FORAGING ECOLOGY OF RED-BILLED TROPICBIRD *PHAETHON AETHEREUS* IN THE CARIBBEAN DURING EARLY CHICK REARING REVEALED BY GPS TRACKING

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ABSTRACT

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Investigating the foraging patterns of tropical seabirds can provide important information about their ocean habitat affinities as well as prey choice. Foraging studies of Red-billed Tropicbird *Phaethon aethereus* populations in the Caribbean are lacking. We sought to rectify this by opportunistically sampling regurgitates at nest sites on the island of St. Eustatius, Lesser Antilles, and by linking the GPS tracks of foraging adults to remotely sensed environmental variables. Diet samples were dominated by Exocoetidae (59.5%) and Belonidae (14.9%), although we were unable to identify 25.5% of samples due to digestion. Tropicbirds nesting on St. Eustatius exhibited diurnal foraging patterns, foraged in deeper waters with higher chlorophyll concentration, and consumed fewer Exocoetidae species compared to travelling behaviour. The maximum distance travelled from the colony was 953.7 km, with an average trip length of 176.8 (± 249.8) km. The biologged birds crossed multiple exclusive economic zones and marine protected areas, and on that basis, we suggest that efforts to protect and conserve this species may require transboundary collaboration throughout the wider Caribbean.

Key words: diet, EEZ, foraging area, MPA, oceanographic variables, *Phaethon aethereus*, seabird

INTRODUCTION

Foraging areas in temperate marine environments are characterised by enhanced primary productivity, which leads to highly predictable foraging resources for pursuit-diving seabirds (Ainley 1977). On the other hand, in the less productive and often oligotrophic tropical oceans where prey is more temporally and spatially patchy (Longhurst & Pauly 1987, Ballance & Pitman 1999, Weimerskirch *et al.* 2005b), a number of seabirds forage by plunging in waters of much greater clarity (Ainley 1977). Birds foraging in tropical oceans require more energetically efficient flight as well (Ainley 1977) to enhance their foraging efficiency, as they often feed in association with highly mobile sub-surface predators that drive prey to shallower depths (Au & Pitman 1986, Ballance *et al.* 1997, Catry *et al.* 2009a). Moreover, oceanographic features that can concentrate prey, such as upwelling associated with specific seasons or topography, provide opportunities for seabirds to forage in tropical waters (Zavala-Hidalgo *et al.* 2006, Weimerskirch 2007, Jodice *et al.* 2015, Oppel *et al.* 2017, Wilkinson *et al.* 2020). Thus, tropical seabird communities are structured by competition (prey abundance/availability) and energetic constraints (flight proficiency) in relation to marine productivity (Ballance *et al.* 1997, Spear *et al.* 2007); only species with relatively low flight costs can forage in areas of low productivity and transit between scattered clumps of prey. Within this context, seabirds tracking in combination with diet studies can provide insight into the relationships between individuals, prey, and oceanographic conditions. The correlation between foraging range and colony size, in both tropical and sub-tropical systems, is also involved (e.g., Jovani *et al.* 2016, Lamb *et al.* 2017, Wilkinson *et al.* 2020). Although many seabird tracking studies have been conducted in mid- and high-latitude regions, analogous studies in sub-tropical and tropical areas have been less frequent.

Among studies of seabird foraging within the tropics, several studies of tropicbirds (family Phaethontidae) have used miniaturised GPS technology (e.g., Sommerfeld & Hennicke 2010, Soanes *et al.* 2016, Diop *et al.* 2018, Santos *et al.* 2019). Soanes *et al.* (2016) identified foraging areas of Red-billed Tropicbirds *Phaethon aethereus* (RBTR) from Anguilla in the eastern Caribbean during the breeding season. Individuals foraged primarily within ~100 km of the colony, but due to the small sample size, the authors were unable to model habitat use or provide detailed data on daily activity patterns or diet. Diop *et al.* (2018) combined GPS tracking, environmental variables, and diet samples to determine the feeding ecology and foraging strategies of RBTR from Senegal's Îles de la Madeleine in the eastern South Atlantic and from St. Helena in the central South Atlantic Ocean. RBTR foraging behaviour was similar but not identical in the two areas, differing with respect to species richness of Scombridae and use of nearshore compared to pelagic waters. In regard to White-tailed Tropicbirds *P. lepturus* (WTTR), Santos *et al.* (2019) tracked the movements of a colony in Brazil, where they showed a preference

for clear, warm surface waters conducive for foraging on flying fish (Exocoetidae; similar to the Hawaiian Islands: Harrison *et al.* 1983). Tropicbirds are also generally considered to be diurnal (Spear *et al.* 2007, Sommerfeld & Hennicke 2010). For example, Diop *et al.* (2018) determined that RBTR from Îles de la Madeleine rested at night and midday while travelling, and foraging peaked around 08h00 and 19h00, which generally matched sunrise and sunset. A similar foraging pattern was observed among Red-tailed Tropicbirds *P. rubricauda* (RTTR) from Christmas Island in the Indian Ocean (Sommerfeld & Hennicke 2010).

We investigated aspects of the foraging ecology of RBTR during the early chick-rearing period (< 21 days old) on St. Eustatius, a small inhabited island in the Lesser Antilles in the northeastern Caribbean. The aim of our study was to examine the species' diet and foraging behaviour, and to characterise foraging locations in relation to oceanographic variables. We hypothesised that the diet of adults and chicks would consist primarily of flying fish and squid, as documented by observations of RBTR in the Gulf of California (Castillo-Guerrero *et al.* 2011) and the eastern Atlantic (Diop *et al.* 2018), as well as RTTR in the central Pacific (Harrison *et al.* 1983, Spear *et al.* 2007). We predicted that RBTR foraging activity would peak at sunrise and sunset, similar to the species' behaviour in the Pacific and eastern Atlantic oceans (Sommerfeld & Hennicke 2010, Diop *et al.* 2018). Finally, we hypothesised that RBTR on St. Eustatius would not forage in low-productivity waters proximal to the colony but rather would commute to deeper waters with higher chlorophyll concentrations and a high species richness of Exocoetidae (i.e., the hypothesised primary prey; Harrison *et al.* 1983.) This last hypothesis is in line with previous studies that have documented tropical seabird species (e.g., RBTR, Masked Booby *Sula dactylatra*, Red-footed Booby *S. sula*) foraging in deeper, more productive waters and ignoring the marine habitat surrounding their colony (Weimerskirch *et al.* 2005a, Diop *et al.* 2018, Wilkinson *et al.* 2020). Determining important marine habitats for seabird species whose populations have not previously been studied can reveal crucial information related to population ecology, foraging strategies, and habitat selection (Wakefield *et al.* 2009).

