Foraging habitat choice of White-tailed Tropicbirds revealed by fine-scale GPS tracking and remote sensing

Carlos D. Santos[1,2,*], Leila F.A.S. Campos[3,*] and Márcio A. Efe[3]

[1] Núcleo de Teoria e Pesquisa do Comportamento, Universidade Federal do Pará, Belém, Brazil
[2] Department of Migration and Immuno-Ecology, Max Planck Institute for Ornithology, Radolfzell, Germany
[3] Laboratório de Bioecologia e Conservação de Aves Neotropicais, Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, Maceió, Brazil
[*] These authors contributed equally to this work.

Corresponding author
Carlos D. Santos,
cdsantos@orn.mpg.de

ABSTRACT

Background. The introduction of animal tracking technology has rapidly advanced our understanding of seabird foraging ecology. Tracking data is particularly powerful when combined with oceanographic information derived from satellite remote sensing, allowing insights into the functional mechanisms of marine ecosystems. While this framework has been used extensively over the last two decades, there are still vast ocean regions and many seabird species for which information is scarce, particularly in tropical oceans.

Methods. In this study we tracked the movement at high GPS recording frequency of 15 White-tailed Tropicbirds (*Phaethon lepturus*) during chick-rearing from a colony in Fernando de Noronha (offshore of Northeast Brazil). Flight behaviours of travelling and searching for food were derived from GPS data and examined in relation to satellite-sensed oceanographic variables (sea surface temperature, turbidity and chlorophyll-a concentration).

Results. White-tailed Tropicbirds showed marked preference for clear and warm sea surface waters, which are indicative of low primary productivity but are likely the best habitat for preying upon flying fish.

Discussion. These findings are consistent with previous studies showing that foraging habitat choices of tropical seabirds may not be driven by primary productivity, as has been widely shown for non-tropical species.

INTRODUCTION

The way how pelagic seabirds move across the vastness of the open ocean have fascinated generations of scientists, but only recently have technological developments provided the tools to uncover that mystery. Tracking devices have become indispensable tools to study the behaviour of seabirds at-sea. Since the early 90s, when the first seabirds were tracked (*Jouventin & Weimerskirch, 1990*; *Prince et al., 1992*), major technological improvements have made tracking devices smaller, more accurate, and more affordable, which diversified

their applications and promoted an increase in the number of species tracked (*Hays et al., 2016*). Similarly, satellite remote sensing has been improved over the last two decades in order to sense relevant oceanographic parameters, such as sea surface temperature (SST) or chlorophyll concentration (*McClain, 2009*; *Blondeau-Patissier et al., 2014*). Taken together, tracks of marine animals and oceanographic variables derived from satellite imagery provide exceptional opportunities to understand the functional mechanisms of marine ecosystems (*Wakefield, Phillips & Matthiopoulos, 2009*). In seabird research the simultaneous use of tracking devices and satellite imagery has escalated since the early 2000s (*Tremblay et al., 2009*). The most recent studies have taken advantage of the increased spatial and temporal resolution of tracking devices and satellite sensors to identify behavioural responses of seabirds to food patches (e.g., *Paiva et al., 2010a*; *Sabarros et al., 2014*; *Poli et al., 2017*). But while the tools necessary to understand how seabirds use their sea environment are now available, large oceanic regions, particularly in the tropics, remain poorly studied (but see *Catry et al., 2009b*; *Kappes et al., 2011*; *Le Corre et al., 2012*; *Legrand et al., 2016*; *Zajkova, Militao & Gonzalez-Solis, 2017* as examples of tracking studies with tropical seabirds).

The vast majority of seabird tracking studies have been conducted in temperate and polar regions. Those have generally shown that seabirds concentrate their foraging in areas of high ocean productivity, typically characterized by high abundance of phytoplankton and low SST (e.g., *Pinaud & Weimerskirch, 2005*; *Suryan et al., 2006*; *Paiva et al., 2010b*). Productive areas normally match with regions of upwelling, where nutrient-rich water rise to the surface, in consequence of specific sea bottom and current profiles, and supports the development of phytoplankton (*Mann & Lazier, 2006*). Seabirds repeatedly commute to these areas from their breeding colonies (*Weimerskirch, 2007*; *Wakefield et al., 2015*), typically travelling in a linear path and constant speed between the breeding colony and the feeding areas where their path becomes highly tortuous and slow (*Weimerskirch, 2007*). In contrast, tropical seabirds tend to show looping movements, where feeding events are sparsely distributed along their loop shaped paths, and they normally present low fidelity to feeding areas (*Weimerskirch, 2007*). Several authors have argued that while polar, temperate and subtropical seabirds feed on areas with predictable productivity (e.g., shelf slopes, ice edges, or ocean fronts), tropical seabirds feed to a large extent in association with subsurface predators (large predatory pelagic fish and cetaceans) that force fish schools towards the surface (e.g., *Catry et al., 2009b*; *Jaquemet et al., 2014*; *Miller et al., 2018*).

Tropicbirds are enigmatic seabirds that typically forage solitarily in tropical and subtropical seas (*Jaquemet, Le Corre & Weimerskirch, 2004*; *Spear & Ainley, 2005*). They have been traditionally grouped with pelicans, cormorants, gannets, boobies and frigatebirds in the order Pelecaniformes, but recently they were found to be more closely related to the Eurypygiformes, that include the Sunbittern (*Eurypyga helias*) and the Kagu (*Rhynochetos jubatus*), based on whole-genome analyses (*Jarvis et al., 2014*). This makes them unique among seabirds taxonomically. Ecologically, they share with boobies, gannets and terns the ability of plunge diving, but unlike these species, they avoid foraging in large multi-species flocks (*Spear & Ainley, 2005*). They are also unusual in that although they fly long distances (comparable to procellariids), they lack the ability to soar (*Spear & Ainley, 1997*; *Mannocci et al., 2014*; *Campos et al., 2018*). This flight behaviour seems to be possible
because they rest for long periods on the water between periods of flight (*Spear & Ainley, 2005*; *Mejias et al., 2017*). Despite these unusual characteristics, tropicbirds have only been tracked in a few studies (*Pennycuick et al., 1990*; *Le Corre et al., 2012*; *Soanes et al., 2016*; *Mejias et al., 2017*; *Campos et al., 2018*), which greatly limits our understanding of their foraging ecology.

