Foraging ecology of tropicbirds breeding in two contrasting marine environments in the tropical Atlantic

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ABSTRACT: Studying the feeding ecology of seabirds is important not only to understand basic aspects of their ecology and threats but also for the conservation of marine ecosystems. In this regard, tropical seabirds have been relatively neglected, and in particular the trophic ecology of tropicbirds is scarcely known. We combined GPS tracking, environmental variables and sampling of regurgitates during incubation and brooding to understand the feeding ecology of red-billed tropicbirds *Phaethon aethereus* as well as how foraging strategies may change between 2 contrasting marine environments: a coastal island in the Canary Current upwelling (Iles de la Madeleine) and an oceanic island in the middle of the south Atlantic (St Helena). Tropicbirds breeding on the Iles de la Madeleine headed west, foraging on and beyond the shelf slope, probably to associate with subsurface predators which bring pelagic fish close to the surface. Birds from St Helena showed a greater foraging effort and a strong attraction to areas with the greatest species richness of Scombridae, possibly due to a greater difficulty in finding prey in the oligotrophic oceanic waters. Tropicbirds ranged much beyond the extension of the protected areas around their colonies, indicating that current protected areas are insufficient for these populations. We found no evidence to suspect direct mortality of tropicbirds in regional fisheries, but overexploitation of small epipelagic fish and tuna may decrease feeding opportunities and lead to competition with fisheries. The substantial differences in foraging behaviour demonstrated by individuals from both colonies indicates that caution should be taken when extrapolating foraging patterns of tropical seabirds breeding in contrasting oceanographic environments.

KEY WORDS: Foraging area · Foraging behaviour · Contrasting environmental features · Red-billed tropicbirds · *Phaethon aethereus* · Eastern tropical Atlantic · Protected areas · Diet · GPS tracking

INTRODUCTION

The different aspects of the feeding ecology of seabirds, such as diet, activity patterns, foraging movements and feeding habitat selection, should ideally be studied in parallel. Doing so can allow a better understanding of the main dimensions of the trophic niche as well as the main factors affecting seabird diet and movements. However, this knowledge is still lacking for many species, particularly among tropical seabirds. In tropical waters, daytime foraging is often related to associations with subsurface predators, such as tunas and, to a lesser extent, cetaceans, which bring the fish close to the surface

and create feeding opportunities for oceanic sea-birds (Spear et al. 2007, Miller et al. 2018). On the other hand, diel vertical migrations are thought to be particularly important in oceanic environments, with many fish and marine invertebrate species being accessible for seabirds mainly during crepus-cular hours (Pinet et al. 2012, Pollet et al. 2014). A number of studies related the occurrence of fish and invertebrates known to perform diel vertical migra-tions in the diet of seabirds to crepuscular foraging, but direct evidence is scarce and somewhat contro-versial (Spear et al. 2007). In this context, combining the information obtained from tracking devices on the feeding grounds and daily activity with diet samples from regurgitations offers an excellent opportunity to understand when and where the dif-ferent prey is taken, the diurnal or nocturnal feed-ing strategies or the use of neritic versus oceanic waters. In addition, this approach is especially use-ful for our understanding of whether direct or indi-rect interactions with fisheries occur (Bertrand et al. 2012, Lewison et al. 2012). Direct interactions occur when seabirds take advantage of fishery discards mainly from trawlers or are caught as by-catch in longline fishing gear, whereas indirect interactions are when seabirds compete with fisheries who tar-get their prey, such as purse-seine fishing or some small artisanal fisheries.

GPS tracking data can also be used in combination with environmental variables of the marine habitat to understand how environmental conditions can influ-ence foraging strategies and feeding habitat selec-tion (Wakefield et al. 2009). These relationships have been used to predict important areas for colonies whose seabirds have not been previously tracked (e.g. Torres et al. 2015, Wakefield et al. 2017, Péron et al. 2018, Yates et al. 2018). However, these pre-dictions are expected to fit better in areas with simi-lar and persistent oceanographic features, such as upwellings, which may provide highly predictable resources (Mannocci et al. 2014). In this context, the association between tropical seabirds and the marine habitat is possibly less intense, since tropical areas are more oligotrophic and less predictable than tem-perate or polar ones (Weimerskirch 2007, Oppel et al. 2017). However, recent work on tropical shear-waters suggests that tropical seabirds show a tighter association to environmental features than previ-ously thought (McDuie et al. 2018, Miller et al. 2018). Nevertheless, whether it is feasible to infer seabird foraging patterns from untracked colonies based on habitat preference in tropical systems is still uncertain.

In tropicbirds, some studies have focussed on diet composition, diving depths, duration of foraging trips and feeding frequency, but mainly in the Indian Ocean and the Pacific (Le Corre 1997, Le Corre et al. 2003, Spear et al. 2007, Sommerfeld & Hennicke 2010). In tropical areas, solitary medium- and small-sized procellariforms typically show important noc-turnal activity, whereas tropicbirds are usually considered diurnal feeders (Spear et al. 2007, Som-merfeld & Hennicke 2010). However, typically diur-nal seabirds, such as Cory's shearwaters *Calonectris diomedea*, have been found to have some plasticity in their diurnal–nocturnal foraging depending on the habitat exploited (Dias et al. 2012); therefore, the assumption of diurnal feeding of tropicbirds deserves some attention. Tropicbirds have not been tracked with high-resolution GPS devices until very recently (Soanes et al. 2016, Campos et al. 2018), and little is known about their feeding ecology and movements at sea. Red-billed tropicbirds *Phaethon aethereus* have a small, pantropical population of fewer than 8000 pairs, occurring in the western Pacific, Atlantic and northern Indian Oceans (Orta 1992, Lee & Walsh-McGehee 2000). This species is classified as 'Least Concern' by the IUCN, although its population trend is decreasing (BirdLife International 2018). Studies of red-billed tropicbirds have so far been lim-ited to their breeding phenology and breeding suc-cess (Stonehouse 1962, Snow 1965, Harris 1969, Beard et al. 2013) and their abundance and distribu-tion based on boat surveys (Spear & Ainley 2005a). A single study investigated the foraging ecology of red-billed tropicbirds and other species breeding in Anguilla (eastern Caribbean) to identify important foraging areas in the region (Soanes et al. 2016). However, this study did not focus on understanding the feeding ecology of the species, and therefore basic information on their habitat preferences, daily activity patterns and diet is still lacking.

In this study, we investigated the feeding ecology of red-billed tropicbirds in 2 areas with contrasting mar-ine environments, i.e. the Iles de la Madeleine (*P. a. mesonauta*) and St Helena (*P. a. aethereus*) (Orta et al. 2016). Madeleine is a coastal island on the African Shelf within a major upwelling system sustaining large fish populations (e.g. Ba et al. 2017, Thiaw et al. 2017). This high prey availability is widely exploited by many pelagic seabirds, both during summer (Ramos et al. 2013, Paiva et al. 2015) and winter (Grecian et al. 2016). St Helena is an oceanic island in the middle of the south Atlantic far from any productive areas. These 2 colonies provide ideal conditions to in-vestigate foraging ecology in the tropical Atlantic and

to understand whether the foraging ecology of red-billed tropicbirds changes in relation to the environment, and therefore whether their foraging patterns can be extrapolated across different breeding colonies. In particular, we aimed to (1) characterize the main dimensions of the trophic niche of tropicbirds in the Atlantic, i.e. diet, activity patterns and foraging areas, (2) understand how tropicbirds modulate their foraging behaviour in relation to the breeding stage, the breeding colony and the oceanographic conditions, and (3) understand the implications for conservation, particularly in terms of potential interactions with fisheries, the delineation of marine protected areas and predicting foraging areas across breeding colonies.

