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LEILA FIGUEIREDO DE ALMEIDA SILVA CAMPOS

PADRÕES DE FORRAGEIO DE *PHAETHON LEPTURUS* NO ATLÂNTICO
EQUATORIAL

MACEIÓ - ALAGOAS
Fevereiro de 2018

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Dissertação apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde. Universidade Federal de Alagoas, como requisito para obtenção do título de Mestre em CIÊNCIAS BIOLÓGICAS, área de concentração em Conservação da Biodiversidade Tropical.

**Orientador: Prof. Dr. Márcio Efe
Co-orientadora: Dra. Sophie Bertrand**

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Leila Figueiredo de Almeida Silva Campos

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*“La mer, une fois qu’elle vous a jete un sort,
Vous tient dans son filet merveilleux pour toujours”*

Jacques Yves Cousteau

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RESUMO

Aves tropicais vivem em ambiente oligotrófico, com presas distribuídas em manchas, e apresentam respostas comportamentais e fisiológicas para as restrições impostas por características oceanográficas. Este estudo investiga a ecologia de movimento da espécie pantropical *Phaethon lepturus* Daundin, 1802 em sua colônia do Atlântico Equatorial utilizando aparelhos miniaturizados de GPS. A espécie tem hábito pelágico, solitário e generalista. Nos oceanos Pacífico e Índico a distância até a colônia limita sua escolha por áreas de forrageio enquanto características oceanográficas como Temperatura Superficial do Mar, Clorofila *a* (utilizada como *proxy* para produtividade primária) e Salinidade ditam a distribuição no mar. Nossos resultados mostram alternância entre viagens curtas e longas, diferença significativa entre padrões de atividade em viagens longas e curtas e associação entre Rabos-de-palha-de-bico-amarelo e Temperatura Superficial do Mar e Turbidez durante a procura por presas. Sugere-se que estes parâmetros estão relacionados à disponibilidade de presas já que peixes voadoras, alimento preferencial destas aves, ocorrem em águas quentes e claras, condições presentes na região onde o maior número de viagens de alimentação foi registrado.

Palavras-chave: Rabos-de-palha, Forrageio dual, Padrões de atividade, Características oceanográficas.

ABSTRACT

Tropical seabirds live in oligotrophic environments with prey patchily distributed and present behavioral and physiological responses to constraints imposed by oceanographic characteristics. This study investigates movement ecology of the pantropical white-tailed tropicbird *Phaethon lepturus* Daudin, 1802 on its Equatorial Atlantic colony, located at Fernando de Noronha Archipelago using miniaturized GPS loggers. The species has a pelagic, solitary and generalist biology. On Pacific and Indian oceans distance from colony limitates its choice on foraging grounds and oceanic features such as Sea Surface Temperature, chlorophyll *a* (as a proxy for primary productivity) and salinity dictate their at-sea distribution. Our results show alternation between short and long foraging trips, alternation between members of a pair in chick-attendance and at-sea occurrence, significant difference between activity modes in short and long trips and association among tropicbirds and STT and turbidity while searching for food patches. We hypothesize that these parameters are related to preys availability, as flyingfish occur in warm oceanic areas and the waters around the Arquipelago are most favorable to their occurrence on its southwest direction.

Key words: Tropicbird, Dual foraging, activity patterns, oceanic features.

APRESENTAÇÃO

Esta dissertação aborda aspectos sobre comportamento e padrões de forrageio do *Phaethon lepturus* Daudin, 1812, conhecido popularmente como Rabo-de-palha-do-bico-laranja ou ainda Rabo-de-junco (como é denominado pelos nativos em sua área de ocorrência), em sua maior colônia em território brasileiro, localizada no Arquipélago de Fernando de Noronha.

O trabalho estrutura-se da seguinte forma: Capítulo um, intitulado “Foraging of Tropical Seabirds: State of the art and research challenges”, que configura revisão da literatura com informações atualizadas sobre os temas abordados nos capítulos dois e três; Capítulo dois: “Foraging of the White-tailed Tropicbird in the Equatorial Atlantic Ocean” a ser submetido à revista *EMU*, que apresenta as atividades de vôo e compara estratégias de forrageio de *Phaethon lepturus*; Capítulo três: “Foraging behaviour and habitat choice of tropicbirds revealed by GPS tracking and remote sensing” que investiga a relação entre as aves e as características oceanográficas em seus locais de alimentação, artigo submetido à revista *PlosOne*; Discussão geral, dividida em tópicos de acordo com os resultados obtidos no trabalho e Conclusão. Ilustrações sobre a área de estudo, procedimentos metodológicos e fotografias de espécimes que não foram adicionadas aos artigos científicos por questões de espaço encontram-se na sessão Apêndices.

Foraging of Tropical Seabirds: State of the art and research challenges

Since Ashmole's (1971) statement that tropical marine systems have low productivity and therefore lower prey abundance and patchy distribution of food items, as well as lower seasonal variation in resources (Weimerskirch 2007) than temperate regions, marine ornithology studies agree that tropical seabirds face different environmental conditions than temperate and polar ones. Oceanic circulation and light availability, for instance, structure ecosystems throughout the oceans by their importance to primary productivity of marine food webs (Sabarros *et al.* 2014).

These and others oceanic features affect prey distribution and consequently the foraging success of predators (Fauchald 2009, Scales *et al.* 2014), and impose high foraging costs by increasing time spent in search for prey patches or extending the prospected area in tropical oceans (Ballance *et al.* 1997, Catry *et al.* 2009a, Fauchald 2009), resulting in a multidirectional dispersal, especially while non-breeding (Spear and Ainley 2005). Oceanic features such as bathymetry, sea surface temperature (SST), salinity and thermocline formation are responsible for these marked differences between tropical and colder oceans. Their influence on seabird ecology, tropicbirds in special, and the strategies developed by seabirds to cope with them is the focus of this chapter.

Foraging strategies at oligotrophic environments

The global distribution of pelagic birds is closely associated with inconsistencies in the marine environment, and ocean circulation patterns are important in determining where these birds feed (Hunt 1991). Indeed, in the absence of global ocean circulation, most nutrients would be unavailable to organisms that feed on the surface, primarily due to the formation of pycnoclines, vertical density gradients that prevent mixing of water masses and are formed primarily from the differential heating of the ocean surface by the sun compared with the water depth. A strong temperature gradient, called the thermocline, is formed. The warmer surface water is less dense than deep cold water, and floats on it, being mixed by winds and forming the epipelagic zone. All the resulting organic matter of the death of above pycnocline

individuals possibly sink towards the ocean floor, creating a layer rich in nutrients at great depths (Shealer 2002).

The depth and temporal stability of pycnocline varies seasonally and geographically. In tropical and temperate oceans, pycnocline is relatively permanent, shallow, and its average depth ranges from 25 meters in the eastern part of the tropical oceans to 250 meters in the center of subtropical gyres (Longhurst 1999). However, in higher latitudes the pycnocline is more dynamic due to strong seasonality of wind speed and solar radiation. Since tropical pycnoclines are better defined and because precipitation typically exceeds evaporation in tropical oceans, these waters have a higher resistance in the mixture layers than at higher latitudes. This reduction in mixture results in lower resources for marine biota (Raymont 1980).

There are areas where characteristics of ocean circulation, either by wind or thermohaline, force the mixture of rich deep water and nutrients in surface layers. Upwelling areas, for example, are formed by turns resulting from land rotation, and focus on the west coasts of America (Humboldt Current) and Africa (Benguela Current). Convergence zones are also important areas of productivity, particularly in areas of open ocean where little mixing occurs (Longhurst 1999).

In tropical oceans productivity is lower, prey more patchily distributed (Jaquemet *et al.* 2004, Weimerskirch 2007) and the environment less seasonal than the one faced by temperate and polar seabirds (Ashmole 1971) and therefore unpredictable events, such as El Niño Southern Oscillation (ENSO) and other climatic phenomena (Schreiber and Schreiber 1984) are responsible for multi-year environmental variations. These conditions may lead to non-seasonal breeding periods and inter-annual variations in the feeding ecology and body conditions of tropical seabirds (Le Corre *et al.* 2003, Castillo-Guerrero *et al.* 2011) along with a large diversity of breeding regimes acquired by different species to live by these environmental constraints (Le Corre 2001).

Tropical seabirds evolved to increase energy intake (Bradshaw *et al.* 2004) by variable strategies, such as “near obligate commensalism” with sub-surface predators (Au and Pitman 1989), plunge diving (Ballance and Pitman 1999), dual foraging strategies (Weimerskirch *et al.* 1994, Congdon *et al.* 2005, Sommerfeld and Henicke 2010, Ochi *et al.* 2016) and association with oceanic fronts or areas of high

chlorophyll concentration (Sabarros *et al.* 2014, Thiers *et al.* 2014). As central place foragers while breeding, distance from colony is also an important limiting factor for the success of tropical seabirds in highly oligotrophic environments (Spear and Ainley 2005).

One way to cope with general low productivity in tropical oceans is to forage at areas with high and predictable prey encounters there are usually related to oceanographic features such as upwellings, eddies, gyres, fronts and seamounts, creating a repertoire of familiar and highly productive foraging sites throughout a breeding season or even at a multi-year approach, both at finer and coarse scales (Hunt *et al.* 1999, Fauchald 1999, Bonadonna *et al.* 2001, Bradshaw *et al.* 2004, Weimerskirch *et al.* 2007, Wakefield *et al.* 2009), as seen in a large number of marine species (Hamer *et al.* 2001, Bradshaw *et al.* 2004, Weimerskirch 2007, Bellquist *et al.* 2008, Montevecchi *et al.* 2009, Bartumeus *et al.* 2010, Kotzerka *et al.* 2011, Lowther *et al.* 2012, Bertrand *et al.* 2014, Sommerfeld *et al.* 2015, Grecian *et al.* 2016).