In this study we GPS-tracked 15 White-tailed Tropicbirds (*Phaethon lepturus*) at high frequency in order to infer their foraging behaviour at sea. All of the tracked individuals were caught during chick-rearing in Fernando de Noronha, a tropical oceanic Archipelago offshore of the Northeast Brazilian coast. Foraging behaviour of White-tailed Tropicbirds at sea was examined in the light of oceanographic variables derived from high spatial resolution Moderate-resolution Imaging Spectroradiometer (MODIS) imagery. With this approach we aimed to understand how White-tailed Tropicbirds respond behaviourally to gradients of chlorophyll-a, SST, and turbidity, which were shown to be major drivers of foraging habitat use by many seabird species (*Henkel, 2006*; *Tremblay et al., 2009*). We hypothesised that White-tailed Tropicbirds will increase their foraging efforts in areas of high primary productivity, which is expected to correlate with prey availability.

METHODS

Study area and data collection

This study was conducted in Fernando de Noronha Archipelago (3.86°S, 32.42°W), 354 km offshore of the Northeast Brazilian coast. The archipelago is composed of 21 islands and islets occupying ca. 26 km^2, and has been protected by Brazilian legislation as a marine national park since 1988. The islands hold large concentration of tropical seabirds, including a breeding population of 100 to 300 of White-tailed Tropicbirds (*Leal et al., 2016*). The climate is tropical with two marked seasons, the rainy season from January to August and the dry season from September to December. The average annual temperature is 27 °C and the rainfall is 1,400 mm (*Leal et al., 2016*). The region is influenced by two main oceanic currents, the near surface westward central branch of the South Equatorial Current and the deeper eastward South Equatorial Undercurrent (*Tchamabi et al., 2017*). The seawater is considered oligotrophic, where phytoplankton productivity is limited by low nutrient concentrations (*de Souza et al., 2013*). Surface salinity ranges between 35.0 and 37.0‰ (*Leal et al., 2016*).

Tracked White-tailed Tropicbirds were captured during chick-rearing (chicks of 1 to 3 weeks old) in Morro do Chapéu islet (Fig. 1), which holds the largest breeding colony of this species in the whole archipelago (*Leal et al., 2016*). The 15 tagged White-tailed Tropicbirds were captured by hand in the nest at dawn (4 to 4:30 am), before they leave for the sea, between August 28th to October 16th 2015. Birds weighted between 315 to 435 g (average 355 g). The data loggers (5 g including battery, Gipsy 4 GPS recorders, Technosmart, Italy) were waterproofed with heat shrink tubing (increasing their weight to 10-15 g) and were attached to the bases of the four central tail feathers with duct tape. The handling of the animals took less than 10 min, after which they were immediately released.
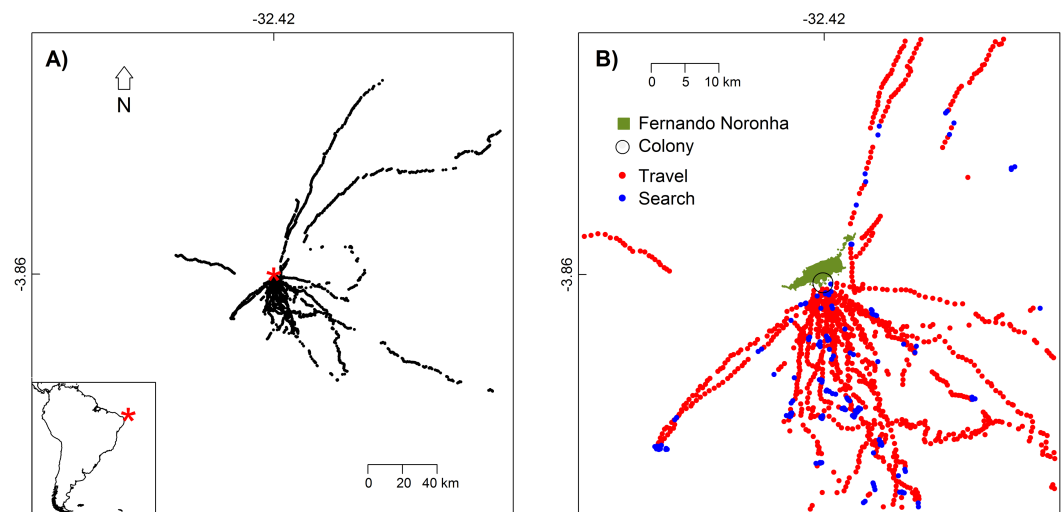
Figure 1 **White-tailed Tropicbirds behaviour at sea classified from First-Passage Time analysis.** (A) Location of the colony (red asterisk) and locations where behaviour was classified (black dots). (B) Flight behaviour classified as travel and search. Only the part of the study area with higher bird use is shown.

The experimental procedures of this study, including bird trapping and the GPS tagging, were approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) through the license SISBIO 27714-4.