MATERIALS AND METHODS

Study area

This study was carried out on 2 islands in the central eastern Atlantic (Fig. 1): Madeleine Island in the Iles de la Madeleine (from November 2015 to February 2016) and St Helena (from August to December 2015). The national park of Iles de la Madeleine (14° 39′ N, 17° 28′ W) is a coastal island of 0.17 km^2 off Senegal on the African continental shelf, less than 100 km from the shelf break. The continental shelf is shallow (<100 m). St Helena (15° 57′ S, 5° 42′ W) is a subtropical oceanic island of 122 km^2 in the middle of the South Atlantic Ocean 1856 km off the West African coast. The sea is about 100 m deep within about 2 km around the island and drops to 3600 m beyond 2 km (Prater 2012).

Ethics

To understand the effect of GPS tracking on breeding success, of 41 monitored nests on Madeleine, 25 were used to deploy GPS devices on adults and 16 were left undisturbed. On St Helena, of 24 monitored nests, 12 were used to track adults and the other 12 were not manipulated. To determine the effect of devices on the body condition of adults and chicks, we weighed tracked (N = 54,
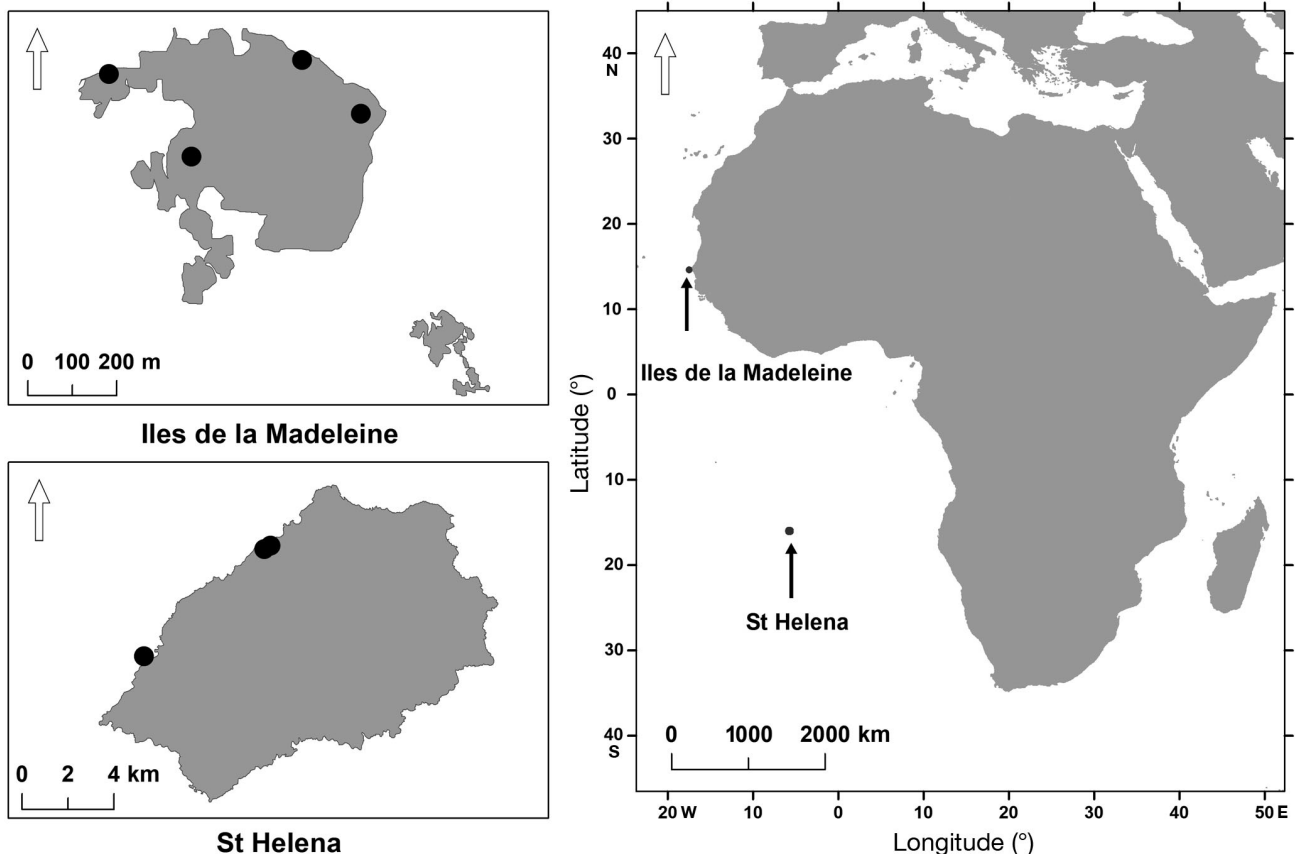

Fig. 1. Location of the 2 study colonies of red-billed tropicbirds (Madeleine and St Helena) in the eastern tropical Atlantic Ocean. Black circles represent nest sites; white arrows indicate north

some animals were weighed repeatedly) and untracked adults (N = 16), as well as 10 chicks from disturbed and 7 from undisturbed nests on Madeleine. To determine potential effects of GPS tracking on the return rate, we compared the return rate to the breeding colony in the following year between tracked and untracked animals by visiting all nests on Madeleine in the next breeding season (data for St Helena not available).

Diet identification through regurgitates

We were only able to collect spontaneous regurgitates from adults and chicks on Madeleine Island, so these data are only available for this breeding site. Samples were placed individually in a zip bag and kept frozen until analyses. Once in the lab, we cleaned regurgitates with water in 2 metallic sieves of 1 and 2 mm mesh size. We separated prey items, scales and otoliths from whole fish to help identify the specimens. Most regurgitates contained only partly digested prey, which could be identified with the help of fish guides of the study area (Seret 1981, Bellemans et al. 1988). We calculated the percentage of frequency of each family of prey. We also weighed each prey item to calculate the percentage of biomass of each family. In order to have information on the potential competition between tropicbirds and fisheries, we searched for the commercial value of the prey we found in regurgitates and the quantity (in tonnes) of the highest commercial value prey captured by fisheries in the exclusive economic zone (EEZ) of Senegal in 2015.

Foraging trajectory

We deployed 41 GPS devices on 34 tropicbirds on Madeleine and 24 devices on 13 tropicbirds on St Helena during incubation and early brooding (chicks <15 d old) in both colonies. Individual birds were caught by hand in the nest and GPS devices were deployed on each partner, alternately, with a maximum of 2 deployments per individual. GPS devices were programmed to record a signal every 5 min and were water-proofed with heat-shrinking tubing. We deployed modified Mobile Action igotU™ GT-120 GPS devices to the top surface of the 4 central rectrices, just below the uropygium, with 3 pieces (diameter: 1.5 cm, length: 10 cm) and 1 piece (diameter: 2 cm, length: 5 cm) of Tesa™ Tape. The size of the GPS devices was 5.0 cm (length), 2.2 cm (width) and 0.8 cm (height). The GPS device and the Tesa tape (18.25 g) weighed on average up to 3% of the weight of the tracked bird on Madeleine (average weight 614.62 ± 6.27 [SD] g; range 520–720 g; ~3%) and St Helena (average weight 701.66 ± 13.26 g; range 600–900 g; ~2.6%). We recaptured the birds on the nest, recovered the GPS device from 3 to 15 d after GPS deployment (depending on nest attendance) and downloaded the data.