Although pelagic bird behavior varies between temporal and spatial scales (Weimerskirch *et al.* 2005), clear associations are seen according to biophysical phenomena that result in disposal of prey in patches. Oceanic features might influence diving behavior (Castillo-Guerrero *et al.* 2011), diet composition (Le Corre *et al.* 2003) and breeding performance (Ramos *et al.* 2002, Catry *et al.* 2013) of tropical seabirds. Besides, the preference displayed by individuals for some foraging sites suggests they may remember these areas with favorable oceanographic features and resource predictability (Hunt and Schneider 1987, Schneider 1993, Weimerskirch 2007, Votier *et al.* 2017).

Several birds show affinity with eutrophic, mesotrophic or oligotrophic waters at small, medium and large scales (Hyrenbach *et al.* 2002, Awkerman *et al.* 2005, Pinaud and Weimerskirch 2005). In the equatorial Pacific, for example, fish-eating birds prefer well stratified water with thorough and well defined thermocline while planktivores prefer more shallow waters and weak thermoclines (Ribic and Ainley 1997, Spear *et al.* 2001, Vilchis *et al.* 2006).

Biological interactions are also important to tropical seabirds' success, such as local enhancement (seabirds use flocks of birds to locate prey patches, Fauchald 2009) and feeding with surface sub predators (Au and Pitman 1989, Ballance *et al.* 1997,

Ballance and Pitman 1999, Jaquemet *et al.* 2004, Jaquemet *et al.* 2014). In fact, the terms “near-obligate commensalism” (Au and Pitman 1989) and “facilitated foraging” (Maxwell and Morgan 2013) are used to show how dependent tropical seabirds are of other marine predators at choosing their foraging site and several studies have shown this interaction (Jaquemet *et al.* 2004, Hebshi *et al.* 2008, Weimerskirch *et al.* 2008, Catry *et al.* 2009a, Yamamoto *et al.* 2010, Maxwell and Morgan 2013, Danckwerts *et al.* 2014, Thiers *et al.* 2014).

Sub-surface predators make prey available for seabirds by indicating prey aggregation (Jaquemet *et al.* 2004), driving prey to the surface, injuring or disorienting prey and providing scraps on which seabirds can scavenge (Ballance and Pitman 1999). Additionally, there is a positive correlation between abundance of seabirds in a given community and their association with sub-surface predators (Ballance and Pitman 1999), as well as an increase in number of individuals from one species in a multi-species flock in facilitated feeding events as evidenced by Jaquemet *et al.* (2004) at Indian Ocean.

Fishing studies in the Equatorial Atlantic express the importance of Yellowfin Tuna *Thunnus albacaris*, Skipjack Tuna *T. alalunga* and *T. atlanticus* for the artisanal fishery in the Fernando de Noronha region, and although their occurrence seems to be more closely related to the coastal areas (<8 km) of the Archipelago (Lessa 1998, Dominguez *et al.* 2016), they might be related to the feeding habits of tropical seabirds that use the area to breed. These feeding opportunities determine indirectly the distribution and abundance patterns of tropical seabirds, providing the basis for a complex community with a predictable structure and intricate interactions (Ballance and Pitman 1999).

Life in an oligotrophic environment also determines physiological evolutionary characteristics, since tropical seabirds must search for food at lower energetic costs than birds from highly productive areas. Thus, tropical seabirds were selected for proficient flight other than swimming, and may search for food in a large oceanic area (Peters 1983, Ballance and Pitman 1999). This ability, however, prevents the development of intricate diving skills, common at polar and temperate seabirds, such as deep diving (Ballance and Pitman 1999).

Tropical seabirds are confined to a two dimensional feeding range, above the sea surface or a few meters below it, and developed behavior such as plunge diving (boobies and tropicbirds), surface plunging (tropicbirds and terns), kleptoparasitism (frigatebirds) and aerial feeding (tropicbirds and frigatebirds), unique to tropical seabirds and presumably evolved in response to volant preys in these oceans (fish from the Exocoetidae family and Ommastrephidae squid, for instance) (Ballance and Pitman 1999). The efficient flight of tropical seabirds and consequent lack of diving adaptations is important to spatial availability of prey items, since prey can swim to deeper waters and avoid consumption by seabirds that are unable to reach more than a few meters of the water column (Fauchald 2009).

Additionally, tropical seabirds tend to be smaller in terms of mean adult body mass and to have reverse sexual dimorphism (females larger than males). This might be related to higher distance from colony of the foraging sites and the consumption of elusive preys, favoring smaller body sizes, as well as the aerial displays while mating. Larger size in incubating females might also offer a buffer against starvation in poor-nutrient waters (Fairbairn and Shine 1993 but see Croxall 1995).

Distance from breeding colony represents an important factor to foraging area selection in central place foragers (Fauchald 1999, Spear and Ainley 2005, Hyrenbach *et al.* 2007, Paiva *et al.* 2010, Avalos *et al.* 2017) and seabirds exploit feeding areas based on travelling capabilities, spatial distribution of prey and the need to return to nests (Fauchald 2009) as well as adaptations of search radius and estimate food patch position by prior successful encounters of high-density patches at small spatio-temporal scale (Fauchald 1999). As shown by Weimerskirch (2007), individuals are more faithful to sites closer to the colony than further from it. This happens because the longer it takes for an individual to return to the same foraging ground, the more likely prey patches might have moved from it or been depleted. In addition, it may be related to a trade-off between long and short trips, with higher foraging site fidelity to closer areas with less prey patches and longer trips for self-provisioning at further but richer foraging sites (Sommerfeld *et al.* 2015).

Dual foraging pattern is observed in many seabird species (Granadeiro *et al.* 1998, Weimerskirch 1998, Congdon *et al.* 2005, Sommerfeld and Henicke 2010, Young *et al.* 2010, Cercere *et al.* 2014, McDuie *et al.* 2015, Shoji *et al.* 2015, Avalos *et al.*

2017) and consists on alternate self-provisioning long trips (usually to more productive foraging areas) and near-colony short trips, responsible for chick provisioning (Weimerskirch *et al.* 1994). Although long trips are more profitable for adults (larger food mass and energy rich), short trips increase feeding frequency for offspring, representing a compromise between chick's need to increase growth rates and survival and adults body condition (Schaffner 1990). In addition, short trips may minimize the risk of long fasting periods for chicks, since pelagic parents forage independently (Weimerskirch *et al.* 1994).

Dual foraging can be triggered by decrease in marine productivity and consequent decline in prey quality (Riou *et al.* 2011, Avalos *et al.* 2017) decrease in adults body mass (Weimerskirch *et al.* 1998, Ochi *et al.* 2010) and chick's body conditions (Ochi *et al.* 2010). Cercere *et al.* (2014) showed that the choice for dual foraging strategy at the Mediterranean Sea by Scopoli's Shearwater is related to low primary productivity around the colony and higher weight in chicks. In fact, adults breeding in areas with higher primary productivity presented unimodal foraging (only short trips) and larger body masses than the ones that used dual foraging for self-provision and chick attendance, much like Cory's Shearwaters in Portuguese neritic and oceanic environments, with contrasting unimodal and bimodal feeding strategies in colonies next to and further from highly productive areas respectively (Avalos *et al.* 2017)

The use of different foraging strategies is related to what Schaffner (1990) called "target payload mass", a hypothetical threshold parents must collect as quickly as their foraging abilities and environmental conditions allow, after satisfying their own energetic needs, in order to provide for their offspring. Swallowing capacity of chick determines the target payload mass the adult will choose to carry and the type of prey they collect (Le Corre *et al.* 2003) since evidence suggest birds could carry much more food than they actually do (Schaffner 1990). The dual foraging strategy may indicate the need to acquire this threshold even if it means to travel to larger and further areas from the colony (Le Corre *et al.* 2003, Cercere *et al.* 2014).

In the Equatorial Atlantic Ocean the low productivity is caused by strong and permanent pycnoclines throughout the year and the impact of oligotrophic Equatorial South Current (Becker 2001, Souza *et al.* 2013) in upper waters (Cordeiro *et al.* 2013, Souza *et al.* 2013, Tchmabi *et al.* 2017). The Fernando de Noronha Chain has

a steep and homogeneous thermocline between 70 and 170m (Souza *et al.* 2013) in the Equatorial Surface Water, with salinity > 35.5 and temperature above 20°C while the South Atlantic Central Water with temperature ranging from 11.3 to 20°C and salinity between 35.5 and 36.4 was present below the thermocline (Cordeiro *et al.* 2013).

Local topography of islands and seamounts (“wakes”) influence changes in temperature and salinity but are not shallow enough to influence the euphotic zone and therefore do not cause nutrient enrichment in the area (Souza *et al.* 2013). Conversely, nutrient enrichment may occur due to wind action (mostly southeastern trade winds blowing from east to west), currents and upwelling events near islands (Becker 2001, Cordeiro *et al.* 2013, Tchmabi *et al.* 2017).

Challenges in telemetry and satellite based research

As early as the 1890`s birds were marked for scientific purposes (Sokolov 2011). Banding of individual birds was the main technique employed during the 20th century and its limitations, such as the need to tag a large number of individuals in order to recapture enough data for analysis, made clear the need to develop new techniques capable of tracking animal movement that became a reality in the 1960s with simple radio transmitters (Sokolov 2001). The use of remote sensing devices attached to animals is called *bio-logging* (Evans *et al.* 2013). Its application in movement ecology and animal conservation is vast, since external attachment of these devices enables researchers to study variables otherwise inaccessible (Culik and Wilson 1991) and ranges from investigation of fisheries’ impacts on wildlife, physiological parameters, foraging strategies, rational development of protected areas and, more recently, impacts of climate change on highly mobile species (Tomkiewicz *et al.* 2010, Sokolov 2011, Bouten *et al.* 2013, Neumann *et al.* 2015, Browning *et al.* 2017).