Data analysis

GPS tracks of White-tailed Tropicbirds flying over the sea were selected from the original dataset. This excluded track segments at the breeding colony or flying over the islands. Some tracks were not round-trip, because the data logger battery ended before the animal returned to the colony. Average GPS recording duration was 8 h and 40 min. GPS data loggers functioned at different rates (from one to six fixes per minute), but to use a consistent dataset we reduced all tracks to the same resolution of 1 fix per minute. Fixes where speed was less than 10 km/h were considered indicative of bird sitting on water (*Weimerskirch et al., 2002*; *Weimerskirch et al., 2005*; *Weimerskirch, Le Corre & Bost, 2008*; *Zavalaga et al., 2012*; *Cecere, Gaibani & Imperio, 2014*) and were removed from further analysis.

In order to classify foraging behaviour of White-tailed Tropicbirds at sea, we used First-Passage Time (FPT) analysis following *Fauchald & Tveraa (2003)*, which we implemented in R (*R Core Team, 2016*) with the function fpt of the package adehabitatLT (*Calenge, 2006*). FPT is defined as the time required to cross a circle with a given radius, and the circle radius associated with the peak log(variance) of FPT is defined as the scale of Area-Restricted Search (ARS; *Fauchald & Tveraa, 2003*). We plotted FPT log(variance) for radii ranging from 5 to 1,000 m for each track and determined the scale at which FPT log(variance) peaked. For latter analysis we used the scale of 434 m, corresponding to the median of scales obtained for individual tracks. Bird behaviour was classified into "travel" or "search" based on the histogram of FPT values shown in Fig. S1. The vast majority

of observations had FPT values concentrated between 50 and 300 s, while the remaining were distributed in low frequencies among a wide range of FPT values higher than 300 s (Fig. S1). The latter observations were classified as "search" as it is expected that foraging effort demands high residency time. Among the former observations, only a half with the lowest FPT values were classified as "travel" (Fig. S1). The remaining observations, with intermediate FPT values, were excluded from further analysis (Fig. S1). We excluded these intermediate observations because there was no clear division in FPT values, but we needed distinct flight behaviours that could be interpreted against oceanographic variables.

White-tailed Tropicbirds behaviour at GPS locations was examined in the light of oceanographic variables derived from MODIS, made available by the NASA's OceanColor Web (http://oceancolor.gsfc.nasa.gov). We used the following variables: (1) Turbidity—The Diffuse Attenuation Coefficient at the 490 nm wavelength (commonly referred as Kd(490)) served as a proxy for water turbidity (*Shi & Wang, 2010*; *Loptien & Meier, 2011*; *Stramska & Swirgon, 2014*). The Kd(490) specifically reflects the diffuse attenuation for downwelling irradiance at 490 nm in m^{-1} (see *O'Reilly et al., 2000* for details). (2) Chlorophyll-a - Near-surface concentration of chlorophyll-a in mg m^{-3}, inferred from remote sensing reflectance in the blue-to-green region of the visible spectrum (see *Hu, Lee & Franz, 2012* for details). (3) SST—Sea surface temperature in °C inferred from the 11 μm and 12 μm long wave infrared bands (see *Kilpatrick et al., 2015* for details). Images made available at ca. 0.009 decimal degrees (1 km) spatial resolution were resampled to 0.05 decimal degrees (ca. 5.57 km) in order to reduce the number of pixels with no data due to cloud cover. We related bird behaviour of each tracking day to images of oceanographic variables obtained in the corresponding day and the day before (values of both days were averaged). We used images from the day before because it is likely that White-tailed Tropicbirds decide their route using recent foraging experience. In fact, some individuals tracked in following days repeated sections of their routes, while there was no route overlap in tracks recorded with greater time-separation. In addition, we standardized the original values of oceanographic variables among the different tracking days. This was necessary because the range of values of the oceanographic variables within the area accessible to the birds varied considerably between tracking days. The standardization was done by ranking the values of the images of the oceanographic variables in a scale varying from 0 to 20. All images were cut to the same geographic range, set by the longest track recorded (range: 5.1134° to 2.6054°S in latitude and 33.6806° to 31.1726°W in longitude).

The effects of oceanographic variables on the behaviour of White-tailed Tropicbirds at GPS locations were modelled with binomial Generalized Linear Mixed Model (GLMM), using the function glmer of the R package lme4 (*Bates et al., 2016*). The response variable was assigned as 1 for the observations classified as "search" and 0 for those classified as "travel". The oceanographic variables were included in the model as fixed factors and bird identity as random factor. Correlations between fixed effects were low (turbidity vs chlorophyll-a: $r = 0.22$; turbidity vs SST: $r = 0.14$; chlorophyll-a vs SST: $r = 0.26$). Model goodness-of-fit was evaluated through marginal R^2 (variance explained by the fixed effects) and the conditional R^2 (the variance explained by the fixed and random effects) following *Nakagawa & Schielzeth (2013)*.

Table 1 Summary of binomial GLMM testing the effects of oceanographic variables on the probability of White-tailed Tropicbirds to exhibit search behaviour at sea. The response variable was assigned as 1 for the observations classified as "search" and 0 for those classified as "travel". The oceanographic variables were included in the model as fixed factors and bird identity as random factor. Conditional and marginal R^2 were calculated following *Nakagawa & Schielzeth (2013)*.

Parameter	Estimate	SE	Z	P-value	R^2 cond./marg.
Intercept	−2.247	0.384	−5.85	<0.001	
SST rank	0.065	0.021	3.05	0.002	0.46/0.09
Turbidity rank	−0.050	0.020	−2.51	0.012	
Chlorophyll-a rank	−0.002	0.020	−0.11	0.912	

RESULTS

We tracked 15 different White-tailed Tropicbirds during one to four trips each. Birds showed higher concentration of movements between the S and SE directions (Fig. 1). Our tracking dataset included 6671 GPS fixes, from which 1792 were used for the classification of bird behaviour.