METHODS

Study species

RBTR are medium-sized (90–107 cm in length and weighing < 700 g; Orta *et al.* 2020), loosely colonial, pelagic-foraging seabirds. They occur in the tropical zones of the Pacific and Atlantic oceans and in the northern Indian Ocean (Orta 1992). Despite their wide distribution, the global population of RBTR is relatively small, estimated to be 8000–15 000 pairs (BirdLife International 2021), including about 1800–3400 pairs in the Caribbean (Lee & Mackin 2008, Lee & Walsh-McGehee 2000). Females lay a single egg, which is incubated by both parents for 40–43 days (Boeken 2016, Schaffner 1991). After hatching, the chick remains in the nest for 70–85 days (Castillo-Guerrero *et al.* 2011, Boeken 2016), during which it is provisioned by both parents.

Study area and data collection

This study was conducted on St. Eustatius (17.29°N, 062.59°W), a small, inhabited island located in the northern Lesser Antilles. St. Eustatius National Marine Park was established in 1996 and is 2750 ha (27.5 km²) in size. It encircles the entire coastline of the island, extending out to waters of 30 m depth, ~3 km offshore

(STENAPA 2022). Two terrestrial Important Bird and Biodiversity Areas (IBA), the Quill IBA to the south and the Boven IBA to the north, were established in 2009 (BirdLife International 2020). The Boven IBA encompasses the majority of cavities in the cliffs where RBTRs nest. RBTR is the only seabird species that nests on St. Eustatius (Lowrie *et al.* 2012). The globally important breeding population here is estimated to be 300–500 pairs (Madden 2019), with Pilot Hill on the west coast being the largest and most accessible nesting area (Fig. 1). Bathymetry within ~2 km of the shoreline ranges from 0 to 200 m (Nieto *et al.* 2013).

Diet identification through regurgitates

Similar to Harrison *et al.* (1983), we collected regurgitated prey items opportunistically from a) chicks that were being weighed during regular monitoring, b) adults that were being identified by band numbers during regular monitoring, and c) items found inside the nest cavity. We stored regurgitate samples frozen (−20 °C) until analysis, at which point we thawed and cleaned them. Most regurgitates contained partly digested prey, some of which could be identified following Humann & Deloach (2002) or local expert opinion. We measured prey items when they were both fresh and dry. Diet was described based on "numerical frequency," defined as the number of items from a given prey family relative to the total number of prey items (Alonso *et al.* 2018).

Foraging trajectory

We deployed Mobile Action igotU™ GT-120 GPS devices on 65 adult tropicbirds between 2016 and 2020; some individuals were tagged more than once over multiple years, thus 83 total devices were deployed. During an initial trial in 2016, we deployed 35 devices on both incubating and brooding birds, but 18 were lost due to incorrect deployment (i.e., on two central rectrices instead of four). An additional eight incubating adults did not leave the nest on foraging trips. In subsequent years, we chose to deploy tags on only adults with chicks < 21 days of age (*sensu* Santos *et al.* 2019) and on only one adult of a given nest, as RBTR parents alternate foraging trips. Individual birds were caught by hand inside the nest cavity. We marked the head of the bird with a permanent marker for ease of identification upon retrieval. We programmed GPS devices to record a location every 3 min, after which they were waterproofed with heat-shrink tubing. We attached devices to the top surface of the four central rectrices using three pieces of Tesa tape (width: 1.5 cm, length: 10 cm). In 2020, we added a zip tie around the device and tape due to concerns about loss of tape adhesion and loss of the devices. The size of the GPS device was 6.0 cm × 2.5 cm × 0.8 cm (length × width × height) and thus small, relative to cross-sectional area of the bird. The GPS device, zip tie and the Tesa tape together weighed 18 g on average, or < 3% of the weight of the tracked bird; birds were weighed pre- and post-deployment. We recaptured birds inside the nest cavity, recovering the tags on average 5.7 ± 1.8 days following GPS deployment.

For ease of comparison, we closely followed the methods described by Diop *et al.* (2018), summarised here. We filtered GPS trajectories in Movebank (www.movebank.org) to remove erroneous locations and locations on land. Because some birds made more than one foraging trip during the tag deployment and because others were tracked more than once over multiple years, we used the R package "track2KBA" (Beal *et al.* 2020) to separate data into individual trips (R environment 3.5.2; R Core Team 2020). For each foraging trip, we calculated the

maximum distance from the colony using the function *Dist2Colony* in the "trakR" package (Fleishman *et al.* 2019) in R, based on the coordinates of the nest site, using a buffer of 0.2 km. We used a Gaussian Mixture Model maximum likelihood estimation algorithm in that package to describe four types of behaviour (resting, intensive search, extensive search, travelling) based on velocity and turning angle. We used kernel density estimations to transform foraging locations (extensive search) into utilisation distributions (UDs; Wood *et al.* 2000) to determine the foraging areas used most by provisioning adults (95%, 75% and 50% UDs). Areas chosen corresponded to maximum range, intermediate range, and core area distributions, respectively (see Diop *et al.* 2018). We downloaded the "North Atlantic EEZ High Seas" (Maritime Boundaries Geodatabase: Exclusive Economic Zones, version 11; Flanders Marine Institute 2020) and "WDPA_WDOECM_marine" (World Database on Protected Areas; UNEP-WCMC & IUCN 2020) shapefiles to calculate the percentage of foraging areas in the total area covered (km^2) that overlaps with exclusive economic zones (EEZ) and marine protected areas (MPAs). To describe the daily habits of RBTR, we calculated the percentage of each behaviour for each hour of the day using the R package "gamm4" (Wood & Sheipl 2020) and graphed the results.