In the past decades tracking devices have evolved from simple Ultra-High-Frequency (UHF) to Small Platform Transmitters (PTTs) and ARGOS receiving system (Vincent *et al.* 2002, Soutullo *et al.* 2007, Sokolov 2011, Chan *et al.* 2015) to light-level based devices (GLS) (Anafasney 2004) and, finally, Global Position Systems (GPS) miniaturized loggers (Evans *et al.* 2013). Alongside with device evolution there was an expansion in the amount of species on which loggers could be used (Evans *et al.* 2013) since device weight is an important feature due to the notion that any

logger attached to birds must weigh less than 3% of the animal's total body mass (Kenward 2001 but see Vandenabeele *et al.* 2012) in order not to interfere with behavior (see Culik and Wilson 1991, Hawkins 2004, Barron *et al.* 2010 for more on bio-logging devices' effects on wildlife). Additionally, the mathematical challenges of spatial models used in the theoretical analysis of animal movements (Fagan and Calabrese 2014) are constantly perfected and now robust investigation of complex data enable researchers to access individual and population behavior and its relation with the surrounding environment (Evans *et al.* 2013, Earl and Zollner 2017).

The Onboard GPS systems (SOB), that acquires and stores data in the unit until further download after recovery (Tomkiewicz *et al.* 2010) has been the most popular tracking device in the past years. It can store both GPS-based location and sensor data, such as diving parameters and temperature, and is used in terrestrial and marine animals. An important limitation in this system is the necessity of recapturing each individual for accessing data due to the impossibility of relay information from the instrumented animal to another location. This might result in loss of devices in the field and the data is never recovered (Afanasyev 2004, Tomkiewicz *et al.* 2010).

Technologies that enable data transfer were created to send data at regular intervals or near-real-time and are mostly used in studies where additional fieldwork or changes in tracking parameters might be necessary (Tomkiewicz *et al.* 2010, Bouten *et al.* 2013). These devices also act as SOBs when needed, providing a backup dataset if some problem prevents further data transfer. The most advanced enable researchers to receive data via GSM/SMS (global system for mobile communication/short message service) but this service is widely available only in Europe and Asia (i.e. Gervasi *et al.* 2006 with brown bears in Sweden and Kojola *et al.* 2009 with wolves in Finland, Santos *et al.* 2017 with Black Kites in Spain) and therefore cannot be used in other areas due to lack of coverage zones (animals might not encounter receiving towers) (Tomkiewicz *et al.* 2010). In places when GSM is not available, satellite-based telephone systems might be used to transfer animal data but biotelemetry companies must have full access to operational systems and hardware designs in order to transfer logger data (Tomkiewicz *et al.* 2010).

Most studies using bio-logging techniques seek to track animal movement for months or even years at a time so the development of long-term attachment and battery

autonomy was necessary (Chan *et al.* 2015). Additionally, power management is an important issue, since a threshold between device weight and operational capability must be found (Tomkiewicz *et al.* 2010). On recent years, solar powered devices were created, enabling researchers to expand the time scale of monitoring (Soutullo *et al.* 2007, Bouten *et al.* 2013, Chan *et al.* 2015). Unfortunately, these loggers are still too heavy (i.e. UvA-BiTS <http://www.uva-bits.nl> weight from 7.2 to 22 g, Bouten *et al.* 12 g) to be used in some species (including the one studied in this dissertation, the *Phaethon lepturus*). Advances in battery autonomy in miniaturized devices are much needed in order to enable small bird's research. Our study, with field work conducted in 2015, could not obtain data beyond 26 hours of logger deployment, and since most birds could travel for more than 10 days at a time, there is an important gap of information due solely to battery limitation.

Animal movement data accessed by remote sensing devices can be associated with coarse-but-frequent (Neumann *et al.* 2015) data (i.e. wind speed, temperature, primary productivity) from satellite sensors such as MODIS (Moderate Resolution Imaging Spectroradiometer – NASA) and LANDSAT (United States Geological Survey and NASA) to access information on how environmental features influence animal behavior (Weimerskirch *et al.* 2008, Young *et al.* 2010, Yamamoto *et al.* 2010, Castillo-Guerrero *et al.* 2011, Catry *et al.* 2013, Thiers *et al.* 2014).

Most of the environmental indices are available from a broad range of remotely-sensed datasets that vary in spatial resolution, wave length, etc. (Neumann *et al.* 2015). Chlorophyll *a*, for instance, used to indicate primary productivity (Grémillet *et al.* 2008), offers an estimate of algal biomass and its spatial and temporal variability (O'Reilly *et al.* 1998), which is important to seabird research since chlorophyll concentration affect phytoplankton productivity that influences feeding behavior of seabirds (Wakefield *et al.* 2009), and can be measured by a band combination of blue, green, red and NIR at a 30 meters resolution in LANDSAT 8 (Jensen 2005) or in bands 8-16 in with 1000 meters spatial resolution in MODIS, for example. Softwares such as SeaDAS and ENVI 5.0 can be used to perform the atmospheric corrections, combine band ratios and provide maps with the environmental indices required for each research (Jensen 2005, Moradi 2016).

Movement ecology

Until recently at sea distribution of seabirds was accessed by on board sightings and ring recovery (Catry *et al.* 2009, Yamamoto *et al.* 2010) and therefore understanding why, how and when animals move (Calabrese and Fegan 2014) was a difficult task. With the development of tracking technologies in the last decades, however, access to the mechanisms and ecological processes shaping organismal movement patterns and their consequences for ecology and evolution (Nathan *et al.* 2008) became simpler and now relocation data of mobile animals at intervals of minutes or seconds provide a temporal sequence of the steps an animal took through space (Edelhoff *et al.* 2016) and key aspects of animal behavior, predator-prey dynamics, infectious diseases management, conservation biology and many other areas hinge upon movement data (Nathan *et al.* 2008, Calabrese and Fegan 2014).

The growing capacity for collecting high resolution movement data requires improvements in data management, processing and analytical techniques (Nathan *et al.* 2008) and new databases (i.e. Movebank, SeaBASS) provide data on movement analysis and environmental indices recorded worldwide. New analytical tools were also developed, as state-space models of individual animal movement (Patternson *et al.* 2008).

Over the years a multitude of analytical approaches have been applied to understand movement ecology. Visual analyses are commonly used to describe animal behaviour, such as Kernel, an estimation of utilization distribution (*UD*) of home range (Calenge 2006). Although still vastly used (i.e. Leal 2013, McDuie *et al.* 2015, Avalos *et al.* 2017, Mejias *et al.* 2017), visual analyses are being replaced by techniques that use track sinuosity or heading variance to access different behavioral states among a single path.

Movement paths are composed by recorded locations on a temporal sequence, and their deconstruction in different behaviors depends on data resolution and sampling frequency (Nathan *et al.* 2008), such as the number of positions acquired at a given time. Once the resolution is sufficiently acquired, the identification of breaking points to different phases is the next step (Nathan *et al.* 2008) and contrasting methodologies were developed to deal with this challenge and relate behaviors in each segment to the surrounding environment (Edelhoff *et al.* 2016).

In this area of movement pattern description, the use of the Correlated Random Walk (hereinafter CRW), a theoretical model that decomposes paths in a series of steps and turning angles (changes of direction, Edelhoff *et al.* 2016) assumes that animal moves usually have a directional persistence and allows researchers to comprehend animal movement in a realistic (but yet simplified) way (Fagan and Calabrese 2014). An important process modeled with CRW is the Area Restricted Search (ARS), the intense search behavior triggered by food encounter where animals use low speed, regular changes in flight direction and large turning angles to remain within the food patch and increase the probability of detecting prey (Fauchald 2009, Wakefield *et al.* 2009, Méthé *et al.* 2015) opposed to fast and nearly straight movements to find another food patch (Weimerskirch 2007, Kappes *et al.* 2011, Méthé *et al.* 2015).

ARS and other continuum behavioral states (Wakefield *et al.* 2009) can be measured by different techniques, such as speed, heading variance, Hidden Markov Models and First Passage Time analysis (Fauchald and Tveraa 2003, Wakefield *et al.* 2009, Dean *et al.* 2013). FPT, for instance, is the time required for an animal to cross a circle of a given radius, and provides an indirect index of ARS since it shows the spatial scale at which birds carry out ARS (Fauchald and Tveraa 2003, Soanes *et al.* 2014).

One aspect to be considered is that inside path geometry some behaviors are measured in a continuum spectrum, such as traveling in between food patches and searching for food within a food patch (ARS) while others are more straight forward and categorical, such as flight and non-flight, and these differences should be considered during the analyses (Wakefield *et al.* 2009). Additionally, the association among tracking data and sea-surface temperature and Chlorophyll *a* must be carefully analyzed since they might be a source of research bias (Grèmillet *et al.* 2008, Scales *et al.* 2014)

With these restriction in mind, along with the small tracking data and the fact that only one type of traveling mode could be accessed completely, our research could not apply some analysis such as Hidden Markov Models and First Passage Time, limitations not un-commonly found in movement ecology studies (Wakefield *et al.* 2009, Avalos *et al.* 2017). However, as we can see in the next section, *in situ*

observation and sensibility analyses of raw data were able to provide interesting and robust results.

Speed parameter: An example of resolution bias

Due to previous logger deployment in *Phaethon aethereus* (a sister species) (Leal 2013) by our research group in Abrolhos Archipelago, we hypothesized at first that foraging trips of the tropicbirds from Ilha do Morro do Chapéu would last no longer than 48 hours. However, *in situ* observation and logger recovery showed that White-tailed tropicbirds (WTTB) breeding in Fernando de Noronha have a dual foraging strategy, found in many tropical seabirds and related to compromise between chick provisioning and adult body condition (Diamond 1975, Schaffner 1990, Congdon *et al.* 2005, Sommerfeld and Hennicke 2010, McDuie *et al.* 2015). This means that parents responsible for nest attendance engage in short trips after dawn and return a few hours later or, at most, in a 21 hours period while its partner engaged in a long trip that might last from four to 11 days. Battery autonomy of our loggers lasted ~ 26 hours depending on the resolution: loggers with 1 fix per 10 seconds would lose battery earlier than those programmed to record 1 fix every 60 seconds.