In general, behaviours classified as "travel" and those classified as "search" were not segregated spatially (Fig. 1B), meaning that the White-tailed Tropicbirds search for food as soon as they leave the breeding colony and all along their route. This is also in agreement with their general route pattern of looping foraging trips rather than commuting foraging trips (Fig. S2).

The oceanographic conditions studied here, turbidity, Chlorophyll-a, and SST, varied considerably during the tracking sampling period (average Pearson's correlation between images available for the sampling period were 0.01, 0.02 and 0.03 for turbidity, Chlorophyll-a, and SST respectively), illustrating a highly unpredictable environment for the White-tailed Tropicbirds. Overall, turbidity ranged from 0.02 to 0.12 m^{-1} (0.03 ± 0.005, mean ± SD), Chlorophyll-a ranged from 0.02 to 0.8 mg m^{-3} (0.12 ± 0.03, mean ± SD), and SST ranged from 9 to 27 °C (24.4 ± 3.2, mean ± SD).

The GLMM model showed significant effects of turbidity and SST on the probability of White-tailed Tropicbirds to exhibit search behaviour, but no effect of Chlorophyll-a was observed (Table 1, Fig. 2). The probability of search behaviour increased with the increase of SST (Fig. 2A) and with the decrease of turbidity (Fig. 2B).

DISCUSSION

We found that White-tailed Tropicbirds searching for food in oligotrophic waters during breeding show preference for areas with higher SST and lower turbidity (Fig. 2), while no influence of chlorophyll-a was observed (Table 1). Our results also indicate that White-tailed Tropicbirds forage along their foraging trips, showing little spatial segregation between searching and travelling behaviours (Fig. 1B). The general shape of White-tailed Tropicbirds tracks are coherent with the foraging patterns described above, being closer to what is usually defined as looping foraging trips, rather than commuting foraging trips (Fig. S2; *Weimerskirch, 2007*).
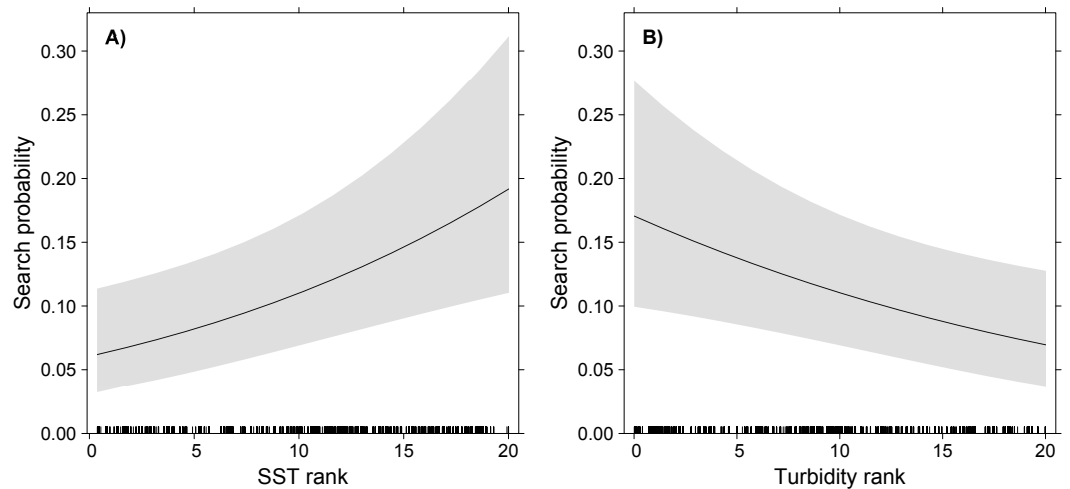
Figure 2 GLMM partial effects of SST (A) and turbidity (B) on the probability of White-tailed Tropicbirds to exhibit search behaviour at sea. The response variable of the model was assigned as 1 for the observations classified as "search" and 0 for those classified as "travel". The oceanographic variables were included in the model as fixed factors and bird identity as random factor. Shading represents 95% confidence intervals.

To some extent, these patterns match with general predictions of habitat use by seabirds breeding in tropical oceanic islands, where the sea is largely unproductive and food resources are unpredictable (*Weimerskirch, 2007*). The sea bottom around tropical oceanic islands is generally deep and flat, with upwelling restricted to scattered seamounts, eddies and frontal zones (*Longhurst & Pauly, 1987*). In addition, breeding seabirds search for food within a limited range of their colony because their chicks need to be fed frequently (*Fauchald, 2009*). Thus areas of predictable upwelling are often too far from their reach. The very low temporal correlation in the oceanographic parameters found in our study area during the sampling period supports the idea that feeding conditions around Fernando Noronha are unpredictable. The high conditional R^2 of our model in comparison with the low marginal R^2 (see Table 1) indicates that much of the variation in searching behaviour probability was related to the individual, which may indicate that different individuals rarely find similar foraging conditions due to the unpredictability of the oceanographic conditions. Interestingly, there were several seamounts within the foraging range of the White-tailed Tropicbirds, but they did not use them as feeding areas (Fig. S3). A study in the same region found that even seamounts that reach a few tens of meters below the surface do not disturb the vertical stratification in the euphotic zone (*de Souza et al., 2013*), thus they are unlikely to create productivity patches usable by the seabirds. In summary, feeding White-tailed Tropicbirds breeding in Fernando de Noronha, seem to be far from areas of predictable productivity, and all the oceanographic parameters measured within their foraging range vary considerably in time and space. This seems to explain why the areas where they feed are scattered and why they develop looping foraging trips (*Weimerskirch, 2007*).