Statistical analyses

All statistical analyses were performed in the R environment 3.5.2 (R Core Team 2020). We assessed data for normality and homogeneity of variance with Q-Q plots, Shapiro-Wilk tests, and Levene's tests. Non-normal data (e.g., behaviour proportions) were arcsine-transformed to approach normality, thus allowing the use of parametric analyses throughout.

Analysis of environmental relationships

One of our objectives was to test whether locations classified as the behavioural state of "foraging behaviour" differed in oceanographic conditions from those classified as "travelling behaviour" (defined below). We 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 bathymetry (1-arc minute ETOPO1), surface current velocity (0.33° of spatial grid resolution, 5-d OSCAR), wave height (0.33° resolution, 5-d OSCAR), day- and nighttime sea surface temperature (SST; 4 km resolution, monthly average MODIS), net primary productivity (NPP; 0.083° resolution, monthly average), euphotic depth; (0.083° resolution, monthly average VIIRS), and chlorophyll *a* concentration (chl *a*, 4 km resolution, monthly average MODIS). We further downloaded the distribution of Exocoetidae species richness (0.5° resolution) from Aquamaps (www.aquamaps.org; Kaschner *et al.* 2019) and salinity from a global analysis at 0.25° resolution (http://marine.copernicus.eu/documents/PUM/CMEMS-GLO-PUM-001-025.pdf). We combined zonal (U) and meridional (V) current velocities to calculate eddy kinetic energy (EKE) using the standard formula $EKE = \frac{1}{2}(U^2 + V^2)$ (Richardson 1983).
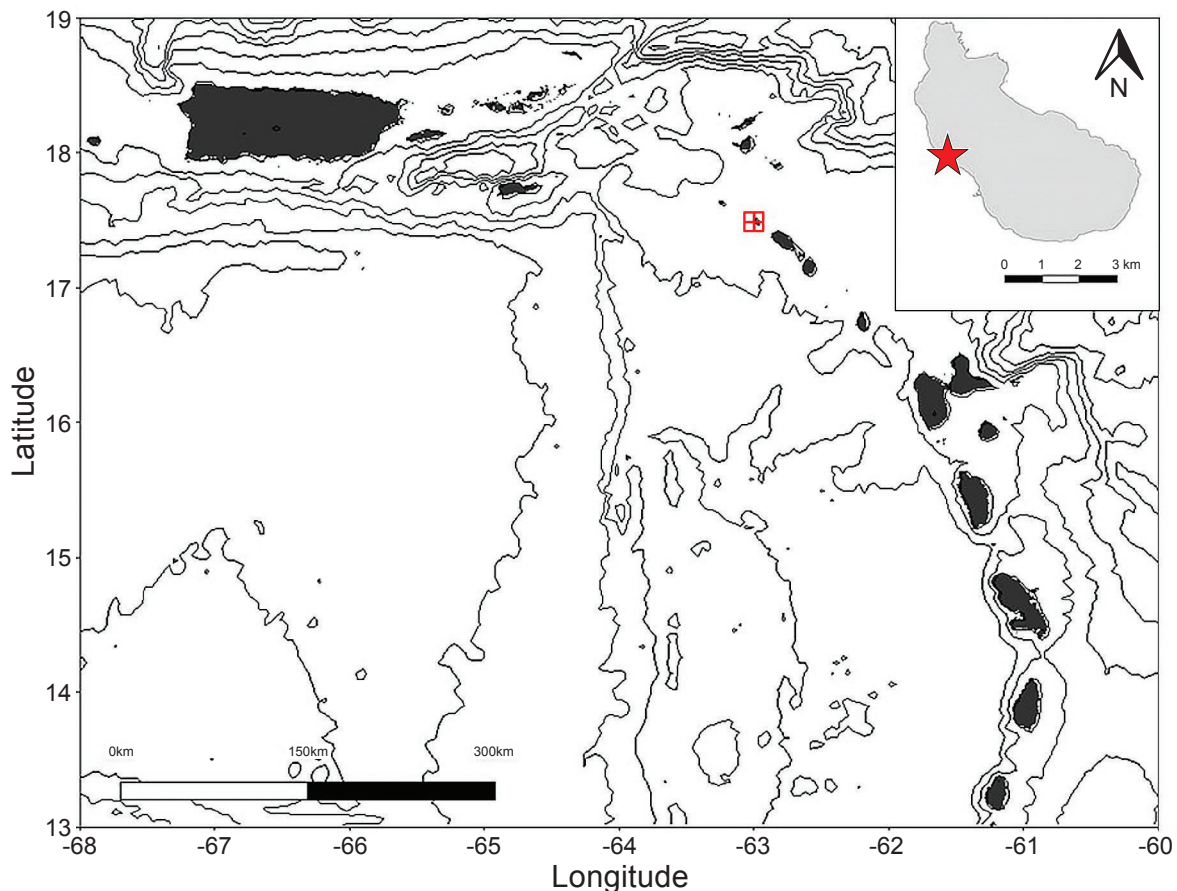

Fig. 1. Map of the Caribbean showing St. Eustatius, Caribbean Netherlands, (red box) and the Pilot Hill study site on St. Eustatius (inset, red star). Black lines denote bathymetry.

After removing one incomplete trip, we used generalised linear mixed models (GLMM) to determine whether the behavioural state was related to the environmental variable (null model). Prior to model exploration, all predictor variables were standardised. We tested for correlation between predictor variables and removed variables that were highly correlated ($r_s > 0.5$; surface current velocity, wave height, NPP, nighttime SST) with multiple other variables. We also ran a generalised linear model with binomial response and logit link function containing the remaining covariates (Table S1 in the Appendix, available on the website). We subsequently examined variance inflation factors for the fitted model for values ≥ 5 to minimise introduced collinearity (see Studwell *et al.* 2017).