The dual foraging pattern meant that while short foraging trips by the attendant parent were correctly accessed, longer foraging trips by the non-attendant parent were not, generating lack of information on our foraging length, area and maximum range. In fact, of the 21 trips only 16 could be used to access total distance and duration, all of them performed by the attendant parent.

Our Gypsy 4 loggers (Technosmart, Italy) recorded data at 10, 30 and 60 seconds intervals and provided a total of 21 tracking without gross errors. Of those, 16 were complete (with no significant loss of signal or battery exhaustion) and 5 were incomplete (with battery exhaustion before the bird's arrival from the foraging trip).

As we can see in Figures 1-2 all three resolutions of GPS fixes presented overall low speed. Different resolution can increase research bias by not properly showing animal behavior (Nathan *et al.* 2008, Edelhoff *et al.* 2016): At 1 fix/60 seconds, for instance, the animal might have performed a dive or turned direction of flight in between fixes, flight speed will appear faster than it really is and the movement will be undervalued. Conversely, resolutions of 1 fix per second would increase data accuracy with the downside of battery reduction. However, the speed parameter of our data seems to agree with previous literature, showing that tropicbirds move

intermittently, alternating between flights and resting on water (Pennycuik 1990, Spear and Ainley 1997, Spear and Ainley 2005, Leal 2013; see McDuie *et al.* 2015 and Avalos *et al.* 2017 for low flight speed in Shearwaters). In fact, their highly energetic costing flapping flight might be responsible for this overall low speed (Spear and Ainley 1997, Mannonci *et al.* 2014) (Figure 2).

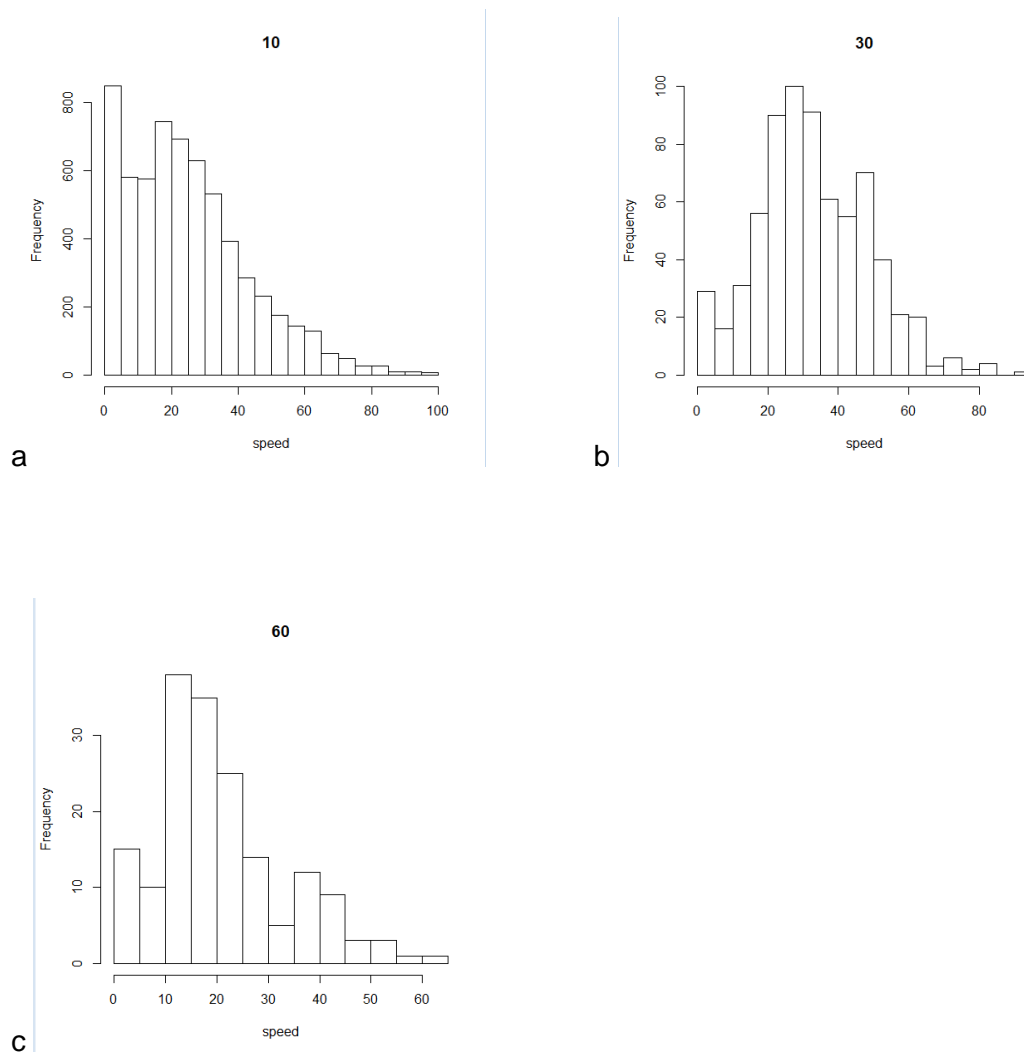


Figure 1- 1 fix/10 sec (a); 1 fix/30 sec (b); 1 fix/60 sec (c). Different data resolution do not seem to influence the speed parameter.

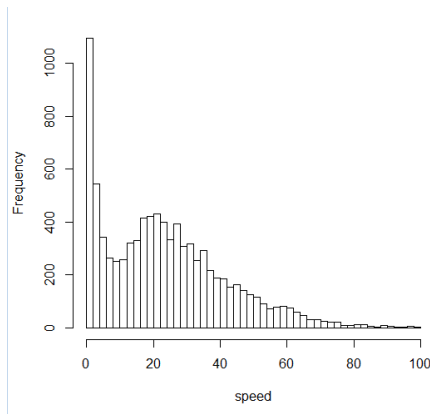


Figure 2- Flight speed of all foraging trips.

With the research limitations in mind, we could access novel information on the flight parameters and overall behavior of the studied species on its largest Brazilian breeding site.

Tropicbirds

Among tropical seabirds species, the tropicbirds (order Phaethontiiformes) are characterized by their offshore (Diamond 1975, Schaffner 1990) and solitary feeding habits, and the white-tailed tropicbird *Phaethon lepturus* (Daudin, 1802) is the one more commonly seen in association with sub-surface predators (Spear and Ainley 2005 but see Jaquemet *et al.* 2004). WTTB breed all year around and therefore do not rely on a unique peak of food availability (Stonehouse 1962, Le Corre 2001, Catry *et al.* 2009c). In fact, during breeding period, distance from the colony seems to be the foraging range limiting factor while oceanographic variables such as sea surface temperature, thermocline structure and salinity play a secondary roll (Spear and Ainley 2005, Mannocci *et al.* 2014). During non breeding season, however, these variables are intimately related to tropicbird distribution, and WTTB is associated to high sea surface salinity and deep thermocline regions, with density decreased with increased sea-surface temperature and thermocline strength at northern Pacific distribution sites (Spear and Ainley 2005).

Some studies suggest that tropicbirds are less prone to breeding fail during food shortage and environmental constraints than other tropical species due to their asynchronous breeding, slow growing chick and generalist feeding behavior (Catry *et*

al. 2013). In fact, Le Corre *et al.* (2003) did not find noticeable variation in breeding performance of the Red-tailed Tropicbird during ENSO events while Catry *et al.* (2013) did not find visible effects of two events (one local and unrelated to oceanic features and one La Niña year) of food shortage on breeding performance of the WTTB, although the species presented lower chick growth rates in these periods. However, both Spear and Ainley (2005) and Castillo-Guerrero (2011) found a direct relation between low tropicbird densities and parental attendance and El Niño events. These contrasting results might evidence that regional scales should be considered as coarse scale variables (Catry *et al.* 2013) as well as longer term studies involving as many environmental and behavioral variables as possible in order to explain tropicbird plasticity and resilience.

Studies describing foraging were conducted in the tropics (Congdon *et al.* 2005, Le Corre *et al.* 2012, Danckwerts *et al.* 2014, Mannocci *et al.* 2014, Weimerskirch *et al.* 2005, Yamamoto *et al.* 2010, Kappes *et al.* 2011, Opper *et al.* 2015) but information on foraging patterns, at-sea behavior and association with oceanic features in the Atlantic ocean is still scarce. This research gap might result of the lack of tradition in marine ornithological research in countries that border this ocean, mainly due to economic limitations (Tavares *et al.* 2016).

In addition, tropicbird populations are declining in the Atlantic breeding sites, with no evidence of re-colonization of abandoned areas or recent events of dispersal to new areas (Lee and Walsh-McGhee 2000). The decline seems to be related to human development issues, such as construction, tourism, use of pesticides and introduction of exotic species (Schaffner 1988, Lee and Walsh-McGhee 1998, Nunes *et al.* 2017), all present at the Fernando de Noronha Archipelago. The fact that both tropicbird species that breed in Brazil are now classified as endangered by the Brazilian government (Brasil 2016) evidences the need of improvements in knowledge of behavioral biology and movement ecology of tropical seabirds in this area as an important conservational tool.