It may seem counter-intuitive, however, that White-tailed Tropicbirds show preference for warmer and clearer waters as these are associated with low primary productivity (*Mann & Lazier, 2006*). And this is somewhat supported by the apparent irrelevance of the chlorophyll-a concentration in the choices of foraging areas by the White-tailed Tropicbirds. However, an increasing number of studies in tropical areas have failed to link chlorophyll-a and SST to foraging habitat use of seabirds, or have found negative relationships between bird occurrence and primary productivity (e.g., *Vilchis, Ballance & Fiedler, 2006*; *Jaquemet et al., 2014*; *Mannocci et al., 2014*; *Poli et al., 2017*). Such results may be explained by spatial mismatches propagated along the trophic chain (*Gremillet et al., 2008*). White-tailed Tropicbirds, as many other tropical seabirds, prey upon flying fish to a large extent (*Stonehouse, 1962*; *Cherel et al., 2008*; *Catry et al., 2009a*), therefore we should expect a positive relationship between the foraging areas selected by White-tailed Tropicbirds and the distribution of flying fish, and not necessarily the distribution of primary productivity. Interestingly, a recent study using airborne LiDAR and covering a large area (approximately 75,000 km^2) in the Gulf of Mexico found that abundance of flying fishes increases with SST and decreases with Chlorophyll-a (*Churnside et al., 2017*). Another recent study confirms the importance of SST explaining the distribution of flying fishes (*Lewallen et al., 2017*), including one species (*Exocoetus volitans*) that is likely a main prey of White-tailed Tropicbirds in Fernando de Noronha (i.e., this species is a key prey item in the Ascension islands (*Stonehouse, 1962*), and is abundant in Fernando de Noronha (*Monteiro et al., 1998*)). In fact, flying fishes are unable to fly at temperatures below 20 °C because their swimming muscles are not able to contract fast enough to take-off (*Davenport, 1994*), and, presumably, higher temperatures improve flight performance. Similarly, White-tailed Tropicbirds may select clearer waters for other reasons than their productivity. The relevance of water transparency for plunge-divers was recognized long ago by *Ainley (1977)*, who hypothesised that plunge-divers should be distributed towards clearer waters, while pursuit-divers should be more associated with turbid waters. While several studies have confirmed or refuted this hypothesis (*Haney & Stone, 1988*; *Henkel, 2006*; *Baptist & Leopold, 2010*), *Haney & Stone (1988)* showed from several plunge-divers that the White-tailed Tropicbird was the only species that was significantly more abundant in clearer waters. We believe that water turbidity and prey abundance may interact for the determination of plunge-divers distribution, but it seems logical for us that given equal prey abundance, increased water transparency should help the birds to locate their prey, therefore improving their foraging success.

CONCLUSION

Overall, our findings are consistent with previous studies showing that foraging habitat choices of tropical seabirds may not be driven by primary production. While these patterns are scientifically interesting, they also illustrate the true challenge of mapping important foraging areas for tropical seabirds. In this context, the direct use of seabird tracks is still the best approach to identify priority areas for the conservation of tropical seabirds (*Le Corre et al., 2012*; *Soanes et al., 2016*). Therefore, additional efforts must be made in order to increase the number of tracking studies in remote areas of the tropical oceans.

ACKNOWLEDGEMENTS

We thank Fernando de Noronha ICMBio staff, CEMAVE, the Capitania dos Portos de Pernambuco and the Diretoria de Articulação e Infraestrutura of the Government of the State of Pernambuco for all the logistic support during the fieldwork. We also thank Teresa Catry for comments on our results and Joseph Smith for proof-reading this manuscript.

Funding

This study was funded by Fundação de Amparo à Pesquisa do Estado de Alagoas (http://www.fapeal.br; a grant to Leila F.A.S. Campos; grant reference: Edital 02/2014), Fundação Grupo Boticário de Proteção à Natureza (http://www.fundacaogrupoboticario.org.br; a grant to Márcio A. Efe; grant reference: 1012_20141) and the Pró-Reitoria de Pesquisa e Pós-Graduação of the Universidade Federal do Pará. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
Fundação de Amparo à Pesquisa do Estado de Alagoas: 02/2014.
Fundação Grupo Boticário de Proteção à Natureza: 1012_20141.
Pró-Reitoria de Pesquisa e Pós-Graduação of the Universidade Federal do Pará.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Carlos D. Santos analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Leila F.A.S. Campos conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
- Márcio A. Efe conceived and designed the experiments, contributed reagents/materials/analysis tools, approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

The experimental procedures of this study, including bird trapping and the GPS tagging, were approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) through the license SISBIO 27714-4.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

The field experiments of this study were approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) through the license SISBIO 27714-4.

Data Availability
Santos CD, Campos LFAS, Efe MA (2018) Data from: Foraging habitat choice of white-tailed tropicbirds revealed by fine-scale GPS tracking and remote sensing. Movebank Data Repository. DOI 10.5441/001/1.649s6f21.

Supplemental Information
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.6261#supplemental-information.

REFERENCES

Ainley DG. 1977. Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. In: Llano GA, ed. *Adaptations within Antarctic ecosystems*. Washington, D.C.: Smithsonian Institution Press.

Baptist MJ, Leopold MF. 2010. Prey capture success of Sandwich Terns Sterna sandvicensis varies non-linearly with water transparency. *Ibis* **152**:815–825 DOI 10.1111/j.1474-919X.2010.01054.x.

Bates D, Maechler M, Bolker B, Walker S. 2016. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-1.2. *Available at https://cran.r-project.org/web/packages/lme4/index.html*.