Model generation

A null GLMM was fitted to RBTR behavioural state using the R function *glmer* in the R package "lme4" (Bates *et al.* 2015). Of the four behavioural states identified (1 = LL (resting), 2 = LH (intensive search), 3 = HL (transiting), and 4 = HH (extensive search)), two were chosen for analysis: extensive search and transiting, hereafter referred to as "foraging" and "travelling," respectively (Diop *et al.* 2018). GLMMs were then constructed, starting with the most highly parameterised linear combinations of predictor variables. Quadratic terms for all variables were also included to account for the possibility of non-linear responses. In one case loggers were attached to the same bird over two separate breeding seasons (2017/18 and 2018/19; Table S2), so trip identity rather than bird identity was incorporated as a random effect. Fixed variables were sequentially removed and evaluated via an information theoretic approach based on Akaike information criterion for small sample size (AICc) values (Burnham & Anderson 2002). When two variables were correlated (Spearman correlation coefficient ≥ 0.5), we removed one variable from the highly correlated pair.

Model selection and fit

Competing models were assessed using a combination of AICc values and Akaike weights. The model with the lowest AICc and highest weight was considered the best-fit model (Akaike 1974, Sugiura 1978). Models with AICc differences of < 2 relative to the best-fit model were also deemed plausible (Arnold 2010; Table S3). When there was no clear single model (ΔAICc < 2), we averaged across all models weighted by AICc to produce a model-averaged prediction (Burnham and Anderson 2002). Model fit was assessed by using marginal R^2 values (R^2m), which assesses the proportion of total variance explained by the fixed effects. Subsequently, the combined fixed and random effects were assessed with conditional R^2 values (R^2c) (Nakagawa & Schielzeth 2013) using the R package "MuMIn" (Bartoń 2016).

RESULTS

Diet identification through regurgitates

Of 47 regurgitates collected, 35 could be identified (73.9%), with remaining samples being too digested to enable identification (Table S4). On the basis of identified items, tropicbird diet was exclusively composed of two families of epipelagic fish, Exocoetidae and Belonidae. Of the 47 useable samples, the diet included 27 samples of Exocoetidae spp. (unidentified to species, 57.4%), one sample of fourwing flyingfish *Hirundichthys affinis*

(Family Exocoetidae, 2.1%), seven samples of Belonidae spp. (needlefish unidentified to species, 14.9%), and 12 fish parts that we were not able to identify (25.5%).

Foraging parameters

We recovered 37 GPS loggers from 83 deployments, resulting in 46 recorded trips (Table S2). The weight of the birds was 621 ± 53 g (mean ± standard deviation) upon capture and 607 ± 45 g upon recovery. Weight loss was not consistent among all tracked birds (73% lost weight, 27% gained weight). The majority ($n = 28$) of loggers were lost in 2016 during the initial trial, owing to incorrect attachment that resulted in loss of tail streamers and devices; loggers lost after the initial trial were due to failure of the Tesa tape. Of the loggers deployed, seven nests failed (8.4%; five during incubation and two during chick rearing). Nest failure among RBTR on St. Eustatius is common during the incubation period (Madden 2019), and these failures were not attributed to GPS deployment; two chicks died from undetermined causes ~4 and 6 weeks following retrieval of loggers. In no case did an adult abandon the nest following logger deployment. Average deployment time was 4.3 (± 2.2) days. Most trips (73.3%) occurred to the southeast and southwest of the colony, while a minority (26.7%) occurred to the north and northeast (Figs. 2–4). Maximum trip length was 953.7 km, with an average of 176.8 (± 249.8) km. Maximum distance travelled from the colony differed by direction, with longer trips occurring to the south (Fig. 2). Average trip duration was 15.3 (± 26.1) hours, of which 34.8% of trips included one or more nights at sea (Table S2). RBTRs travelled and foraged primarily between 05h00 and 18h00, with foraging activity peaking between 07h00 and 10h00. Birds tended to be inactive between 18h00 and 05h00 (Fig. 5).
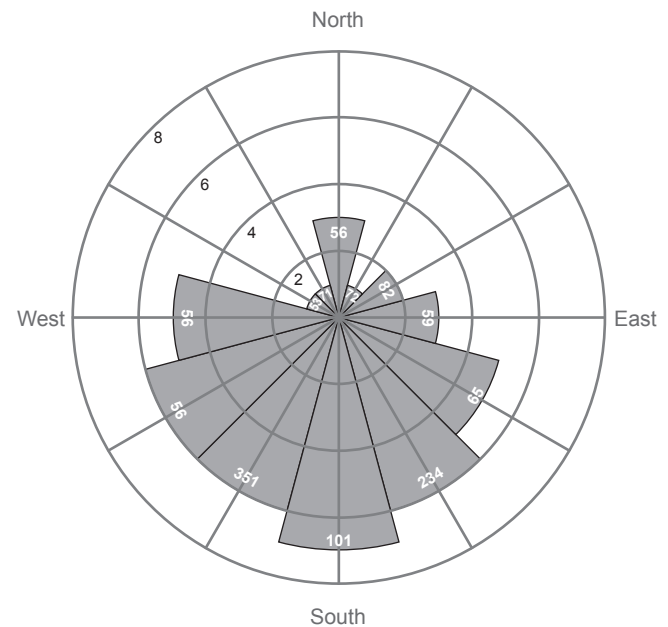