We used R to filter GPS trajectories, by removing positions on land and erroneous locations (i.e. positions that would have required travel with an average speed of >80 km h^{-1}). We then split the trajectories with more than 1 foraging trip into respective foraging trips that were delineated by the bird's intermittent return to the colony. For each foraging trip, we calculated the maximum distance from the colony, the total duration of the trip and the distance travelled. We used a Gaussian Mixture Model maximum likelihood estimation algorithm provided in the EMbC package in R to describe 4 types of behaviour (resting, intensive search, extensive search, relocation) (Garriga et al. 2016). The algorithm classifies each type of behaviour based on the speed and the turning angle of the trajectory: resting is low speed, low turning angle; intensive search is low speed, high turning angle; extensive search is high speed, high turning angle; and relocation is high speed, low turning angle. We also used hidden Markov models (HMM) with 4 states to classify locations, as HMMs can be more successful in identifying actual foraging behaviour (Bennison et al. 2018). However, when visually inspecting the classification, we did not find substantial differences between methodologies and we kept the EMbC (see Supplement 1 and Fig. S1 at www.int-res.com/articles/suppl/m607p221_supp.pdf). Both EMbC and HMM algorithms often classified locations as intensive search when the bird was actually resting, probably due to the location error of the GPS devices when animals are resting, which resulted in artificially high turning angles with very low speed (see Supplements 2 & 3 and Figs. S2 & S3 to understand the reasoning of this conclusion). Therefore, we decided to pool locations classified as intensive search and resting into the same category as 'resting behaviour'. Foraging behaviour was then inferred from locations classified by the EMbC as 'extensive search'.

We used kernel density estimations (KDEs) to transform foraging positions into utilization distributions (Wood et al. 2000) in order to determine the most important foraging areas at each colony. We calculated the kernel density for 95 and 50%, corresponding to home range and core area distributions,

respectively. To describe the daily habits of the animals, we calculated the percentage of each behaviour for each hour of the day, i.e. we divided each foraging trip into hourly intervals and estimated the percentage of each behaviour in each hour. We graphed the results using the R package 'gamm4'. We pooled together incubation and brooding since there were no differences in the daily pattern. We only included Madeleine in this analysis, since St Helena data included very few locations at night, possibly as a consequence of water covering the GPS device while resting.

Statistical analyses

All statistical analyses were carried out with R 3.2.5 (R Core Team 2016). We assessed data for normality and homogeneity of variance with Q–Q plots, Shapiro-Wilks Levene's tests, resulting in the use of parametric analyses throughout. Non-normal data (e.g. behaviour proportions) were arcsine transformed to approach normality.

To address the effect of GPS devices on hatching and fledging success of tropicbirds, we performed chi-squared tests between manipulated and control groups on Madeleine and St Helena. To address GPS effects on the body condition of chicks, we ran a linear mixed-effects model (LMM) with chick mass as the response variable, manipulated/non-manipulated nest as a fixed effect and chick age as a random effect. To address the GPS effect on adult condition, we performed an LMM with adult mass as the response variable, tracked/non-tracked as a fixed effect and individual as a random effect. LMMs were conducted with the function 'lmer' (package 'lme4', Bates et al. 2015). We used chi-squared tests to compare the return rate of tracked and non-tracked birds. We also performed chi-squared tests to address the differences in the proportion of families of prey found in regurgitates.

We ran further LMMs with colony and breeding stage (either incubation or brooding) as fixed factors and individual as a random factor, to test variation in resting, foraging and relocation between colonies and breeding stages. We created competing models with all variables and the interaction between fixed factors, and selected the most parsimonious models based on Akaike's information criterion corrected for small sample sizes (AICc) using the function 'dredge' (R package 'MuMIn', Barton 2016). Since we found an interaction between colony and breeding stage, we divided the dataset into subsets to test each param-

eter in each colony and breeding stage separately, performing LMM with the factor of interest as the fixed factor and individual as the random intercept.

To address the differences in the proportion of resting, foraging and relocation between breeding stages on Madeleine, we performed LMMs with breeding stage as a fixed factor and individual as a random factor. We performed analysis of variance with the size of the 95% kernel utilization distribution for each foraging trip to test for differences in the size of the foraging area used for tropicbirds from Madeleine and St Helena.

Analysis of environmental relationships

To test whether locations classified as 'foraging behaviour' differed in oceanographic conditions from those classified as 'travelling behaviour', we first downloaded environmental variables corresponding spatially and temporally with the tracking data from the Env-DATA system in Movebank (Dodge et al. 2013) and from other oceanographic data sources. We downloaded day- and night-time sea surface temperature (SST; 4 km resolution, monthly average), net primary productivity (NPP, 0.083 degree resolution, monthly average), chlorophyll *a* concentration (chl *a*, 4 km resolution, monthly average), surface wind vectors (10 m above ground, from Global Atmospheric Reanalysis of the European Centre for Medium-Range Weather Forecasts, 6 h average) and ocean depth (from ETOPO1 Global Relief Model). We further downloaded monthly mean bottom temperature, current velocity, the depth of the mixed surface layer, salinity and sea surface height from a global analysis at a 0.25 degree resolution (http://marine.copernicus.eu/documents/PUM/CMEMS-GLO-PUM-001-025.pdf). In addition, we acquired the location of major seamounts from bathymetric charts because they can be hotspots of biodiversity (Morato et al. 2008), and downloaded the species richness of Scombridae, subsurface predatory fish that can drive prey fish species for tropical birds to the surface, from Aquamaps (www.aquamaps.org; Kaschner et al. 2016).

We combined surface wind vectors (zonal and meridional velocities) to calculate wind speed (in m s^{-1}), and ignored wind direction given that both colonies have very consistent prevailing wind fields (SE winds at St Helena, NE winds at Madeleine). We combined zonal (U) and meridional (V) current velocities to calculate eddy kinetic energy (EKE) using the standard formula EKE = ½(U^2+V^2). We cal-

culated the bathymetric slope for each grid cell using the function 'terrain' in the R package 'raster' based on the depth of surrounding grid cells. For each grid cell, we also calculated the Euclidian distance to the colony and nearest seamount.

For each environmental variable we fitted 2 binomial generalised linear mixed models (GLMMs), examining whether the behavioural state ('foraging' or 'relocating') was related to the environmental variable and varied by colony (environment × colony interaction), or whether the behavioural state was unrelated to the environmental variable (null model). Each of these 2 models included the breeding status and the colony as a fixed factor, and a random intercept for the individual foraging trip to account for non-independence of locations along the same foraging trip. We then used a likelihood-ratio test to examine whether the environmental differences were supported by the data (Lewis et al. 2011). To assess the explanatory power of the full model, we calculated the variance explained (R^2) following Nakagawa & Schielzeth (2013), and we present mean values and associated standard deviations for each environmental variable.

Next, we explored whether all environmental variables together (see Table 4) could reliably distinguish between locations classified as 'foraging' and the general marine environment to assess whether red-billed tropicbirds may select certain environmental features for foraging. For this we first downloaded environmental variables for a regular grid of locations spaced 20 km apart and covering the entire marine area within the radius corresponding to the maximum foraging travel distance from the colony of red-billed tropicbirds at both colonies using the same data sources in the Env-DATA system in Movebank (Dodge et al. 2013) and the global physical reanalysis. The oceanographic variables obtained from the background locations coincided temporally with the month in which tracking data were obtained at the respective colony.