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Dual Foraging Strategy of the White-tailed Tropicbird in the Equatorial Atlantic Ocean

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Abstract

Tropical seabirds present behavioral and physiological adaptations to oligotrophic environments, such as asynchronous breeding, generalist feeding habits and dual foraging strategy. The White-tailed Tropicbird *Phaethon lepturus* (WTTB) is a fairly well studied species, but data on its movement behavior are still scarce. In this paper we studied breeding WTTB from the Fernando de Noronha Archipelago in northeastern Brazil, the largest breeding site of the species in the Equatorial Atlantic Ocean. With miniaturized GPS loggers, we calculated speed, distance from colony and trip duration and determined different behavioral states (sitting on water, searching for food and travelling) and the proportion of time spent in each behavior. Comparisons between behaviors within foraging strategies were made. The study accessed 21 foraging trips that evidenced dual foraging strategy, with theoretical foraging radius for short trips of 94.97 km and 279.52 km for long trips. Overall flight speed had a mean of 32.58 (± 16.26 km.h⁻¹), whereas proportion of time spent in each behavior was significantly different between short and long trips for sitting on water, searching and travelling behaviors.

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In general, our results corroborate previous studies elsewhere on both tropicbirds and other tropical seabirds, and demonstrate that during chick rearing, as much constrained to the environment close to the colony, adults present different activity patterns for long and short trips, engaging into long trips to further foraging grounds while short trips must enable parents to quickly reach food patches and return to colony. In addition, we suggest that WTTB in Fernando de Noronha know the coarse scale direction of food patches but search for unpredictable patches in small temporal scales.

Key words: tropicbird, movement ecology, GPS, activity patterns, Equatorial Atlantic.

Introduction

Tropical seabirds live in highly oligotrophic environments (Ashmole 1971) where prey exhibit patchy distributions. Therefore, tropical seabirds present important physiological and behavioral adaptations for foraging on such resources (Weimerskirch *et al.* 2005, Weimerskirch 2007). Tropical oceanic features, such as current systems, thermocline depth and low primary productivity (Bertrand *et al.* 2014; Sabarros *et al.* 2014) imply extended foraging radius and high foraging costs for seabirds (Ballance *et al.* 1997; Catry *et al.* 2009a; Fauchald 2009).

Among the adaptations required to cope with environmental constraints, tropical seabirds rely on surface plunging or aerial feeding (Ballance and Pitman 1999; Chang *et al.* 2016), which may be facilitated by commensalism with sub-surface predators such as tunas and dolphins (Au and Pitman 1989; Ballance *et al.* 1997; Jaquemet *et al.* 2004; Maxwell and Morgan 2013). Dual foraging pattern is also common in those ecosystems, with parents alternating short trips for chick attendance and long trips to distant foraging grounds for self-provisioning (Weimerskirch *et al.* 1994; Sommerfeld and Hennicke 2010; McDuie *et al.* 2015)

In pelagic environments tropicbirds usually feed solitarily, with no large multispecies feeding flocks ((Diamond 1975; Schaffner 1990; Jaquemet *et al.* 2004; Spear and Ainley 2005). Tropicbirds have a plastic phenology with asynchronous breeding, slow chick growth and generalist trophic niche (Ramos *et al.* 2005; Catry *et al.* 2013) and, as it is usual in seabirds, their oceanic distribution is reduced during the breeding stage to a certain distance from colony (Spear and Ainley 2005; Mejías *et al.* 2017).

Previous studies on the tropicbird family focused mostly on breeding performance, response to environmental variables at local scales, feeding habits and conservation issues (Schaffner 1990; Le Corre *et al.* 2003; Catry *et al.* 2009b; Sommerfeld and Hennenke 2010, Catry *et al.* 2013; Leal *et al.* 2016; Mejías *et al.* 2017; Nunes *et al.* 2017). New research tools have been used to access foraging parameters of pelagic seabirds, such as miniaturized GPS loggers (Evans *et al.* 2013). In this paper, the first to our knowledge to provide high resolution movement description (high frequency GPS tracking data) of white-tailed tropicbirds, we aim to: 1) determine foraging behavior of WTTB; 2) understand how movement metrics are related to foraging preferences.

Methods

Study site

The study was conducted at Morro do Chapéu (32°25'30"W, 3°51'57"S), an islet located at Fernando de Noronha Archipelago, northeastern Brazil. The Archipelago is influenced by trade winds and by two oceanic currents, the South Equatorial Current at surface and the deeper South Equatorial Undercurrent, both oligotrophic (Cordeiro *et al.* 2013; Tchmabi *et al.* 2017). The islet supports the largest White-tailed Tropicbird colony of the Equatorial Atlantic (around 200 individuals, Mancini *et al.* 2016) and birds nest into cavities in the sedimentary rocks, the “caracas” (Figure 1).

Sampling

The study area was checked daily from August 12th to October 31st 2015 and parents with chicks with age ranging from hours to 3 weeks were selected for GPS deployment. Birds were captured by hand preferably before dawn, individualized by stainless steel bands from CEMAVE/ICMBio and received Gypsy 4 GPS loggers (Technosmart, Italy) on their four central tail feathers. Logger were waterproofed with a heat-shrinking tube and attached to the rectrices with TESA® tape (Wilson *et al.* 1997). The devices recorded date, time, longitude, latitude, instant speed ground, altitude, number of satellites and HDOP (Horizontal Dilution of Precision). Positions with HDOP above 6 were withdrawn for the analysis. A total of 21 trips were collected, with sampling period of 10, 30 and 60 seconds. This resolution parameter does not allow determining directly dive events, as points accessed at 60 s interval might hide a diving bout performed in between fixes. However, battery autonomy was insufficient at finer resolution (e.g. 10 seconds) to record complete trips, even the short ones.

Movement parameters

Speed values were calculated as the ratio between the distance and time elapsed between consecutive GPS positions (Zavalaga *et al.* 2012). Positions at the colony and with speed values above 100 km.h⁻¹ (considered as artifacts generated by position errors, n=36) were removed from the analysis (Figure 2; see also Pennycuick *et al.* 1990; Spear and Ainley 1997) in all 21 trips tracked (but see Wakefield *et al.* 2009 for problems in this procedure).

An examination of the frequency distribution of the speed values allowed a separation into three behavioral states, as indicated by previous studies: points with speed below 10 km.h⁻¹ were considered as “sitting on the water” since birds could be both sitting on the water or engaging in diving bouts, a distinction our data cannot solve (Weimerskirch *et al.* 2005; Weimerskirch *et al.* 2008; Zavalaga *et al.* 2012; Cercere *et al.* 2013). Area Restricted Search behavior was characterized by speed between 10 and 40 km.h⁻¹; travelling (return to colony or

flight between food patches) with speeds between 40 and 100 km.h⁻¹ (Pinaud 2008; Soanes *et al.* 2014). Distance between search areas was calculated as the area between the last search position detected in a given location and the next consecutive search point after a series of travelling positions (Sommerfeld *et al.* 2015).

White-tailed Tropicbirds present dual foraging strategy (Campos *et al.* 2018) and therefore short (trips performed by nest-attendant parent) and long (incomplete trips performed by the non-attendant parent) (Sommerfeld and Hennicke 2010; McDuie *et al.* 2015; Ochi *et al.* 2016) were treated differently. Each behavior state was used to calculate proportion of time spent in different activities for both short and long foraging trips.

Since foraging metrics of long trips could not be thoroughly accessed due to battery exhaustion, we estimated a theoretical foraging radius (Pennycuick *et al.* 1990; Le Corre *et al.* 2003; Sommerfeld and Hennicke 2010) of WTTB engaging in long trips, using proportion of time spent in flight of 78 % (based on short trips), mean flight speed value of 34.13 km.h⁻¹ and mean trip duration of 10.5 hours, the maximum value obtained in logger data. The result was compared to a calculated theoretical foraging radius using the known short trip metrics for proving.

Statistics

A Shapiro-Wilk test was performed in all movement metrics to investigate normal distribution of data. The proportion of time spent sitting on water, searching and travelling behaviors in short and long trips were compared with Pearson's Chi-squared test with $p < 0.05$, with five short trips randomly selected for comparison with long trips. All statistics were computed with R software (R Core Team 2017).

Results

16 complete trips (whole foraging trip presented in data) and five incomplete trips (battery exhaustion caused incomplete recording) from 14 animals were accessed, with 9.031 position

points. WTTB leave the colony at dawn in order to perform short foraging trips and return to colony before dusk while attending the chick. While in long foraging trips, however, birds do not access roosting islets or return to colony for 4-11 days.

Mean speed values of $32.58 \pm 16.26 \text{ km.h}^{-1}$ were observed for flight behavior (searching and travelling) considering both foraging strategies whereas short trips presented mean flight speed of $31.22 \pm 15.45 \text{ km.h}^{-1}$ and long trips presented mean speed of $34.13 \pm 17.01 \text{ km.h}^{-1}$ (Figure 2).

WTTB from Fernando de Noronha spent most of their short foraging trips in search for food patches (60%) while sitting on the water and travelling represented 20 and 18% of their time, respectively. While long trips were not thoroughly accessed, the proportion of time spent sitting on the water was $43 \pm 18 \%$, searching for food patches of $39 \pm 20 \%$ and travelling was of $14 \pm 9 \%$ (Figure 3). Activity parameters in both short and long foraging trips were statistically different. The proportion of time spent in each behavior was significantly different between short and long trips for sitting at water ($\chi = 0.861$, $p = 0.93$, $df = 4$), searching ($\chi = 0.452$, $p = 0.97$, $df = 4$) or travelling ($\chi = 0.173$, $p = 0.99$, $df = 4$).

The theoretical foraging radius was of 94.97 km for short trips and 279.52 km for long trips. Birds commute between foraging areas and the colony in a looping direction while mean distance between search areas was of $4.25 \pm 3.04 \text{ km}$. Long foraging trips of WTTB lasted from four to 11 days (*in situ* observation) and the miniaturized GPS loggers (i.e. ‘Gypsy 4’, 5 g) used did not have such battery autonomy (Chan *et al.* 2015). Therefore the results for long trips should be treated with caution. However, it is clear that WTTB cope with environmental constraints by using dual foraging strategy with different behavioral strategies and that long trips are related to areas further from colony than short trips.