Blondeau-Patissier D, Gower JFR, Dekker AG, Phinn SR, Brando VE. 2014. A review of ocean color remote sensing methods and statistical techniques for the detection., mapping and analysis of phytoplankton blooms in coastal and open oceans. *Progress in Oceanography* **123**:123–144 DOI 10.1016/j.pocean.2013.12.008.

Calenge C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**:516–519 DOI 10.1016/j.ecolmodel.2006.03.017.

Campos LFAS, Andrade AB, Bertrand S, Efe MA. 2018. Foraging behavior and at-sea distribution of White-Tailed Tropicbirds in tropical ocean. *Brazilian Journal of Biology* **78**:556–563 DOI 10.1590/1519-6984.173578.

Catry T, Ramos JA, Jaquemet S, Faulquier L, Berlincourt M, Hauselmann A, Pinet P, Le Corre M. 2009a. Comparative foraging ecology of a tropical seabird community of the Seychelles western Indian Ocean. *Marine Ecology Progress Series* **374**:259–272 DOI 10.3354/meps07713.

Catry T, Ramos JA, Le Corre M, Phillips RA. 2009b. Movements., at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. *Marine Ecology Progress Series* **391**:231–242 DOI 10.3354/meps07717.

Cecere JG, Gaibani G, Imperio S. 2014. Effects of environmental variability and offspring growth on the movement ecology of breeding Scopoli's shearwater *Calonectris diomedea*. *Current Zoology* **60**:622–630 DOI 10.1093/czoolo/60.5.622.

Cherel Y, Le Corre M, Jaquemet S, Menard F, Richard P, Weimerskirch H. 2008. Resource partitioning within a tropical seabird community: new information from stable isotopes. *Marine Ecology Progress Series* **366**:281–291 DOI 10.3354/meps07587.

Churnside JH, Wells RJD, Boswell KM, Quinlan JA, Marchbanks RD, McCarty BJ, Sutton TT. 2017. Surveying the distribution and abundance of flying fishes and other epipelagics in the northern Gulf of Mexico using airborne lidar. *Bulletin of Marine Science* **93**:591–609 DOI 10.5343/bms.2016.1039.

Davenport J. 1994. How and why do flying fish fly? *Reviews in Fish Biology and Fisheries* **4**:184–214 DOI 10.1007/BF00044128.

de Souza CS, Da Luz JAG, Macedo S, Montes MDF, Mafalda PO. 2013. Chlorophyll a and nutrient distribution around seamounts and islands of the tropical south-western Atlantic. *Marine and Freshwater Research* **64**:168–184 DOI 10.1071/MF12075.

Fauchald P. 2009. Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series* **391**:139–151 DOI 10.3354/meps07818.

Fauchald P, Tveraa T. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* **84**:282–288 DOI 10.1890/0012-9658(2003)084[0282:UFPTIT]2.0.CO;2.

Gremillet D, Lewis S, Drapeau L, Van Der Lingen CD, Huggett JA, Coetzee JC, Verheye HM, Daunt F, Wanless S, Ryan PG. 2008. Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology* **45**:610–621 DOI 10.1111/j.1365-2664.2007.01447.x.

Haney JC, Stone AE. 1988. Seabird foraging tactics and water clarity: are plunge divers really in the clear? *Marine Ecology Progress Series* **49**:1–9 DOI 10.3354/meps049001.

Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen WD, Caley MJ, Costa DP, Eguíluz VM, Fossette S, Friedlaender AS, Gales N, Gleiss AC, Gunn J, Harcourt R, Hazen EL, Heithaus MR, Heupel M, Holland K, Horning M, Jonsen I, Kooyman GL, Lowe CG, Madsen PT, Marsh H, Phillips RA, Righton D, Ropert-Coudert Y, Sato K, Shaffer SA, Simpfendorfer CA, Sims DW, Skomal G, Takahashi A, Trathan PN, Wikelski M, Womble JN, Thums M. 2016. Key questions in marine megafauna movement ecology. *Trends in Ecology & Evolution* **31**:463–475 DOI 10.1016/j.tree.2016.02.015.

Henkel LA. 2006. Effect of water clarity on the distribution of marine birds in nearshore waters of Monterey Bay., California. *Journal of Field Ornithology* **77**:151–156 DOI 10.1111/j.1557-9263.2006.00035.x.

Hu CM, Lee Z, Franz B. 2012. Chlorophyll a algorithms for oligotrophic oceans: a novel approach based on three-band reflectance difference. *Journal of Geophysical Research: Oceans* **117**:Article C01011 DOI 10.1029/2011jc007395.

Jaquemet S, Le Corre M, Weimerskirch H. 2004. Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FA'Ds). *Marine Ecology Progress Series* **268**:281–292 DOI 10.3354/meps268281.

Jaquemet S, Ternon JF, Kaehler S, Thiebot JB, Dyer B, Bemanaja E, Marteau C, Le Corre M. 2014. Contrasted structuring effects of mesoscale features on the seabird community in the Mozambique Channel. *Deep-Sea Research II* **100**:200–211 DOI 10.1016/j.dsr2.2013.10.027.