We tested for correlation between predictor variables and removed 1 of 2 highly correlated ($r_S > 0.7$) variables; on St Helena we found a very strong correlation between NPP and chl a ($r_S = 0.885$) and between day-and night-time SST ($r_S = 0.967$), and therefore removed NPP and night-time SST from further analyses. In Madelaine, we found a very strong correlation between bottom temperature and bathymetry ($r_S = 0.822$), between bottom temperature and mixed layer depth ($r_S = -0.710$) and between day- and night-time SST ($r_S = 0.912$), and therefore removed bottom temperature and night-time SST

from further analyses. Because there was only a single seamount in the foraging range of red-billed tropicbirds around Madelaine, distance to colony and distance to the seamount were also highly correlated ($r_S = 0.792$); we therefore removed distance to the seamount from further analyses.

We then fitted an algorithmic random forest model to classify locations as either background or foraging locations for each colony separately because this algorithm is a powerful method that can include and account for interactions among many different variables (Breiman 2001, Cutler et al. 2007, Hochachka et al. 2007). We fitted this model in the R package 'randomForest' (Liaw & Wiener 2002) with 1500 trees allowing 3 variables to be tried for each node in each tree, and internally cross-validated the model by using 65% of data to construct trees and the remaining 35% to assess the classification success. The importance of variables was assessed via a permutation procedure, where the values of each variable were randomly permuted and the decrease in classification success was calculated (Strobl et al. 2007). We re-scaled the decrease in classification accuracy and present relative variable importance (scaled to 100% for the most important variable) together with the classification success of the model based on internal cross-validation.

Because seabird tracking data can be highly autocorrelated in space and time, we evaluated whether the random forest model was effective in capturing the spatial and temporal variation in the data using the included environmental variables. We tested for spatial autocorrelation in model residuals by calculating Moran's I (Moran 1950) for the 50 nearest neighbouring grid cells in each month using the function 'moran.test' in the R-package 'spdep'. Moran's I ranges from −1 (perfect dispersion) to +1 (perfect correlation), with 0 indicating complete lack of autocorrelation, and we concluded that the random forest model adequately accounted for spatial autocorrelation in the data if the absolute value of Moran's I of residuals was <0.1.

Algorithmic models can overfit the data, and we therefore externally validated each model using data from the other colony to assess whether the ecological relationships identified by the random forest model were generalisable across the tropical Atlantic (Elith & Leathwick 2009, Oppel et al. 2012, Torres et al. 2015). We evaluated what proportion of St Helena locations were accurately classified by the model trained with data from Iles de la Madeleine, and vice versa, and report the classification success of these external validations.

RESULTS

Ethics

On Madeleine, some birds failed during the study period but the percentage of tracked birds that failed to hatch (25%) or to fledge (16%) did not differ from those found for the control group (0 and 25%, respectively) (hatching χ^2_1 = 2.782, N = 41, p = 0.095; fledging χ^2_1 = 0.065, N = 35, p = 0.799). Similarly, on St Helena, tracked birds that failed to hatch (25%) or to fledge (88.9%) did not differ from those found for control birds (53.8 and 33.3%, respectively) (hatching χ^2_1 = 1.129, N = 24, p = 0.288; fledging χ^2_1 = 2.813, N = 15, p = 0.094). Chick or adult mass between tracked and control birds did not differ significantly (chick mass tracked = 706 ± 49.93 g; untracked = 692.86 ± 89.2 g; $t_{4.89}$ = −0.169, p = 0.873; adult mass tracked = 614.63 ± 46.21 g; untracked 596.86 ± 51.21 g; $t_{56.95}$ = 1.367, p = 0.177). Return rates to the breeding site the following year between tracked and untracked birds did not differ significantly (tracked 75.61%; untracked birds 62.5%; χ^2_1 = 0.438, N = 57, p = 0.508).

Diet identification through regurgitates

The diet of tropicbirds on Madeleine during the breeding period was exclusively composed of 4 families of epipelagic fish: Belonidae (46.7%), Exocoetidae (31.1%), Carangidae (11.1%) and Scombridae (11.1%) (Table 1). Belonidae and Exocoetidae were consumed in greater frequency than Scombridae and Carangidae (χ^2_3 = 16.067, N = 45, p = 0.001). In terms of biomass, these 4 families were consumed in similar quantities: Belonidae (19.7%), Exocoetidae (32.6%), Carangidae (17.8%) and Scombridae (29.2%), although the proportion of Scombridae and Exocoetidae was slightly higher than that of the other 2 families (χ^2_3 = 8.17, N = 111, p = 0.04). The species that occurred in the diet inhabit the surface layer to 100 m depth (Table 1). These fish families include a number of species consumed by tropicbirds that have disparate commercial value, ranging from minor commercial value (Exocoetidae) to high commercial value (Carangidae and Scombridae) (Table 1). In 2015, fisheries captured 12 174.08 t of *Scomber japonicus*, 515.92 t of *S. scomberus*, 5129.03 t of *Caranx rhonchus* and 10 362.37 t of *Trachurus trecae* in the EEZ of Senegal (DPM 2015).

Foraging parameters

From the 41 deployments on Madeleine and 24 on St Helena, we could only obtain 22 and 15 complete foraging trips, respectively, due to loss of the devices. Of the 22 complete trips conducted by Madeleine tropicbirds, all headed in a westerly direction (Fig. 2A), whereas St Helena tropicbirds always headed north of the island (Fig. 2B). The best model explaining the maximum distance from the colony included colony and breeding stage, as well as the interaction between them (Akaike weight = 1; interaction $t_{33.02}$ = 5.26, p < 0.001). We found that the maximum distance from the colony was on average shorter for tropicbirds from Madeleine than for those from St Helena during incubation (Table 2; $t_{1,13}$ = 53.85, p < 0.001), but did not differ during brooding ($t_{20.01}$ = 1.12, p = 0.27). On St Helena, maximum distance from the colony was on average greater during the incubation

Table 1. Summary of prey items from diet samples of red-billed tropicbirds on Madeleine (N: number of specimens obtained). The commercial value of each species/family, depth range in which the species are most commonly found and the source of information are also presented