Fig. 2. Direction of foraging trips of adult Red-billed Tropicbirds *Phaethon aethereus* from St. Eustatius, Caribbean Netherlands, tracked between 2016 and 2020. The mean maximum distance (km) per 30° bearing is shown in white text and the sample size is shown in black text.
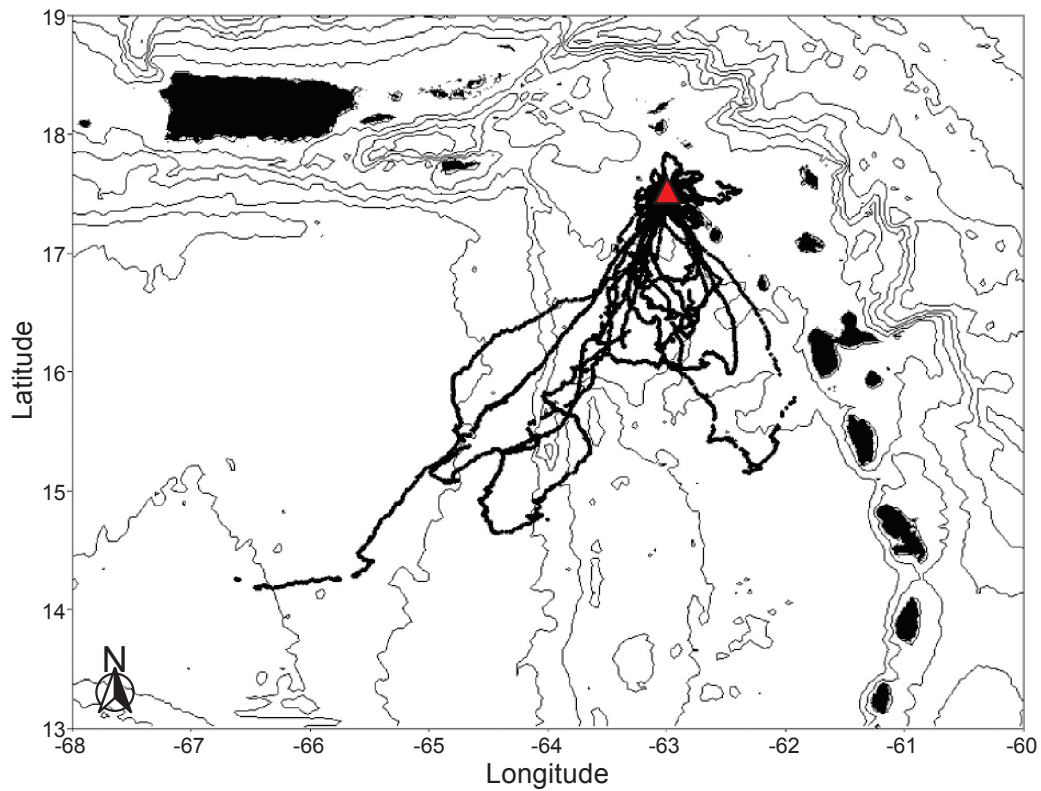
Fig. 3. GPS tracks (*n* = 45) of adult Red-billed Tropicbirds *Phaethon aethereus* during early chick rearing (chicks 0–21 days of age) on St. Eustatius, Caribbean Netherlands, between 2016 and 2020. The red triangle marks St. Eustatius and thin black lines represent bathymetry (GEBCO Bathymetric Compilation Group 2020).
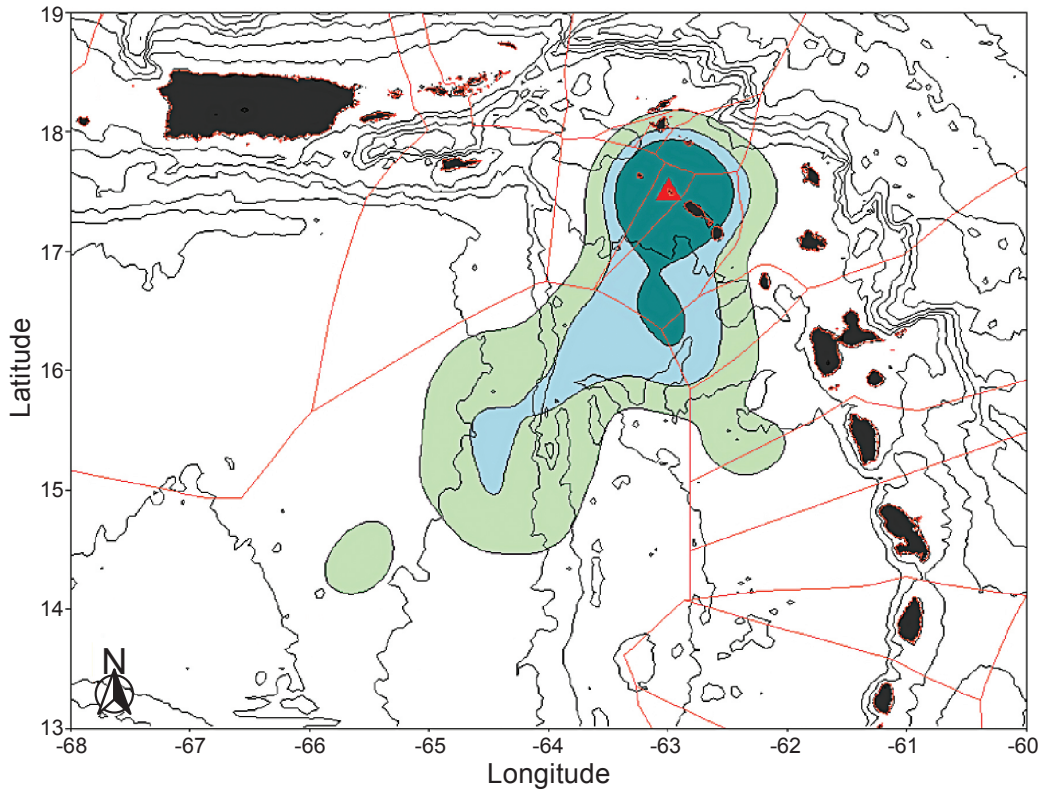

Fig. 4. Kernel density estimates (KDE) of foraging areas of Red-billed Tropicbirds *Phaethon aethereus* nesting on St. Eustatius, Caribbean Netherlands, (red triangle) between 2016 and 2020 (*n* = 45). Percentage volume KDE contours show the proportion of foraging locations by individuals. Dark green indicates core foraging area (50%), light blue is intermediate (75%), and light green is the maximum (95%) foraging area. Red lines outlining black areas denote exclusive economic zones. Black lines represent bathymetry. (GEBCO Bathymetric Compilation Group 2020).