Jarvis ED, Mirarab S, Aberer AJ, Li B, Houde P, Li C, Ho SYW, Faircloth BC, Nabholz B, Howard JT, Suh A, Weber CC, da Fonseca RR, Li J, Zhang F, Li H, Zhou L, Narula N, Liu L, Ganapathy G, Boussau B, Bayzid MS, Zavidovych V, Subramanian S, Gabaldón T, Capella-Gutiérrez S, Huerta-Cepas J, Rekepalli B, Munch K, Schierup M, Lindow B, Warren WC, Ray D, Green RE, Bruford MW, Zhan X, Dixon A, Li S, Li N, Huang Y, Derryberry EP, Bertelsen MF, Sheldon FH, Brumfield RT, Mello CV, Lovell PV, Wirthlin M, Schneider MPC, Prosdocimi F, Samaniego JA, Velazquez AMV, Alfaro-Núñez A, Campos PF, Petersen B, Sicheritz-Ponten T, Pas A, Bailey T, Scofield P, Bunce M, Lambert DM, Zhou Q, Perelman P, Driskell AC, Shapiro B, Xiong Z, Zeng Y, Liu S, Li Z, Liu B, Wu K, Xiao J, Yinqi X, Zheng Q, Zhang Y, Yang H, Wang J, Smeds L, Rheindt FE, Braun M, Fjeldsa J, Orlando L, Barker FK, Jønsson KA, Johnson W, Koepfli K-P, O'Brien S, Haussler D, Ryder OA, Rahbek C, Willerslev E, Graves GR, Glenn TC, McCormack J, Burt D, Ellegren H, Alström P, Edwards SV, Stamatakis A, Mindell DP, Cracraft J, Braun EL, Warnow T, Jun W, Gilbert MTP, Zhang G. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **346(6215)**:1320–1331 DOI 10.1126/science.1253451.

Jouventin P, Weimerskirch H. 1990. Satellite tracking of wandering albatrosses. *Nature* **343**:746–748 DOI 10.1038/343746a0.

Kappes MA, Weimerskirch H, Pinaud D, Le Corre M. 2011. Variability of resource partitioning in sympatric tropical boobies. *Marine Ecology Progress Series* **441**:281–294 DOI 10.3354/meps09376.

Kilpatrick KA, Podesta G, Walsh S, Williams E, Halliwell V, Szczodrak M, Brown OB, Minnett PJ, Evans R. 2015. A decade of sea surface temperature from MODIS. *Remote Sensing of Environment* **165**:27–41 DOI 10.1016/j.rse.2015.04.023.

Leal GR, Serafini PP, Simão Neto I, Ladle RJ, Efe MA. 2016. Breeding of White-tailed Tropicbirds (*Phaethon lepturus*) in the western South Atlantic. *Brazilian Journal of Biology* **76**:559–567 DOI 10.1590/1519-6984.16514.

Le Corre M, Jaeger A, Pinet P, Kappes MA, Weimerskirch H, Catry T, Ramos JA, Russell JC, Shah N, Jaquemet S. 2012. Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. *Biological Conservation* **156**:83–93 DOI 10.1016/j.biocon.2011.11.015.

Legrand B, Benneveau A, Jaeger A, Pinet P, Potin G, Jaquemet S, Le Corre M. 2016. Current wintering habitat of an endemic seabird of Reunion Island, Barau's petrel *Pterodroma baraui*, and predicted changes induced by global warming. *Marine Ecology Progress Series* **550**:235–248 DOI 10.3354/meps11710.

Lewallen EA, Van Wijnen AJ, Bonin CA, Lovejoy NR. 2017. Flyingfish (Exocoetidae) species diversity and habitats in the eastern tropical Pacific Ocean. *Marine Biodiversity* **48(4)**:1755–1765.

Longhurst AR, Pauly D. 1987. *Ecology of tropical oceans.* New York: Academic Press.

Loptien U, Meier HEM. 2011. The influence of increasing water turbidity on the sea surface temperature in the Baltic Sea: a model sensitivity study. *Journal of Marine Systems* **88**:323–331 DOI 10.1016/j.jmarsys.2011.06.001.

Mann KH, Lazier JRN. 2006. *Dynamics of marine ecosystems.* Malden: Blackwell Publishing.

Mannocci L, Laran S, Monestiez P, Doremus G, Van Canneyt O, Watremez P, Ridoux V. 2014. Predicting top predator habitats in the Southwest Indian Ocean. *Ecography* **37**:261–278 DOI 10.1111/j.1600-0587.2013.00317.x.

McClain CR. 2009. A decade of satellite ocean color observations. *Annual Review of Marine Science* **1**:19–42 DOI 10.1146/annurev.marine.010908.163650.

Mejias MA, Wiersma YF, Wingate DB, Madeiros JL. 2017. Distribution and at-sea behavior of Bermudan White-tailed Tropicbirds (*Phaethon lepturus catesbyi*) during the non-breeding season. *Journal of Field Ornithology* **88**:184–197 DOI 10.1111/jofo.12198.

Miller MGR, Carlile N, Phillips JS, McDuie F, Congdon BC. 2018. Importance of tropical tuna for seabird foraging over a marine productivity gradient. *Marine Ecology Progress Series* **586**:233–249 DOI 10.3354/meps12376.

Monteiro A, Vaske T, Lessa RP, El-Deir ACA. 1998. Exocoetidae (Beloniformes) off North-eastern Brazil. *Cybium* **22**:395–403.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4(2)**:133–142 DOI 10.1111/J.2041-210x.2012.00261.X.

O'Reilly JE, Maritorena S, O'Brien MC, Siegel DA, Toole D, Menzies D, Smith RC, Mueller JL, Mitchell BG, Kahru M, Chavez FP, Strutton P, Cota GF, Hooker SB, McClain CR, Carder KL, Muller-Karger F, Harding L, Magnuson A, Phinney D, Moore GF, Aiken J, Arrigo KR, Letelier R, Culver M. 2000. *SeaWiFS Postlaunch Calibration and Validation Analyses. SeaWiFS postlaunch technical report series: Part 3 NASA Tech Memo 2000-206892, Vol 11*, Greenbelt: NASA Goddard Space Flight Center.

Paiva VH, Geraldes P, Ramirez I, Garthe S, Ramos JA. 2010a. How area restricted search of a pelagic seabird changes while performing a dual foraging strategy. *Oikos* **119**:1423–1434 DOI 10.1111/j.1600-0706.2010.18294.x.