| Family	N	Species	Commercial value	Depth range (m)	References
Belonidae	8	*Tylosurus crocodilus*	Minor	0–13	Froese & Pauly (2017)
Belonidae	13	*Strongylura senegalensis*	Minor	0– ?	
Carangidae	2	*Trachurus trecae*	High	20–100	Mbengue (2012), DPM (2015), Froese & Pauly (2017)
Carangidae	3	Not identified (digested)			
Exocoetidae	1	*Parexocoetus mento atlanticus*	Minor	0–-20	Froese & Pauly (2017)
Exocoetidae	2	*Exocoetus* sp.	Minor	0–20	Froese & Pauly (2017)
Exocoetidae	1	*Cypselurus* sp.	Minor	0–20	Froese & Pauly (2017)
Exocoetidae	10	Not identified (digested)			
Scombridae	2	*Auxis thazard*	High	0–100	Mbengue (2012), DPM (2015), Froese & Pauly (2017)
Scombridae	3	Not identified (digested)			
Unknown fish	6	Not identified (digested)			
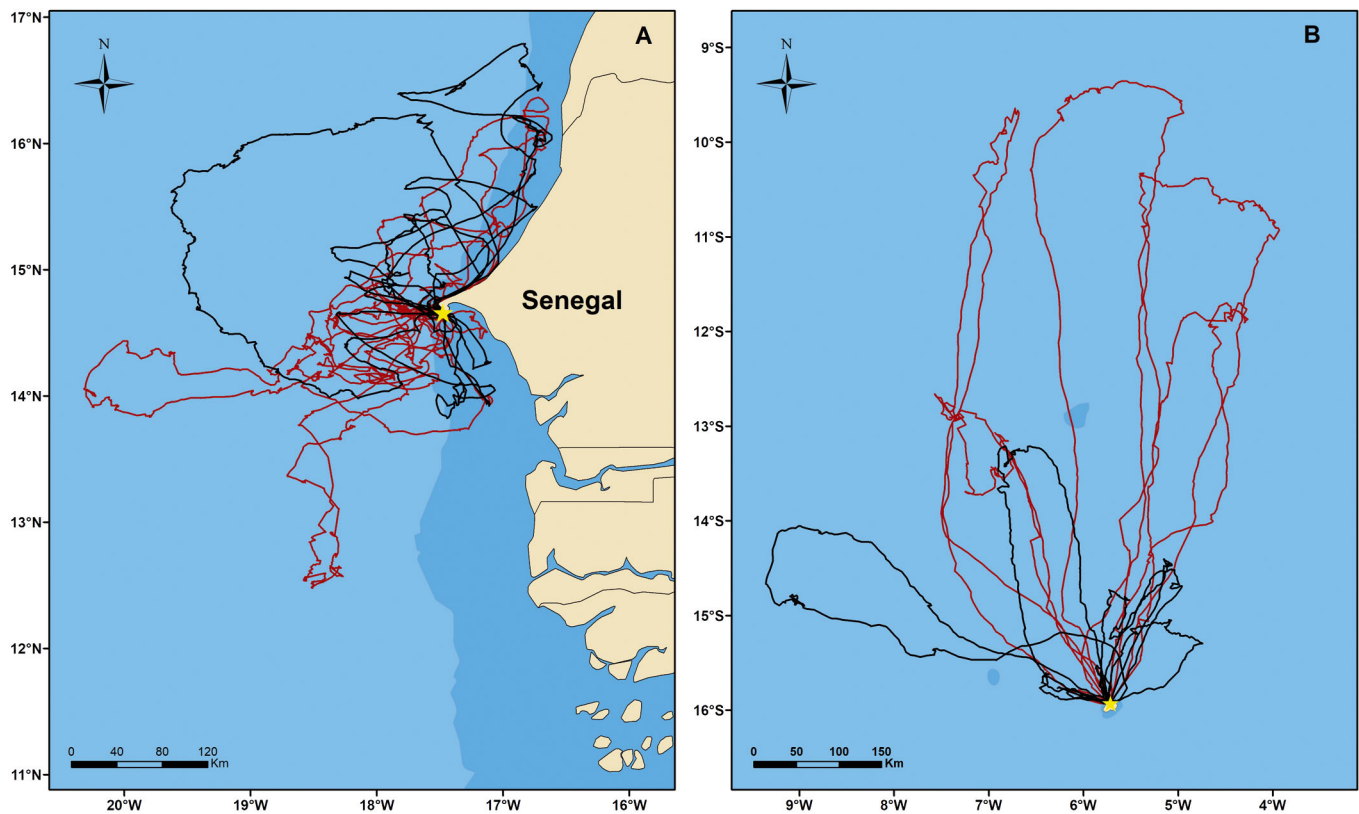
Fig. 2. Red-billed tropicbirds foraging trips during incubation and brooding periods in (A) Madeleine (10 incubating trips, 12 brooding trips) and (B) St Helena (6 incubating trips, 9 brooding trips). Red (black) lines indicate incubating (brooding) trips, dark blue shows the isobath at 200 m, yellow star is the breeding colony

stage than during brooding (Table 2; $t_{12.99} = 6.07$, p < 0.001), although it did not differ between breeding stages on Madeleine ($t_{19.68} = 1.16$, p = 0.26). Regarding trip duration, the best model also included colony and breeding stage and the interaction between them (Akaike weight = 0.86; interaction $t_{32.99} = 2.83$, p = 0.01). Trip duration was shorter on Madeleine than on St Helena during incubation (Table 2; $t_{1,13} = 13.51$, p = 0.003), but did not differ during brooding (Table 2; $t_{20} = -0.45$, p = 0.66). On St Helena, trip duration was on average larger during incubation than brooding (Table 2; $t_{13} = 7.23$, p < 0.001), and on

Madeleine trip duration was marginally longer in incubation than in brooding ($t_{19.99} = 2.08$, p = 0.05). Regarding distance travelled, the best model included colony and breeding stage and the interaction between them (Akaike weight = 0.98; interaction $t_{33} = 3.36$, p = 0.002). Distance travelled was shorter on Madeleine than on St Helena during incubation ($t_{1,13} = 22.05$, p < 0.001), but not during brooding ($t_{20.15} = -0.08$, p = 0.94). Distance travelled was on average larger during incubation than brooding on St Helena ($t_{12.99} = 6.2$, p < 0.001), but not on Madeleine ($t_{19.91} = 1.63$, p = 0.12).

Table 2. Total distance covered, maximum distance, duration and size of the area with 95% kernel density estimations during incubation and brooding stages of red-billed tropicbirds (mean ± SE) on Madeleine and St Helena. N: number of foraging trips, tkm²: thousands of km²

Stage	Colony	N	Total dist. (km)	Max. dist. (km)	Duration (h)	Area (tkm²)
Incubation	Madeleine	10	680.20 ± 115.39	142.22 ± 31.70	115.69 ± 18.94	17.01 ± 4.64
Incubation	St Helena	6	1520.47 ± 97.16	596.28 ± 61.40	182.88 ± 36.95	201.07 ± 4.83
Brooding	Madeleine	12	411.39 ± 116.21	97.26 ± 23.58	56.67 ± 20.52	12.11 ± 4.95
Brooding	St Helena	9	397.94 ± 117.09	149.17 ± 42.09	49.31 ± 17.21	21.17 ± 9.89

The size of the home range (95% KDE) foraging area was greater on St Helena than on Madeleine ($F_{1,35}$ = 8.25, p = 0.01; Fig. 3). Foraging grounds in both colonies completely overlapped with the EEZs (Fig. 3).

Environmental variables

There was strong statistical support for environmental differences between locations classified as 'travelling' and 'foraging', but the magnitude of the differences and the explanatory power of all environmental variables were small (Fig. S4 in Supplement 4; Table 3). Tropicbirds foraged in warmer and much more nutrient-rich and shallower stratified water off the coast of Madeleine compared to St Helena (Table 3), where the environment is characterized by much deeper water with steeper seafloor slopes and a greater number of distinct seamounts (Table 3). Distance to the colony and the number of Scombridae species had the greatest explanatory power in GLMMs (Table 3), and indicated that foraging locations were on average farther from the colony than travelling locations, with slightly higher richness of Scombridae species in St Helena than in Madeleine.