TABLE 1
Percentage overlap between Red-billed Tropicbird
***Phaethon aethereus* foraging areas (50%, 75%, and**
95% utilisation distribution (UD) ranges) and
exclusive economic zones in the Caribbean region[a]

Country	Territory	50% UD	75% UD	95% UD
St. Kitts & Nevis	St. Kitts & Nevis	48.6	31.0	13.2
Saba	Netherlands	16.7	9.7	7.4
St. Eustatius	Netherlands	16.4	7.1	2.9
St. Martin	France	11.5	7.1	5.3
Montserrat	UK	3.5	9.6	6.7
Venezuela	Venezuela	2.1	33.5	52.8
St. Maarten	Netherlands	1.1	1.4	0.6
Anguilla	UK	-	-	0.1
Antigua & Barbuda	Antigua & Barbuda	-	0.5	3.0
Dominica	Dominica	-	-	1.4
Guadeloupe	France	-	-	6.4

[a] Countries that overlap with 50% UD ranges are responsible for protection in the core area

TABLE 2
Percentage overlap between Red-billed Tropicbird
***Phaethon aethereus* foraging areas (50%, 75%, and**
95% utilisation distribution (UD) ranges) and
marine protected areas (MPAs) in the Caribbean[a]

Marine Protected Area	Country	50% UD	75% UD	95% UD
Yarari Sanctuary	Caribbean Netherlands	33.1	16.8	10.3
Agoa	Martinique	10.9	6.9	11.7
Saba Bank National Park	Netherlands	8.9	5.1	2.9
Marine Management Area	St. Kitts & Nevis	2.9	1.3	0.5
St. Mary's	St. Kitts & Nevis	0.3	0.1	0.0
St. Eustatius National Marine Park	Netherlands	0.2	0.1	0.0
Redonda	Antigua & Barbuda	-	-	0.3

[a] MPAs that overlap with 50% UD ranges are responsible for protection in the core area

The maximum (95%), intermediate (75%), and core (50%) RBTR foraging areas are presented in Fig. 4. Core foraging areas overlapped with multiple EEZs (Table 1) and multiple MPAs (Table 2).

Environmental variables

Time spent in foraging behaviour was strongly correlated with bathymetry, chlorophyll *a* concentration, and Exocoetidae species richness (Table 3). Specifically, RBTR commuted to forage in deeper waters with higher chlorophyll *a* concentration but fewer Exocoetidae species compared to travelling locations (Fig. 6, Table 3). The total variance explained by the combined fixed and random effects of the most plausible models was 37.0% (R^2c), while the total variance explained by the fixed effects only (bathymetry, Exocoetidae species richness, and chlorophyll *a*) was 15.9% (R^2m). Thus, the variables used in our model explain only a small proportion of the variation in the foraging preferences of RBTR.

DISCUSSION

During the nesting season, seabirds are central-place foragers and return to the nesting colony within a limited timeframe. Studies in temperate and polar regions indicate that seabirds commute to reach prey patches, in some cases using short-term memory (e.g., Weimerskirch *et al.* 2005b, Cook *et al.* 2006, Phillips *et al.* 2017). In the tropics, however, such resources are less predictable, thus seabird foraging behaviour is often considered less predictable (Weimerskirch 2007). Prey predictability, of course, depends on the spatial and temporal scales considered (Hunt & Schneider 1987) and the marine habitat in question. For tropicbirds, it also depends on the presence of sub-surface predators such as tuna and marine mammals, which are highly mobile (Au & Pitman 1986, Spear *et al.* 2007). Prior tracking studies from the Caribbean have revealed that

foraging seabirds key in on bathymetric features (Wilkinson *et al.* 2020) and cross numerous EEZs in the process (Soanes *et al.* 2015). Other studies indicate that predictability of foraging behaviour can be affected by breeding strategy (Soanes *et al.* 2021). Our study demonstrated that RBTR from St. Eustatius crossed over nearshore waters to forage in deeper waters that had higher chlorophyll concentrations compared to travelling points. These areas may also support sub-surface predators such as tuna and porpoises, though our data were unable to confirm this.

Diet and behavioural patterns

Diet specimens from RBTR nesting on St. Eustatius primarily included two families of epipelagic fish (Exocoetidae and Belonidae), similar to results from Senegal where nesting RBTR fed exclusively on four families of epipelagic fish (Diop *et al.* 2018). We did not observe squid in the diet, as was observed in diets of RBTR from Trinidad and Tobago and the Gulf of California (Castillo-Guerrero *et al.* 2011). A 2019 study from nearby Saba (*n* = 55 samples) showed RBTR diets that were composed primarily of fish, although the diversity observed was higher than in our study (Exocoetidae 65.5%, Scombridae 7.3%, Carangidae 9.1%, squid 1.8%; M. Leopold & M. Boeken unpubl. data). In contrast, Schaffner (1988) recorded a high proportion of squid (73% and 64%), followed by Exocoetidae (49%), Carangidae (40% and 46%), and Scombridae (32%), among samples collected from chick-rearing WTTR at two colonies (*n* = 45, 22 samples) on Culebra, Puerto Rico, between 1984 and 1986. Squid have occasionally been observed in regurgitates from St. Eustatius (HM unpubl. data); however, none were collected during our study. Because squid beaks do not break down and can remain in the stomach longer than other prey items (Furness *et al.* 1984), we posit that the lack of squid found in regurgitates was not a result of sampling bias but may instead reflect foraging behaviour and diet choices.

