” and occasionally by briefly plunging into the surface without complete submersion (Ashmole and Ashmole, 1967). During ocean voyages in the Seychelles, c. 30 flocks of <500 feeding sooty terns were observed, always in association with predatory fish, such as tuna and mackerel (Feare, unpublished data). Most commonly, the birds chased prey at the water surface or above it by means of highly aerobic maneuvers and did not settle on the water. This likely accounted for the low values of contact with seawater recorded by the GLS loggers.

CONCLUSION

This is the first study describing the at-sea movements of the sooty tern, the most abundant tropical seabird. The results support the long-held belief that the sooty tern is one of the most pelagic of all terns. Those that breed on Bird Island (Seychelles), have extensive longitudinal migrations and four large pelagic non-breeding core areas. They practically never enter the water and probably sleep in flight. The findings of this study have also important consequences for sooty tern conservation. Our finding that different individuals of the Bird Island population utilize different core areas during the non-breeding period, and yet another area for the pre-laying exodus, shows that the birds can be vulnerable to adverse conditions far from the breeding colonies. These can include excessive commercial exploitation of pelagic predatory fish, especially tuna (Pillai and Satheeshkumar, 2013; Danckwerts et al., 2014). The most used core area, the Bay of Bengal, is highly contaminated by industrial pollutants and by plastic microparticles (Eriksen et al., 2014). The latter have a capacity to adsorb and concentrate toxicants and pharmaceuticals (Gaw et al., 2014). Some of these could have implications for the birds' breeding performance when in Seychelles. The northern Indian Ocean, and especially the Bay of Bengal, is prone to cyclones, whose frequency and intensity are increasing (Singh et al., 2001). This has been associated with increasing atmospheric pollution (Evan et al., 2011). The

2011 die-off of sooty terns in Sri Lanka, mentioned above, was contemporaneous with the development of a tropical depression off the east coast of Sri Lanka (IMD, 2011). This suggests that while the use of large core foraging areas might buffer sooty terns against some vagaries in food availability, there are risks that environmental changes in some core areas could threaten birds that utilize these.

AUTHOR CONTRIBUTIONS

AJ helped design the study, collected field data, performed data analysis and drafted the manuscript. CF conceived and designed the study, collected field data and drafted the manuscript. RS helped design the study, collected field data and helped draft the manuscript. CL and CSL collected field data. ML helped design the study and helped draft the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2017.00394/full#supplementary-material>

Supplementary Figure 1 | Density distributions of sooty terns ($N = 36$ birds and 53 annual tracks) from Bird Island (white triangle) during the non-breeding, pre-laying and breeding periods. Density contours encompass home ranges (90% kernel). For the non-breeding period, locations were concentrated in four main areas: in the Bay of Bengal (**A**), on each side of the Chagos-Laccadive plateau (**B**), on each side of the 90 East Ridge (**C**), and around Comoros (**D**). Units are in degrees.

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