The random forest models were able to distinguish foraging from random background locations based on environmental variables, with very good classification success for both St Helena (misclassification rate from internal cross-validation; foraging: 6.6%, background: 3.1%) and Madeleine (foraging: 1.8%, background: 17.4%). There was no spatial autocorrelation in model residuals (Moran's I for St Helena: −0.011 to 0.098, for Madeleine: −0.005 to 0.015), indicating that the available environmental variables adequately captured the spatial variation in the data. The most important predictor variables differed between colonies, and only distance to colony achieved >80% relative importance at both colonies (Table 4); the richness of Scombridae and salinity were the most important variables around St Helena, while chl a concentration and distance to colony were the most important variables off the coast of Madeleine (Table 4; Fig. S5 in Supplement 4). Tropicbirds appeared to forage in waters with a greater richness of Scombridae around St Helena, but with an intermediate richness of these predatory fish and with intermediate chl a concentration off the coast of Madeleine (Fig. S5). At both colonies, more than 5 predictor variables achieved a relative variable importance >50%, indicating that foraging locations are unlikely to be determined by simple environmental gradients or features. Despite the excellent classification success in internal cross-validation, the models were not transferable to another spatially segregated colony in the Atlantic Ocean, likely because of major environmental differences between the colonies in bathymetry, chl a concentration, sea surface temperature and mixed layer depth. The misclassification rate for foraging locations from St Helena, when predicted from the model trained with data from Madeleine was 100%. For Madeleine, locations predicted from the model trained with data from St Helena was 87.6%. This occurred because each colony-specific model was too closely fitted to the environmental data and pre-
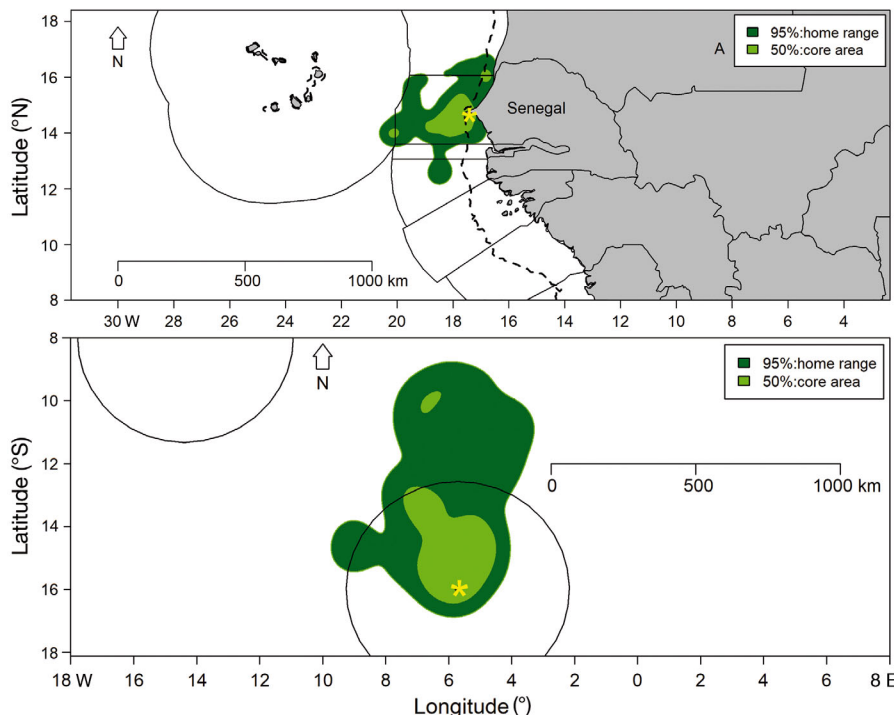

Fig. 3. Kernel density of red-billed tropicbird foraging areas during incubation and brooding overlapped to exclusive economic zones (EEZs) in (A) Madeleine (22 foraging trips) and (B) St Helena (15 foraging trips). Dashed black line is the 200 m isobath, solid black lines mark the EEZ, yellow star indicates the breeding colony

Table 3. Mean ± SD of environmental conditions at foraging and travelling locations of red-billed tropicbirds tracked from Iles de la Madeleine and St Helena during the breeding season in 2015/2016 (incubation and chick-rearing combined); n: number of locations from which environmental data were available, R^2: proportion of variance explained by the generalised linear mixed model with a colony × environment interactive fixed effect. The p-value indicates whether the environmental parameter in the model is different from 0. SST: sea surface temperature

Parameter	Colony	Behavioural stage	n	SST (°C) Mean	SD	R^2	p
SST (°C)	Madeleine	Foraging	1285	25.0	1.3	0.045	0.003
		Travelling	2025	24.8	1.2		
	St Helena	Foraging	513	21.2	0.7		
		Travelling	1155	21.1	0.6		
Nighttime SST (°C)	Madeleine	Foraging	1285	24.3	1.3	0.048	0.001
		Travelling	2025	24.1	1.2		
	St Helena	Foraging	445	20.9	0.7		
		Travelling	1017	20.8	0.6		
Net primary productivity (mg C m^{-2} d^{-1})	Madeleine	Foraging	1288	1662.6	1081.2	0.038	0.044
		Travelling	2018	1775.3	1217.5		
	St Helena	Foraging	540	590.7	96.3		
		Travelling	1212	589.2	87.9		
Wind speed (m s^{-1})	Madeleine	Foraging	1309	6.9	1.3	0.036	0.64
		Travelling	2088	6.9	1.4		
	St Helena	Foraging	540	7.1	0.9		
		Travelling	1212	7.1	0.8		
Chlorophyll a (mg m^{-3})	Madeleine	Foraging	1090	1.5	1.9	0.049	0.41
		Travelling	1737	1.5	2.5		
	St Helena	Foraging	197	0.2	0.1		
		Travelling	462	0.2	0.1		
Depth (m)	Madeleine	Foraging	1634	−1775.5	1409.7	0.068	<0.001
		Travelling	2543	−1592.8	1319.4		
	St Helena	Foraging	625	−3947.3	737.4		
		Travelling	1386	−3871.1	765.8		
Slope of seafloor (°)	Madeleine	Foraging	1634	1.1	0.8	0.062	<0.001
		Travelling	2543	1.2	0.9		
	St Helena	Foraging	625	2.0	1.9		
		Travelling	1386	2.1	2.1		
Bottom temperature (°C)	Madeleine	Foraging	1337	8.6	8.0	0.044	0.51
		Travelling	2112	8.5	7.6		
	St Helena	Foraging	491	2.4	1.7		
		Travelling	1121	2.4	1.8		
Distance to colony (km)	Madeleine	Foraging	1634	110.0	77.9	0.085	<0.001
		Travelling	2543	100.1	71.1		
	St Helena	Foraging	625	263.0	191.9		
		Travelling	1386	232.7	171.5		
Distance to seamount (km)	Madeleine	Foraging	1634	89.9	49.0	0.06	<0.001
		Travelling	2543	85.7	43.3		
	St Helena	Foraging	625	64.7	43.4		
		Travelling	1386	56.7	33.2		
Eddy kinetic energy (m s^{-1})	Madeleine	Foraging	1337	0.011	0.010	0.052	0.027
		Travelling	2112	0.011	0.010		
	St Helena	Foraging	491	0.010	0.006		
		Travelling	1121	0.010	0.006		
Mixed layer depth (m)	Madeleine	Foraging	1337	19.0	4.0	0.057	<0.001
		Travelling	2112	19.3	3.8		
	St Helena	Foraging	491	45.0	14.6		
		Travelling	1121	46.9	15.0		
Salinity (g kg^{-1})	Madeleine	Foraging	1337	34.90	0.34	0.048	0.71
		Travelling	2112	34.91	0.32		
	St Helena	Foraging	491	36.56	0.15		
		Travelling	1121	36.59	0.14		
Sea surface height (m)	Madeleine	Foraging	1337	−0.041	0.041	0.053	0.004
		Travelling	2112	−0.043	0.041		
	St Helena	Foraging	491	−0.085	0.027		
		Travelling	1121	−0.081	0.025		
Scombridae species (n)	Madeleine	Foraging	1594	6.21	1.94	0.09	<0.001
		Travelling	2490	6.32	1.90		
	St Helena	Foraging	625	7.27	1.01		
		Travelling	1386	7.31	0.96		