Discussion

WTTBs breeding in Fernando de Noronha present a coordinated dual foraging strategy with different activity patterns while in chick-rearing. Even if biased by the lack of complete access to long trip data due to battery exhaustion, our results show differences in movement behaviour on foraging trips in both searching for food and travelling behaviour and provide insights on the movement ecology of tropicbirds on their equatorial colony.

Our results corroborate previous studies on both tropicbirds and other tropical seabirds and demonstrate that adults in chick rearing, as much constrained to the environment close to the colony, present different activity patterns while in long and short trips, engaging into long trips to further foraging grounds while short trips must enable parents to quickly reach food patches and return to colony (Congdon *et al.* 2005, Spear and Ainley 2005, Catry *et al.* 2009a; Fauchald 2009; McDuie *et al.* 2015, Tyson *et al.* 2017)

Dial activity patterns

WTTB present a coordinated dual foraging strategy in Fernando de Noronha, with marked differences in nest attendance and trip duration in short and long trips. It is unclear how parents coordinate their trips, but during the first two weeks of chick-rearing, synchronous burrow attendance seems to be the trigger to alternation between the attendant partner, who will perform daily short trips, and the bird who will immediately engage in a long trip, as seen in Tyson *et al.* (2017).

Tropicbirds have high energetic demands due to their flapping flight (Mannocci *et al.* 2014) and therefore some of their traveling time to foraging grounds is resting on water, both at day and night, much like Red-billed Tropicbird *Phaethon aethereus* in Abrolhos Archipelago Leal (2013), Red-tailed Tropicbirds *Phaethon rubricauda* in Christmas Island (Sommerfeld and Hennicke 2010), Nazca Boobies *Sula grantii* in the Galápagos (Zavalaga *et al.* 2012), and WTTB in the Sub-tropical Atlantic (Mejías *et al.* 2017).

The fact that tropicbirds engage in long foraging trips to distant foraging grounds (Campos *et al.* 2018) despite their costly flight, might represent an energetic constraint imposed by the highly oligotrophic environment around Fernando de Noronha (Cordeiro *et al.* 2013; Souza *et al.* 2013; Tchmabi *et al.* 2017). This environment seems insufficient for adult provision and therefore a coordinate dual foraging strategy is necessary.

Flight speed

The mean speed of $31.22 (\pm 15.45)$ and $34.13 (\pm 17.01)$ km.h^{-1} for short and long trips is lower than found by Schaffner (1990) of 46.8 km.h^{-1} flight speed (based on a theoretical calculation) of Puerto Rican WTTB, Pennycuik *et al.* (1990) of 44.28 km.h^{-1} for WTTB, Leal (2013) in RBTB of $44.2 (\pm 14.9) \text{ km.h}^{-1}$ and Spear and Ainley (1997), who predicted flight speeds of tropicbirds ranging from 50.29 to 60.26 km.h^{-1} depending on wind direction.

Considering the different and less precise logger data used in earlier studies, the lack of information on removal of high speed values in previous studies and based on proportion of time spent on each behavior and visual analysis of the trips, searching behavior comprehends a great proportion of the foraging trips of birds from Fernando de Noronha and, therefore, the lower speed values can be related to this activity throughout most of the time.

Activity patterns and foraging radius

WTTB engaged in searching for food as soon as they left the colony and this behavior occupied the majority of time spent in short foraging trips, a pattern distinct from non-breeding WTTB from the Bermudan colonies, who spent more time in water in 2014-2015 (59 and 58% of the time with a mean of 7 hours) than in flying mode (41 and 42% of the time with mean value of 5 hours) during the day (Mejías *et al.* 2017).

Leal (2013) found random movements, i.e. (non-directional flight) in 58% of the time spent in foraging trips of RBTB in Abrolhos Archipelago and 42% in feeding events. However, since

this study provides the same speed values for both feeding and sitting at water surface it seems clear how similar at-sea behavior of the sister species are at the Tropical Atlantic. Sommerfeld and Hennicke (2010) found that in breeding RTTB the proportion of time spent in flying mode varied greatly between incubating and chick-rearing adults, when birds spend on average 62.4 ± 17.3 and $90.1 \pm 8.6\%$ of day time flying, respectively. The authors hypothesized that the large amount of time spent in flight mode by chick-rearing birds was expected since the brevity of their foraging trip (like in our study, short foraging trips by the attendant parent lasted no longer than a few hours) would reduce time available for searching behavior and therefore high flying proportion would increase the chance of finding food patches.

Tropicbirds presented difference in activity patterns in short and long trips, an evidence of their plastic behavior (Catry *et al.* 2013). In short trips, time constraints and nesting attendance induce high proportion in searching behavior (Sommerfeld and Hennicke 2010) in oligotrophic areas, while in long trips birds must balance energetic cost of commuting to distant areas with the necessity of high food intake (Pettex *et al.* 2010). The larger theoretical foraging radius for long trips shows that those trips represent not only more time to encounter prey, but intentional travel to further feeding areas, evidencing that the ocean around the Archipelago would not provide enough food for adults even if they spent long periods in the same area used in short trips.

WTTB in Fernando de Noronha did not restrict search and sitting on the water (either resting or feeding) to areas next to the maximum distance achieved but presented search behaviour along most the trip, with looping strategy, indicating that prey encounters were scattered in the area. Prey availability is related to patchily distribution, and seabirds must cope with different spatial and temporal scales in order to reach foraging areas (Weimerskirch 2007, Paiva *et al.* 2010). Searching behaviour represents individual response to changes in prey

distribution (Paiva *et al.* 2010), increased productivity (Weimerskirch 2007) and time constraints (Votier *et al.* 2017). While commuting is usually associated to previous knowledge of food patches, looping trips represent increase search effort for unpredictable prey encounters (Weimerskirch 2007).

We do not know if birds started search behaviour due to proximity to previous known areas of foraging (Pettex *et al.* 2010; Votier *et al.* 2017) or if the behavior was triggered by detection of food patches. If the first, tropicbirds would remember where to forage in a small spatial scale, much like seabirds from polar and temperate waters (Fauchald 1999; Weimerskirch 2007; Votier *et al.* 2017). However, in the second scenario, the presence of an unpredictable food patch would induce searching behavior (Paiva *et al.* 2010). Our data is more consistent with the second hypothesis since birds presented low speed values and high proportion of time in searching through most of the trips, returning to colony at high speeds after successful feeding in looping trips.

Our data suggests that birds departing from colony use visual cues of returning birds to derive information on the direction of successful food encounters in a small temporal scale (Boyd *et al.* 2016) or that a colony memory-based system knows the coarse scale direction of food patches (i. e. the area located southeast of the Archipelago) but search for nested unpredictable patches in small temporal scales. Some of the tagged birds in departure might have used the return direction of other WTTB to locate the coarse direction of food patches but more investigations are needed in order to determine the search strategy that best represents direction choice at the Archipelago. However, both strategies indicate a highly oligotrophic and unpredictable environment, which is reinforced by the small distance between searching areas, a proxy for prey encounter rates (Sommerfeld *et al.* 2015), and by the dual foraging strategy, an evidence of less predictable resource availability near the colony (Paiva 2010). This explains the extent of the theoretical foraging radius of the colony,

corroborating previous studies in oligotrophic waters (Weimerskirch 2007; Soanes *et al.* 2016).

Previous studies show that long foraging trips to distant foraging grounds in tropical seabirds are related to self-provision (Weimerskirch *et al.* 1994; Weimerskirch *et al.* 1998; Ochi *et al.* 2010; Riou *et al.* 2011; Avalos *et al.* 2017) and to oceanic features related to increase in prey availability, such as seamounts (Morato *et al.* 2010; McDuie *et al.* 2015). In Fernando de Noronha the presence of nutrient mixture in seamounts does not reach the euphotic zone and therefore the area is overall highly oligotrophic (Becker 2001; Souza *et al.* 2013; Tchmabi *et al.* 2017). It might be that southeastern waters are more favorable to WTTB preferred prey (Diamond 1975) the Exocoatidae flyingfish (Zainuddin 2011; Lewallen *et al.* 2017) or that although prey might be patchily distributed in the oceanic environment around the Archipelago, its availability is higher in this particular area in the studied temporal scale (Carroll *et al.* 2017).

The chosen foraging area of seabirds is a result of previous knowledge, colony size, competition and environmental features (Soanes *et al.* 2016) and therefore future research should examine the relationship of WTTB with all these variables, especially the oceanic environment surrounding Fernando de Noronha to elucidate whether birds' bearings and activity patterns are influenced by the ocean's physical conditions.

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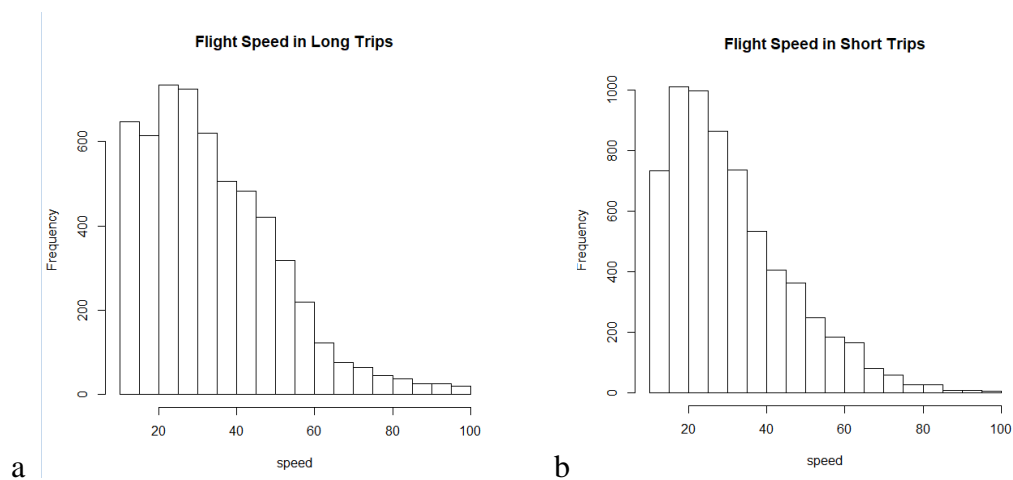
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Figures



Figure 1. Study site: Caracas rocks at Morro do Chapéu Islet, Fernando de Noronha.