Thirteen Exocoetidae species occur in the Caribbean (Table S5, Fig. S1), but the relationship between RBTR foraging and flying fish species richness is not clear. Despite the relatively high species richness in our study area, our models suggest that RBTR forage in areas of low richness of flying fish species (Table 3). Although we cannot be certain how many species occurred in the diet of tracked RBTR, the regurgitate samples contained just two families (Exocoetidae and Belonidae) of which Exocoetidae occurred in high abundance (59.5%). A diet of low species richness but high abundance of flying fish has been observed elsewhere for tropicbirds. For example, a study of WTTR diet in the Seychelles was characterised by low species richness but a high abundance of flying fish, which was the most consumed prey (Catry *et al.* 2009b). Similarly, RTTR and WTTR on Aldabra consumed high frequencies of three and four species of flying fish, respectively (Diamond 1975), and in the eastern Tropical

Pacific, the diet diversity of RTTR was low but was dominated by flying fish (Harrison *et al.* 1983, Spear *et al.* 2007). In the tropical epipelagic zone, dense clumps of prey can exist but may be scattered (Fauchald *et al.* 2000). We therefore tentatively speculate that RBTR forage areas of dense clumps of prey among a very scattered background of prey, rather than focusing on areas of high species richness. These dense clumps of prey could also form a proxy for tuna or porpoise schools, though we were unable to confirm this.

Oceanographic variables

We present the first study, though incomplete, reporting habitat characteristics of where RBTR forage in the Caribbean. Regional oceanographic conditions are important species-specific predictors of the foraging behaviour of tropical seabirds (Hennicke & Weimerskirch 2014, McDuie *et al.* 2015, McDuie & Congdon 2016, McDuie *et al.* 2018). For example, Soanes *et al.* (2021) found that SST and depth correlated negatively with Brown Booby *Sula leucogaster* foraging but that the correlation with chlorophyll *a* concentration was positive in the vicinity of Dog Island, Anguilla; this is the opposite of what was found for Masked Booby *S. dactylatra*. Poli *et al.* (2017) tracked Masked Boobies in the Gulf of Mexico and found strongest correlations with sea surface height anomalies and water velocity. We found that RBTR nesting on St. Eustatius may be travelling over low-productivity areas to forage in more productive waters. Our reasoning is that in tropical waters, zooplankton and fish abundance are often positively correlated with chlorophyll concentration (Piontkovski & Williams 1995, Jaquemet *et al.* 2005, Takarina *et al.* 2019), presumably resulting in an increase in prey availability for seabirds (Monticelli *et al.* 2007). Thus, higher productivity of pelagic waters in the northeastern Caribbean Sea may well support a more predictable supply of prey for RBTR (Fig. S2). Alternatively, the larger body size and flight proficiency of RBTR may allow them to travel extensively between prey patches in productive areas (Ballance *et al.* 1997).
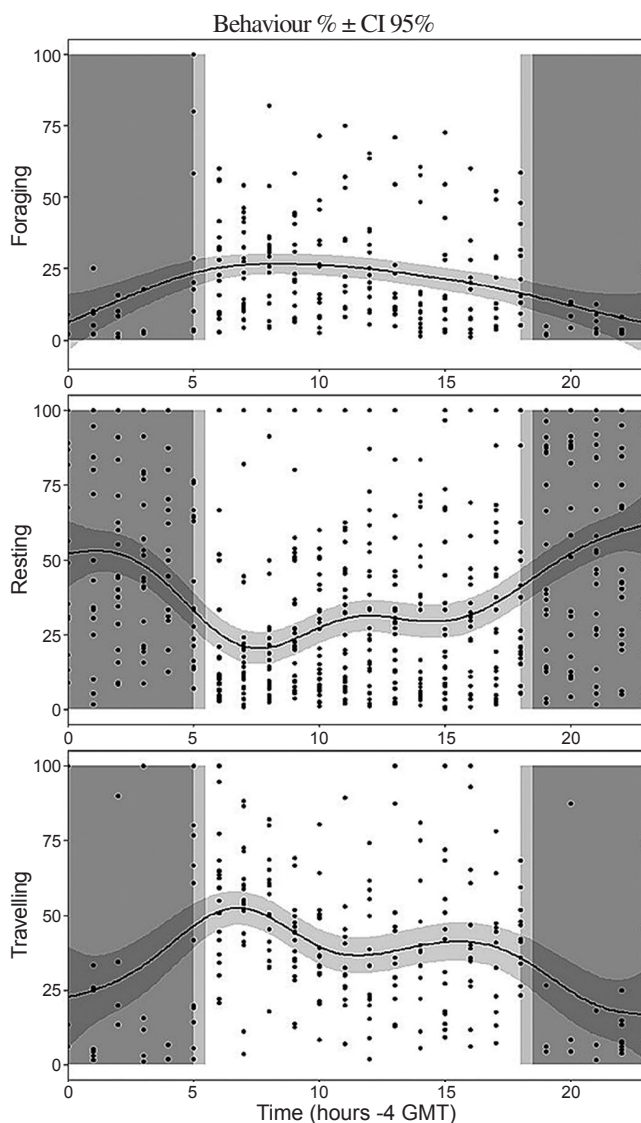

Fig. 5. Behavioural modes of Red-billed Tropicbirds *Phaethon aethereus* nesting on St. Eustatius, Caribbean Netherlands, based on GPS tracking data collected between 2016 and 2020. Dark grey areas represent darkness, light grey areas represent sunrise and sunset periods, and white areas represent daylight. CI is confidence interval.
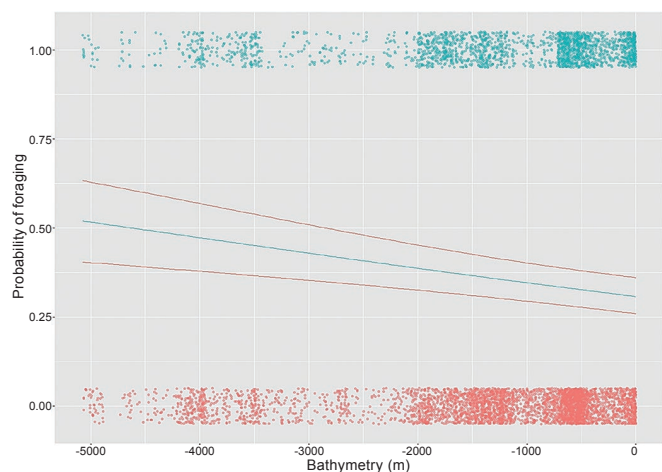

Fig. 6. Probability of foraging of Red-billed Tropicbirds *Phaethon aethereus* (0 = travelling; 1 = foraging) on St. Eustatius, Caribbean Netherlands, in relation to bathymetry (m). The blue line represents fit, while red lines represent upper and lower 95% confidence intervals. Coloured dots showing behaviour are scattered vertically to show distribution.