Table 4. Relative importance of environmental predictor variables to distinguish between red-billed tropicbird foraging locations and the general environment (random background locations) around Iles de la Madeleine and St Helena during the breeding season in 2015/2016. Variable importance is derived from a permutation procedure based on a random forest algorithm, where the increase in the mean squared error (MSE) indicates the decrease in classification accuracy when a variable is randomly permuted. Relative importance is scaled to 100% for the most important variable

Variable	St Helena		Madeleine	
	Increase in MSE	Relative importance (%)	Increase in MSE	Relative importance (%)
Bottom temperature	49.3	57.8	Not used	
Chlorophyll *a*	62.1	72.8	145.4	100.0
Depth	47.1	55.2	64.4	44.3
Distance to colony	69.1	81.0	120.1	82.6
Distance to seamount	60.1	69.8	Not used	
Eddy kinetic energy	53.0	62.1	81.0	55.7
Mixed layer depth	47.1	55.2	57.0	39.2
Month	47.6	55.8	32.9	22.6
Net primary productivity	Not used		68.8	47.3
Salinity	75.1	88.0	61.4	42.2
Sea surface height	59.4	69.6	63.9	44.0
Sea surface temperature	50.4	59.1	76.5	52.6
Slope of seafloor	39.4	46.2	70.8	48.7
Species richness of Scombridae	85.3	100.0	98.6	67.8
Wind speed	65.2	76.5	93.9	64.5

dicted either universally high (St Helena to Madeleine) or universally low (Madeleine to St Helena) suitability for foraging at the other colony.

Activity pattern and behaviour

We found a higher proportion of resting during incubation than during brooding ($t_{17.79}$ = 2.78, p = 0.01), and a lower proportion of travelling during incubation than brooding ($t_{19.34}$ = −2.53, p = 0.02). We did not find a significant difference in the proportion of foraging between breeding stages ($t_{18.34}$ = −1.34, p = 0.19). Tropicbirds on Madeleine rested mainly during the night and midday and showed travelling and foraging peaks around 08:00 and 19:00 h, generally matching with sunrise and sunset periods (Fig. 4).

DISCUSSION

This study provides the first data on the feeding ecology of red-billed tropicbirds in the eastern tropical Atlantic where the species has been poorly studied. We provide the first insights on the diet, daily activity patterns, foraging movements and feeding habitat selection of this species in the Atlantic and

show how the foraging behaviour of tropicbirds can vary substantially between 2 areas with contrasting oceanographic conditions.

On Madeleine, red-billed tropicbirds fed exclusively on epipelagic fish of Belonidae Exocoetidae, Carangidae and Scombridae during their breeding period. This diet contrasts with that described for the same species in the Gulf of California and Trinidad and Tobago; these more oceanic environments provided a diet that was composed not only of fish but also squid (Castillo-Guerrero et al. 2011). The first 3 families are typically predated by tropical seabirds in association with large sub-surface predators during the day (Spear et al. 2007). Indeed, Madeleine birds showed mainly diurnal foraging activity patterns, with most of the resting taking place at night, but also with a peak of resting during the central and hottest hours of the day. This result aligns with that of red-tailed tropicbirds *Phaethon rubricauda* on Christmas Island during incubation (Sommerfeld & Hennicke 2010). In the eastern Pacific, 46% of the feeding red-billed tropicbirds were associated with sub-surface predators or travelling cetaceans for feeding (Spear & Ainley 2005b). On Madeleine, the shelf break is less than 100 km from the breeding colony, and tropicbirds mainly foraged on the shelf slope and beyond. The same foraging grounds are also exploited by Cape Verde shearwaters *Calonectris edwardsii* during their incubation period in June (Paiva et al. 2015). Indeed, seabird species diversity and abundance in the Canary Current generally peak within 20 km of either side of the shelf break (Camphuysen et al. 2013). In the Canary Current, the megafauna also concentrates around the shelf break (Zeeberg et al. 2006, Camphuysen et al. 2013). Altogether, these patterns indicate that the association with subsurface predators on the shelf break in front of Madeleine takes place during the day and might be an important tropicbird feeding strategy.

This area is also important for small migratory epipelagic species, such as horse mackerel (*Trachurus* spp.), that are particularly abundant in winter and early spring (Arístegui et al. 2009) when
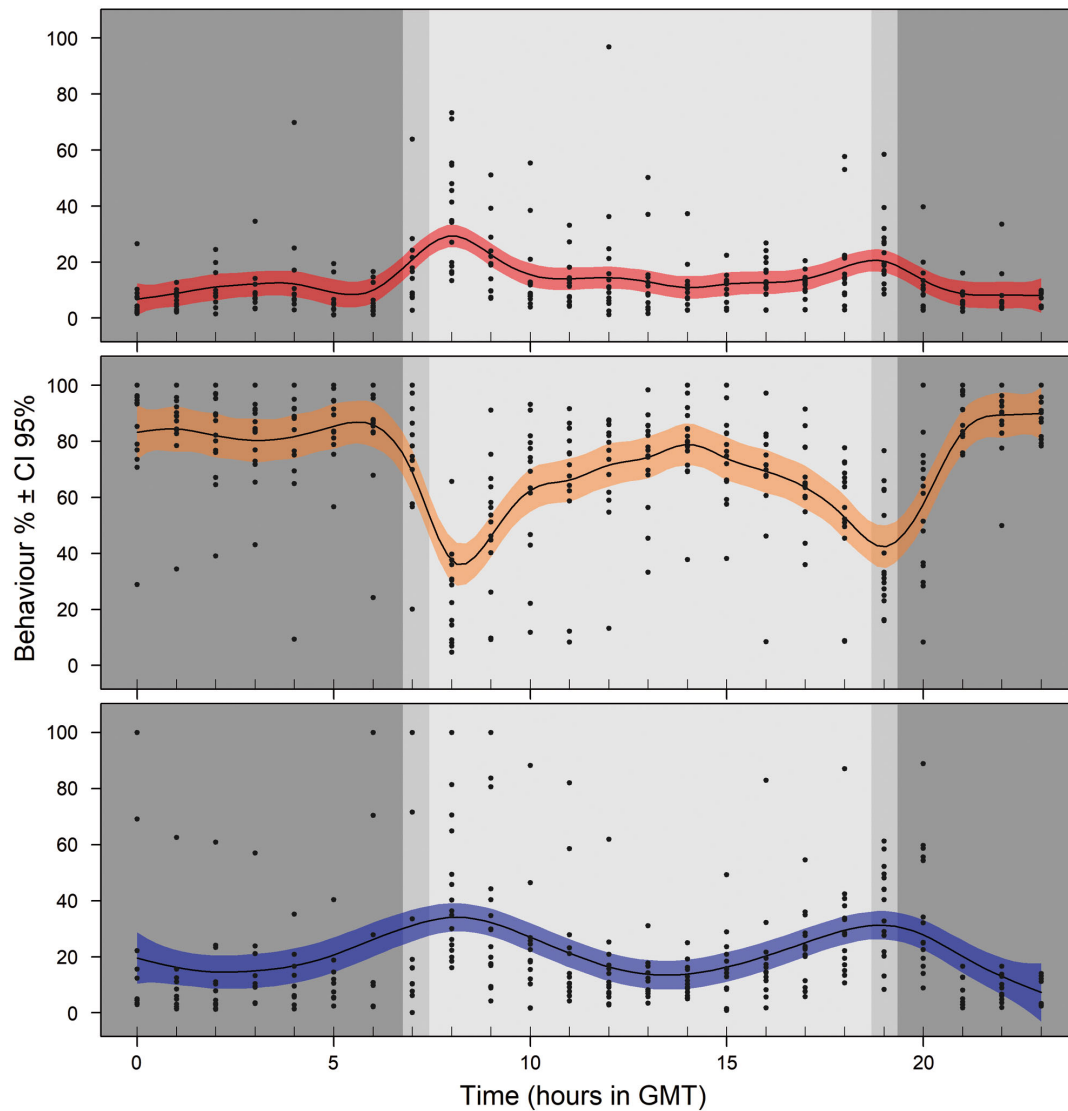
Fig. 4. Behavioural modes throughout the day during the breeding period of red-billed tropicbirds (incubation and brooding) on Madeleine. Dark grey areas correspond to darkness, light grey areas to sunrise and sunset periods and lightest grey areas to daylight. Orange represents resting, red is foraging, and blue is relocation