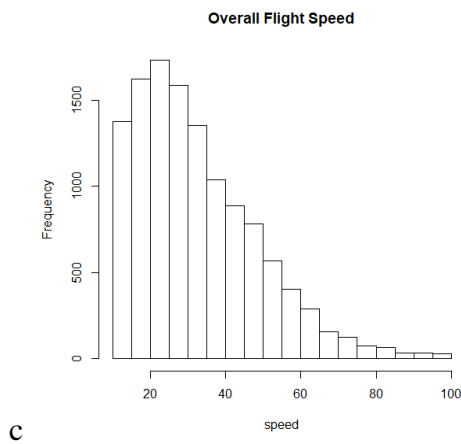


Figure 2. Histogram of flight speeds for short trips (n=16; a), long trips (n=5; b) and pooling all foraging trips together (n=21; c).

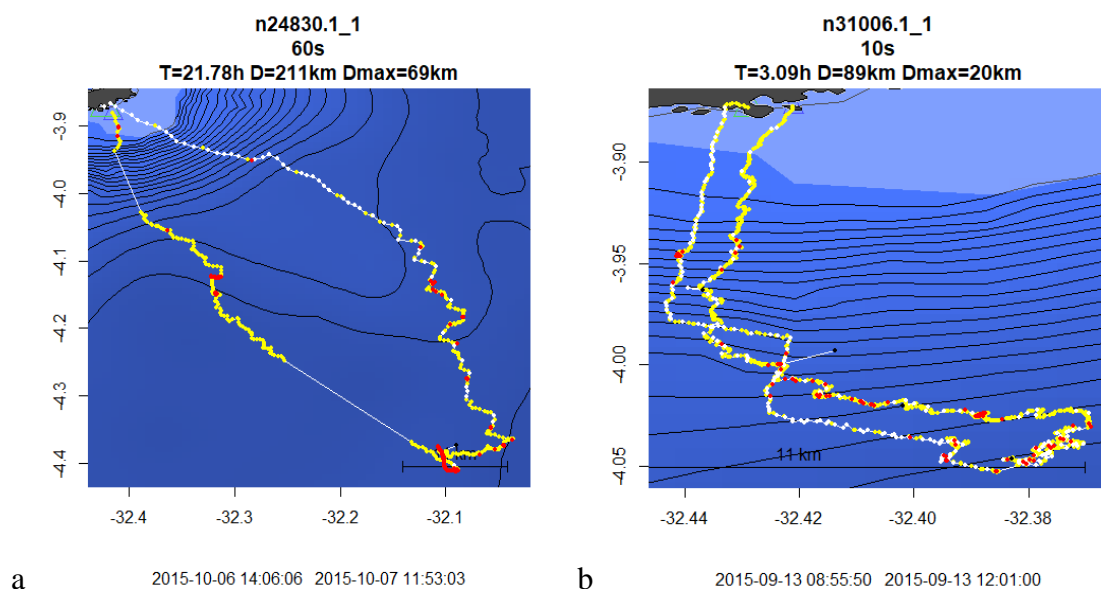


Figure 3. Activity patterns in foraging trips. a) On water ($<10 \text{ km}\cdot\text{h}^{-1}$) and searching points ($10 <$ and $<40 \text{ km}\cdot\text{h}^{-1}$) in most of the track. Travelling behavior (<40 and $<100 \text{ km}\cdot\text{h}^{-1}$) at return to the colony. b) Foraging trip with high proportion of searching and on water behaviors. Traveling comprehends a smaller portion of time. Colors: On water in red; searching in yellow; travelling in white; black dots represent speeds above $100 \text{ km}\cdot\text{h}^{-1}$.

Foraging habitat choice of white-tailed tropicbirds revealed by fine-scale GPS tracking and remote sensing

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Abstract

The foraging ecology of seabirds has developed enormously after the introduction of animal tracking technology. Tracking data is particularly powerful when combined with oceanographic information derived from satellite remote sensing, allowing to understand the functional mechanisms of marine ecosystems. While this framework has been greatly used over the last two decades, there are still vast ocean regions and many seabird species for which information is very scarce, particularly in tropical oceans. In this study we tracked for the first time a tropicbird species with GPS dataloggers. We followed the movement at sea of 15 white-tailed tropicbirds (*Phaethon lepturus*) during chick-rearing from a colony in Fernando de Noronha (offshore of Northeast Brazil) at high GPS rate. Flight behaviours of travelling and searching for food were derived from GPS data and examined in the light of satellite sensed oceanographic variables. White-tailed tropicbirds showed clear preference for clear and warm sea surface waters, which are indicative of low productivity but are likely the best habitat for preying upon flying fish. These findings are consistent with previous studies showing that foraging habitat choices of tropical seabirds may not be driven by productivity, as it has been widely shown for non-tropical species.

Introduction

The way pelagic seabirds move across the vastness of the open ocean have fascinated generations of scientists, but only recently technological developments provided the tools to uncover that mystery. It was only in the early 90s that the movement of seabirds at-sea was first followed with tracking devices [1, 2]. Since then, major technological improvements have made tracking devices smaller, more accurate, and more affordable, which boosted their use in ecological studies, particularly on seabirds [3, 4]. 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 abundance [5, 6]. When set together, tracks of marine animals and oceanographic variables derived from satellite imagery provide exceptional opportunities to understand the functional mechanisms of marine ecosystems [7]. In seabird research the simultaneous use of tracking devices and satellite imagery has escalated since the early 2000s [8]. 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. 9, 10, 11]. 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 12, 13-15, 16 as examples of tracking studies with tropical seabirds].

By far the majority of seabirds 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. 17, 18, 19]. 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 phytoplankton [20]. Seabirds tend to show high fidelity to these areas and typically develop commuting movements from their breeding colony [21, 22]. In

commuting movements birds travel in a linear path and constant speed between the breeding colony and the feeding areas where their path becomes highly tortuous and slow [22]. 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 [22]. 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. 12, 23, 24].

Tropicbirds are enigmatic seabirds that mostly forage solitarily in tropical and subtropical seas [25, 26]. 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 kagus, based on whole-genome analyses [27]. 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 [26]. They are also unusual by the fact that they fly long distances, comparable to procellariids, but they lack the ability to soar [28-30]. This flight behaviour seems to be possible because they rest long periods on the water [26, 31]. Despite these intriguing characteristics tropicbirds were only tracked three times [14, 31, 32] before our study and never with GPS, which greatly limits our understanding of their foraging ecology.

In this study we GPS-tracked 15 white-tailed tropicbirds (*Phaethon lepturus*) at high frequency (between 1 and 6 fixes per minute) in order to infer on their foraging behaviour at sea. Animals were caught during chick-rearing in Fernando de Noronha, a tropical oceanic Archipelago offshore of the Northeast Brazilian coast. Foraging behaviour of birds at sea was

examined in the light of oceanographic variables derived from high spatial resolution Moderate-resolution Imaging Spectroradiometer (MODIS) imagery in time frames of two days. With this approach we aimed to understand how birds 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 [8, 33].

Materials and Methods

Ethics Statement

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.

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 by 21 islands and islets occupying ca. 26 km², and it is protected by Brazilian legislation as a marine national park since 1988. The islands hold large concentration of tropical seabirds, including a breeding population between 100 and 300 of white-tailed tropicbirds [34]. 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 1400 mm [34]. 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 [35]. The seawater is considered oligotrophic, where phytoplankton productivity is limited by low nutrient concentrations [36]. Surface salinity ranges between 35.0 and 37.0‰ [34].

Tracked birds 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 [34]. The 15 tagged birds were captured by hand in the nest at dawn (4 to 4:30 am), before they leave to the sea, between August 28th to October 16th 2015. The data loggers (5 g, Gipsy 4 GPS recorders, Technosmart, Italy) were waterproofed with shrink tube (increasing their weight to 10-15 g) and were attached to the basis of the four central tail feathers with duct tape. The handling of the animals took less than 10 minutes and after which they were immediately released.

Data analysis

GPS tracks of animals flying over the sea were selected from the original dataset. These only excluded track sections of animals at the breeding colony or flying over the islands. GPS data loggers functioned at different rates (from 1 to 6 fixes per minute), but to use a coherent dataset we reduced all tracks to the same resolution of 1 fix per minute. Some tracks were not round-trip, because the data logger battery ended before the animal returned to the colony. Tracks were divided in segments of 5 minutes and classified as “on-water”, “travelling” and “searching” from GPS parameters as following:

On-water: Track segments where the mean speed was less than 10 Km/h, which comprises on-water drift due to sea currents.

Travelling or searching: These behaviours were separated based on track tortuosity. Track tortuosity was calculated as horizontal displacement (distance between the track ends) divided by the track length. If the horizontal displacement was less than 30% of the track length, the track segment was classified as “searching” otherwise it was classified as “travelling”.

Track segments classified as “on-water” were excluded from further analysis, as we aimed to infer on foraging by plunge diving. This excluded the few track segments collected during the night, as birds were resting on the water during that period.

We related the foraging behaviour of birds to oceanographic variables derived from MODIS, made available by the NASA's OceanColor Web (<http://oceancolor.gsfc.nasa.gov>). We used the following variables:

Turbidity: The Diffuse Attenuation Coefficient at the 490 nm wavelength (commonly referred as $K_d(490)$) served as a proxy for water turbidity [37-39]. The $K_d(490)$ specifically reflects the diffuse attenuation for downwelling irradiance at 490 nm in m^{-1} (see [40] for details).