TABLE 3
Model-averaged summary statistics of Red-billed Tropicbird *Phaethon aethereus* foraging behaviour in the Caribbean Sea and southern Atlantic Ocean[a,b,c]

Model parameter	Coefficient		Z score	P value
	Estimate	SE		
Intercept	0.16	0.20	0.57	0.57
Bathymetry (m)	**−0.63**	**0.14**	**4.64**	**< 0.001**
Sea surface temperature	−0.14	0.13	1.10	0.27
Exocoetidae species richness	**−0.57**	**0.10**	**5.48**	**< 0.001**
Chlorophyll α (mg·m^{-3})	**0.38**	**0.09**	**3.97**	**< 0.001**
Euphotic depth (cm)	0.14	0.09	1.64	0.10
Salinity (g·kg^{-1})	0.06	0.05	1.17	0.24
Exocoetidae species richness^2	0.05	0.19	0.25	0.80
Sea surface temperature^2	−0.01	0.03	0.20	0.84
Chlorophyll α (mg·m^{-3})^2	0.002	0.009	0.18	0.85
Euphotic depth (cm)^2	−0.001	0.009	0.10	0.92
Bathymetry^2	−0.003	0.03	0.10	0.92

[a] All generalised linear mixed model parameters were standardised for comparative purposes.

[b] The superscript 2 symbolises 'squared'. SE = Standard Error

[c] Significant terms are highlighted in bold typeface.

In the Caribbean, bathymetric features such as banks can form areas of increased and more predictable productivity, within which some seabird species forage (Poli *et al.* 2017). For example, Wilkinson *et al.* (2020) revealed that Masked Boobies breeding on Jamaica exhibited high foraging site fidelity to Pedro Bank. However, despite the close proximity of the Saba Bank, an isolated submarine platform (20–50 m below sea level) located approximately 19 km northwest of St. Eustatius (Macintyre *et al.* 1975), our results indicate that RBTR do not rely on this bathymetric feature but instead travel to areas of more productive open ocean. It is likely that the Saba Bank is too shallow for Exocoetidae species, which prefer a more pelagic habitat (Lewallen *et al.* 2017), and thus this bank does not offer suitable foraging opportunities for RBTR on St. Eustatius.

Despite the number of relevant tracking studies in recent years (e.g., Poli *et al.* 2017, Diop *et al.* 2018, Soanes *et al.* 2021), the relationship between tropical seabird foraging and environmental covariates (if they exist) is still not clear. St. Eustatius, in the northern Lesser Antilles, is surrounded by oligotrophic waters and RBTR nesting there may require a foraging strategy that involves commuting to more productive waters within flight capability. This is comparable to the foraging patterns of RBTR nesting on St. Helena, which is also surrounded by oligotrophic waters where RBTR expend greater foraging effort, due perhaps to a lower quality marine habitat (Diop *et al.* 2018) or to depletion of foraging facilitators in the region (Peterson *et al.* 2007, Hebshi 2008, Grémillet & Boulinier 2009). Similarly, Castillo-Guerrero *et al.* (2011) revealed that nest initiation, feeding conditions, and parental attendance of RBTR in the Gulf of California

were influenced by chlorophyll concentration and anomalies in SST. Overall, however, congruent with Diop *et al.* (2018), the environmental variables in our study had limited power to explain RBTR foraging. Given the ephemeral nature of prey patches in tropical marine environments, RBTR on St. Eustatius may travel opportunistically until they discover a productive patch or a sub-surface predator.

CONCLUSIONS

Tracking studies enable researchers to locate key foraging areas of particular populations of interest. Our study, together with others (e.g., Soanes *et al.* 2014, 2015, 2016, 2021), highlights the benefit of a regional perspective when considering the ecology of seabird populations in the Lesser Antilles and wider Caribbean Sea (Jodice & Suryan 2010, Soanes *et al.* 2014, Jodice *et al.* 2015). As with other seabird tracking studies, the degree of association between RBTR with other seabirds, including competitors, and with sub-surface predators remains unclear. Such information could well be important, as our review revealed.

Understanding the foraging ecology of RBTR in the Caribbean can serve as a model to conserve and manage the species in the region. For RBTR nesting on St. Eustatius, core foraging areas occur primarily within the jurisdiction of the Netherlands, St. Kitts & Nevis, France, Venezuela, and the United Kingdom Overseas Territories (Flanders Marine Institute 2020). The management plan for the natural resources of the EEZ of the Dutch Caribbean states that "common sustainable management of marine biodiversity… includes the protection of species and habitats in the waters" (Meesters *et al.* 2010). The same report acknowledges a lack of data on the distribution, abundance, and dependencies of seabirds, and therefore the results of our study will contribute a better understanding of RBTR foraging patterns within and across regional EEZs and MPAs. Our data demonstrated that key areas for RBTR from St. Eustatius were not protected by MPAs, and it may be an important consideration in the creation of future protected sites such as Specially Protected Areas of Caribbean Importance. Finally, by replicating our methods on other significant RBTR populations in the Caribbean (e.g., Saba, Anguilla, Trinidad & Tobago), we may be able to better identify core foraging areas and evaluate whether, as suggested above, a wider regional network of special MPAs may be warranted. The results of our study can be replicated by researchers studying the species elsewhere in the Caribbean, and may be useful for conservation organisations to assess the strategies necessary to protect key RBTR foraging areas in the region.

comments greatly improved our paper, for which we are thankful. Handling and banding of birds was conducted under permit #B97, issued by Vogeltrekstation (Netherlands bird banding authority). The authors declare no conflict of interest. The data that support the findings of this study are available from the corresponding author upon reasonable request. We appreciate the comments of reviewers and the editor, which helped us to improve our paper.

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