local upwelling is more intense (Menna et al. 2016). This may explain why tropicbird breeding peaks at this time (Diop et al. in press). Although tropicbirds in Senegal feed in areas with artisanal gillnets and high demersal trawler activity, which discard around 40% of their catch (Belhabib et al. 2014), the diet composition indicates that tropicbirds do not rely on demersal discards. However, the possibility that tropicbirds may partly feed on discards cannot be excluded, since large pelagic trawlers fishing on small pelagic fish also operate in the area and may discard pelagic species found in the diet of the tropicbirds (ter Hofstede & Dickey-Collas 2006).

One of the major drivers of foraging behaviour is the breeding stage, since the energy demands and the breeding duties change across the breeding season, limiting foraging in time and space (Phillips et al. 2017). In red-billed tropicbirds, foraging distance, foraging range, trip duration, distance travelled and depth of the foraging areas were greater during incubation than during brooding. These variations are usually attributed to the constraints of the brooding behaviour, when adults are forced to forage on a possibly suboptimal area close to the colony to ensure small chicks are fed frequently (Phillips et al. 2017). During brooding, foraging adults need to meet the energy requirements of their chicks, forcing birds to

increase their effort. In agreement, we found tropicbirds spending less time resting during brooding than during incubation trips, whereas travelling was higher during brooding than during incubation. Such changes are common in albatrosses, petrels and penguins (Phillips et al. 2017), and have previously been noted in tropicbirds (Sommerfeld & Hennicke 2010).

Oceanographic conditions at regional scales may play an important role in the foraging behaviour of tropical seabirds (Hennicke & Weimerskirch 2014, McDuie et al. 2015, 2018, McDuie & Congdon 2016, Weimerskirch et al. 2016, Miller et al. 2018). The more southerly St Helena is remote and surrounded by oceanic waters that are almost exclusively used by seabirds from this island, where the predictability and abundance of prey is presumably lower than on the permanent upwelling system of the African Shelf (Weimerskirch 2007, Harding et al. 2013). This would explain why net primary productivity and chl *a* concentration of waters used by the tropicbirds from Madeleine were, respectively, 3- and 7-fold greater than those used by birds from St Helena, which may indicate lower food availability in the latter locality. This difference in food availability probably explains a greater foraging effort (trip duration and distance travelled) of tropicbirds breeding on St Helena and a stronger attraction to areas with the greatest species richness of Scombridae than those on Madeleine. However, overall the environmental variables had only limited power to explain where tropicbirds searched for food, and distance to the colony was one of the most important predictors at both colonies (Table 4), similar to other tropical seabirds (Oppel et al. 2017). In the case of Madeleine, tropicbirds did not exploit upwelling colder waters of the continental shelf and mainly foraged westwards on the shelf slope and beyond, possibly to feed in association with subsurface predators, as explained above. However, tropicbirds on Madeleine did not associate with species richness of Scombridae, although this might be because only a single or few species of tuna might be abundant in the area. On St Helena, tropicbirds showed a stronger directional bias in their distribution than the birds near Africa, despite a much larger area of available open ocean over which they may theoretically have dispersed. In contrast to masked boobies *Sula dactylatra* of St Helena, which used waters all around the island (Oppel et al. 2015), tropicbirds always travelled to the north. Several underwater seamounts exist between St Helena and Ascension, 1200 km to the north-east, and seamounts may attract some marine top predators (Morato et al. 2008). However, tropicbirds from St Helena did not appear to spend more time in the vicinity of seamounts (Fig. 3). The birds we tracked all breed on the north and north-eastern coast of St Helena, and other tropicbird colonies exist on the west and south coasts, but those birds nest on precipitous cliffs and were therefore not accessible for sampling. Although the tropicbird colonies on St Helena are generally small (10–30 pairs), it is possible that there is spatial partitioning at sea, and the birds we tracked therefore avoided marine areas to the south of the island presumably used by birds breeding in other colonies around St Helena (Ceia et al. 2015). An alternative explanation for the northward movement could be the prevalent gradient in water temperature, with warmer waters north of St Helena than south of the island. St Helena is the southernmost breeding locality of the species in the Atlantic Ocean, and the preferred prey of tropicbirds or the tuna they associate with may be mostly found in warmer waters north of the island.

One potential threat for tropicbirds is the interaction with fisheries. The prey of tropicbirds are also targeted by regional fisheries, which may result in negative interactions (Zydelis et al. 2013). On Madeleine, the foraging grounds of tropicbirds are not within a marine protected area. Indeed, the only protection is the 50 m seawards extension of Madeleine protected area around the colony (DPN 2010), which is clearly too small for this species (Oppel et al. 2018). However, the foraging grounds completely overlap with that of the EEZ of Senegal and surrounding countries. Artisanal fisheries, such as the Atlantic sailfish fisheries operating in the area, may pose a risk of by-catch for tropicbirds, since this fishery uses horse mackerel as bait (Sow 2016). However, worldwide by-catch of tropicbirds seems to be scarce, only documented on 2 occasions (Pott & Wiedenfeld 2017), and it is unlikely that fisheries operating in the area cause a direct impact on tropicbirds. Senegalese fisheries may also pose an indirect competitive threat to tropicbirds (Cury et al. 2011), as Cunene horse mackerel *T. tracea*, an important component of tropicbird diet, are of high commercial value and are extensively fished (Mbengue 2012, DPM 2015). In fact, small pelagic fish stocks in Senegal are over-exploited, and the ecosystem is deteriorating due to climate change (Belhabib et al. 2014, Coll et al. 2016), enhancing interspecific competition with seabirds, which could ultimately affect the productivity and viability of their populations (Arístegui et al. 2009, Sambe et al. 2016). In addition, tuna catches in the Canary Current seem to be dropping for at least 2 of the 3 most common species in the area (Braham & Corten 2015),

which may reduce feeding opportunities for tropicbirds or, alternatively, increase pelagic fish abundance due to reduced predation pressure (Montevecchi 2002). On the other hand, fishing activities around St Helena are regulated and licensed to comply with the objectives of the marine protected area and exploit inshore waters not far from the island (St Helena Government 2016). These only partially overlap with the tropicbird's foraging grounds, which may reduce this competitive interaction.

Ultimately, our study reveals that red-billed tropicbirds can breed in localities that display contrasting marine environments. The differential colony-specific foraging movements and feeding habitat selection demonstrate that patterns of activity and environmental characteristics cannot easily be extrapolated across breeding colonies. Finally, foraging grounds of tropicbirds on Madeleine completely overlap with EEZs of surrounding countries, which indicates that the conservation of the species totally depends on national governments. Indirect competition with fisheries that overexploit the prey of tropicbirds and target large sub-surface predators, in conjunction with the increase in SST in the Canary Current, may be of particular concern for tropicbirds. Further research is needed to fully understand the impact of these at-sea threats on the western African population of this species.

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