Paiva VH, Geraldes P, Ramirez I, Meirinho A, Garthe S, Ramos JA. 2010b. Oceanographic characteristics of areas used by Cory's shearwaters during short and long foraging trips in the North Atlantic. *Marine Biology* **157**:1385–1399 DOI 10.1007/s00227-010-1417-5.

Pennycuick CJ, Schaffner FC, Fuller MR, Obrecht HH, Sternberg L. 1990. Foraging Flights of the White-Tailed Tropicbird (*Phaethon lepturus*): radiotracking and Doubly-labelled Water. *Colonial Waterbirds* **13**:96–102 DOI 10.2307/1521574.

Pinaud D, Weimerskirch H. 2005. Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology* **74**:852–863 DOI 10.1111/j.1365-2656.2005.00984.x.

Poli CL, Harrison AL, Vallarino A, Gerard PD, Jodice PGR. 2017. Dynamic oceanography determines fine scale foraging behavior of Masked Boobies in the Gulf of Mexico. *PLOS ONE* **12**:e0178318 DOI 10.1371/journal.pone.0178318.

Prince PA, Wood AG, Barton T, Croxall JP. 1992. Satellite tracking wandering albatross Diomedea exulans in the South Atlantic. *Antarctic Science* **4**:31–36 DOI 10.1017/S0954102092000075.

R Core Team. 2016. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. *Available at https://www.R-project.org/*.

Sabarros PS, Gremillet D, Demarcq H, Moseley C, Pichegru L, Mullers RHE, Stenseth NC, Machu E. 2014. Fine-scale recognition and use of mesoscale fronts by foraging Cape gannets in the Benguela upwelling region. *Deep-Sea Research II* **107**:77–84 DOI 10.1016/j.dsr2.2013.06.023.

Shi W, Wang MH. 2010. Characterization of global ocean turbidity from Moderate Resolution Imaging Spectroradiometer ocean color observations. *Journal of Geophysical Research: Oceans* **115**:Article C11022 DOI 10.1029/2010JC006160.

Soanes LM, Bright JA, Carter D, Dias MP, Fleming T, Gumbs K, Hughes G, Mukhida F, Green JA. 2016. Important foraging areas of seabirds from Anguilla, Caribbean: implications for marine spatial planning. *Marine Policy* **70**:85–92 DOI 10.1016/j.marpol.2016.04.019.

Spear LB, Ainley DG. 1997. Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis* **139**:221–233 DOI 10.1111/j.1474-919X.1997.tb04620.x.

Spear LB, Ainley DG. 2005. At-sea behaviour and habitat use by tropicbirds in the eastern Pacific. *Ibis* **147**:391–407 DOI 10.1111/j.1474-919x.2005.00418.x.

Stonehouse B. 1962. The Tropic Birds (*Genus Phaethon*) of Ascension Island. *Ibis* **103B**:124–161 DOI 10.1111/j.1474-919X.1962.tb07242.x.

Stramska M, Swirgon M. 2014. Influence of atmospheric forcing and freshwater discharge on interannual variability of the vertical diffuse attenuation coefficient at 490 nm in the Baltic Sea. *Remote Sensing of Environment* **140**:155–164 DOI 10.1016/j.rse.2013.08.043.

Suryan RM, Sato F, Balogh GR, Hyrenbach KD, Sievert PR, Ozaki K. 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. *Deep-Sea Research II* **53**:370–386 DOI 10.1016/j.dsr2.2006.01.012.

Tchamabi CC, Araujo M, Silva M, Bourlas B. 2017. A study of the Brazilian Fernando de Noronha island and Rocas atoll wakes in the tropical Atlantic. *Ocean Modelling* **111**:9–18 DOI 10.1016/j.ocemod.2016.12.009.

Tremblay Y, Bertrand S, Henry RW, Kappes MA, Costa DP, Shaffer SA. 2009. Analytical approaches to investigating seabird-environment interactions: a review. *Marine Ecology Progress Series* **391**:153–163 DOI 10.3354/meps08146.

Vilchis LI, Ballance LT, Fiedler PC. 2006. Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. *Marine Ecology Progress Series* **315**:279–292 DOI 10.3354/meps315279.

Wakefield ED, Cleasby IR, Bearhop S, Bodey TW, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC. 2015. Long-term individual foraging site fidelity—why some gannets don't change their spots. *Ecology* **96**:3058–3074 DOI 10.1890/14-1300.1.

Wakefield ED, Phillips RA, Matthiopoulos J. 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series* **391**:165–182 DOI 10.3354/meps08203.

Weimerskirch H. 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Research II* **54**:211–223 DOI 10.1016/j.dsr2.2006.11.013.

Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G, Lipp HP. 2002. GPS tracking of foraging albatrosses. *Science* **295**:1259–1259 DOI 10.1126/science.1068034.

Weimerskirch H, Le Corre M, Bost CA. 2008. Foraging strategy of masked boobies from the largest colony in the world: relationship to environmental conditions and fisheries. *Marine Ecology Progress Series* **362**:291–302 DOI 10.3354/meps07424.

Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F. 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? *Proceedings of the Royal Society B-Biological Sciences* **272**:53–61 DOI 10.1098/rspb.2004.2918.

Zajkova Z, Militao T, Gonzalez-Solis J. 2017. Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic. *Marine Ecology Progress Series* **579**:169–183 DOI 10.3354/meps12269.

Zavalaga CB, Emslie SD, Estela FA, Muller MS, Dell'Omo G, Anderson DJ. 2012. Overnight foraging trips by chick-rearing Nazca Boobies *Sula granti* and the risk of attack by predatory fish. *Ibis* **154**:61–73 DOI 10.1111/j.1474-919X.2011.01198.x.