Chlorophyll-a: near-surface concentration of chlorophyll-a in $mg\ m^{-3}$, inferred from remote sensing reflectances in the blue-to-green region of the visible spectrum (see [41] for details).

SST: sea surface temperature in $^{\circ}C$ inferred from the 11 μm and 12 μm long wave infrared bands (see [42] 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 examined bird selection of turbidity, chlorophyll-a and SST by comparing the conditions of those variables at the sites used by birds and those available all around the island within the range of the longest track recorded. The area of considered available for birds was squared, to facilitate raster analysis, ranging from 5.1134 $^{\circ}$ to 2.6054 $^{\circ}S$ in latitude and from 33.6806 $^{\circ}$ to 31.1726 $^{\circ}W$ in longitude. Since the spatial distribution of oceanographic variables varied largely during the sampling period (average Pearson's correlation between images available for the sampling period were nearly zero for all variables), we decided to examine each day of tracking in the light of the images available for that day and the day before. We used images of the day before because it is likely that birds 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 more separated in time. Thus, images of daily availability for each oceanographic variable were produced by averaging images of the tracking day and the day before. Available conditions and those used by the birds were then combined into a daily selection score. To produce that score we first ranked each availability image between 0 and 20. This brought the availability images of different tracking days to the same scale. The daily selection score was obtained by replacing the original values of oceanographic variables at sites chosen by birds (track segment centroids) by the corresponding ranks of the standardized scale of the availability images. For each variable the availability ranks will show a uniform distribution centred at 10. The distribution of selection scores should be similar to that of availability ranks if no selection of oceanographic conditions exists, otherwise we may conclude that birds show patterns of selection (see Fig. S1). Patterns of selection may be based on deviance from uniform distribution and/or deviance of distribution centre (i.e. not centred at 10). We considered that patterns showing deviance of distribution centre were the most robust evidence of selection, and conservatively we interpreted only those patterns. Thus, we made conclusions on bird selection of oceanographic conditions only if selection scores were significantly different from 10, based on one sample Student's t-tests. We were unable to perform multivariate modelling because there was mismatch in the missing values of the different oceanographic variables, and the removal of all missing values would dramatically decrease our sample size and compromise the power of our analysis. We prevented problems of multiple comparisons by applying Bonferroni corrections to our Student's t-tests. Although, turbidity and chlorophyll-a had some degree of correlation (Pearson's correlation, $r=0.48$), we considered that they differed enough to be interpreted separately. These two variables had virtually no correlation with SST (turbidity vs SST: $r= -0.04$; chlorophyll-a vs SST: $r= 0.04$). All data analysis procedures were conducted with the software R [43].

Data accessibility

All data are available at ...

Results

We tracked 15 different birds 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 we classified the behaviour of birds for 1230 track segments of 5 minutes each. From these, 519 were classified as “on-water” and were excluded from the analysis, and the 711 remaining were analysed regarding their relation to oceanographic variables. In general, behaviours classified as “travelling” and those classified as “searching” were not segregated spatially (Fig. 1), meaning that the birds 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 from the birds. Nevertheless, regions to the NW direction of the island tend to be warmer at surface (based on SST) than those to the SE direction (Fig. S3).

Birds showed a preference for clearer (low turbidity) and warmer surface (high SST) waters while they flew over the sea, but showed no clear preference regarding Chlorophyll-a concentrations (Fig. 2; Student’s t-tests Bonferroni corrected: $t = -2.9$, $df = 576$, $p\text{-value} = 0.010$; $t = -1.7$, $df = 576$, $p\text{-value} = 0.276$; $t = 2.6$, $df = 681$, $p\text{-value} = 0.032$; for turbidity,

Chlorophyll-a, and SST respectively). Matching and clearer results were found when we considered only the track segments classified as “searching”. Birds searching for food showed strong preference for warmer and clearer waters, and no clear preference with regards to Chlorophyll-a concentrations (Fig. 3 low pannel; Student’s t-tests Bonferroni corrected: $t = -3.5$, $df = 249$, $p\text{-value} = 0.002$; $t = -0.7$, $df = 249$, $p\text{-value} = 1$; $t = 3.7$, $df = 288$, $p\text{-value} = 0.0008$; for turbidity, Chlorophyll-a, and SST respectively). In contrast, for track segments classified as “travelling” there was no clear association with any of the oceanographic variables (Fig. 3 top pannel; Student’s t-tests Bonferroni corrected: $t = -0.9$, $df = 326$, $p\text{-value} = 1$; $t = -1.6$, $df = 326$, $p\text{-value} = 0.335$; $t = 0.4$, $df = 392$, $p\text{-value} = 1$; for turbidity, Chlorophyll-a, and SST respectively).

Discussion

We showed that white-tailed tropicbirds searching for food in oligotrophic waters during breeding tend to use areas with higher SST and lower turbidity than that available within their foraging range (Fig. 3), while no clear patterns of selection for chlorophyll-a were observed (Fig. 3). For track segments where birds were travelling there was no evidence for selection of any of the oceanographic parameters examined (Fig. 3). Our results also indicate that white-tailed tropicbirds forage along their foraging trips, therefore, in a wide view, there is no spatial segregation between searching and travelling track segments (Fig. 1). 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. 2S, [22]).

To some extent, these patterns match with general predictions of habitat use by seabirds breeding tropical oceanic islands, where the sea is largely unproductive and the food resources are unpredictable [22]. The sea bottom around tropical oceanic islands is generally

deep and flat, and upwelling is restricted to scattered seamounts, eddies and frontal zones [44]. In addition, breeding seabirds search for food within a limited range of their colony, because their chicks need to be fed frequently [45]. 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. Interestingly, there were a few seamounts within the foraging range of the birds, 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 [36], thus they unlikely create productivity patches usable by the birds. In fact, we did not see any patterns in the oceanographic parameters indicative of productivity in the areas where these seamounts are located (Fig. S3). 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 feeding 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 [22].

It may seem counter-intuitive, however, that birds show preference for warmer and clearer waters as these are associated with low productivity [20]. And this is somewhat supported by the apparent irrelevance of the chlorophyll-a concentration in the choices of foraging areas by the birds. 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 ocean productivity [e.g. 10, 23, 29, 46]. This may be explained by spatial mismatches propagated along the trophic chain [47]. White-tailed tropicbirds, as many other tropical seabirds, prey upon flying fish to a large extent [48-50], therefore we should expect a positive relationship between the foraging areas selected by

white-tailed tropicbirds the distribution of flying fish, and not necessarily the distribution of sea productivity. Interestingly, a recent study using airborne LiDAR and covering a large area (approximately 75,000 km²) in the Gulf of Mexico found that abundance of flying fishes increases with SST and decreases with Chlorophyll-a [51]. Another recent study confirms the importance of SST explaining the distribution of flying fishes [52], including one species (*Exocoetus volitans*) that is likely a main prey of white-tailed tropicbirds in Fernando de Noronha (i.e. this species is preyed in Ascension islands [50], and abundant in Fernando de Noronha [53]). 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 [54], and, presumably, higher temperature improves flight performance. Similarly, birds may select clearer waters for other reasons than their productivity. The relevance of water transparency for plunge-divers have been recognized long ago by Ainley [55], 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 [33, 56, 57], Haney and Stone [57] showed from several plunge-divers that the white-tailed tropicbird was the only significantly more abundant in clearer waters. We believe that water turbidity and prey abundance may interact for the determination plunge-divers distribution, but it seems logic for us that in equal conditions of prey abundance an increased water transparency should help the birds to locate their prey, thus improving foraging success.

It should be also noted that while birds selected foraging areas with high SST within the scale of their movement, they did not move towards regions that were in average warmer than those used (see Fig. S3). We believe that other reasons than oceanographic parameters may explain the large scale movement of the birds. Wind direction may be influential in the large scale patterns of movement of seabirds [8]. However, our birds tended to leave the colony with wind assistance and return against the wind (wind direction: mean = 302.8°, SD = 0.28, data

from the three nearest weather station buoys, available at <http://www.goosbrasil.org>). This contradicts the prediction that birds should not choose to return to the colony with headwind, since they carry extra load of food for the chicks [58]. We believe that birds move preferentially towards SE because their colony is facing that direction in the main island of Fernando de Noronha, therefore in their return to the colony they do not have to fly over, or around, the main island. Crossing over or around the main island would imply extra energy expenditure and would expose the birds to kleptoparasitism by the abundant frigatebirds (*Fregata magnificens*) flying over in the island. In fact, none of our tracked birds crossed the main island or went around it in their return to the colony, but some did when leaving the colony.

Overall, our findings are consistent with previous studies showing that foraging habitat choices of tropical seabirds may not be driven by productivity. 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 [14]. Therefore, additional efforts must be made in order to multiply tracking studies in remote areas of the tropical oceans.

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Figures

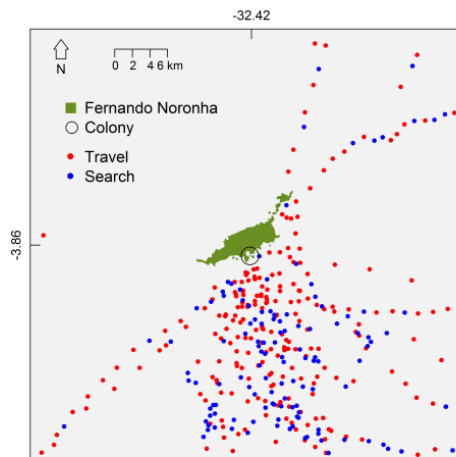


Figure 1. White-tailed tropicbirds flight behaviour at sea classified from GPS tracking parameters. Tracks were segmented into sections of 5 minutes and classified as “travel” if tortuosity was low or “search” if tortuosity was high (see methods section for further details). Only the part of the study area with higher bird use is shown. Colony is located at the islet in the centre of the circle.

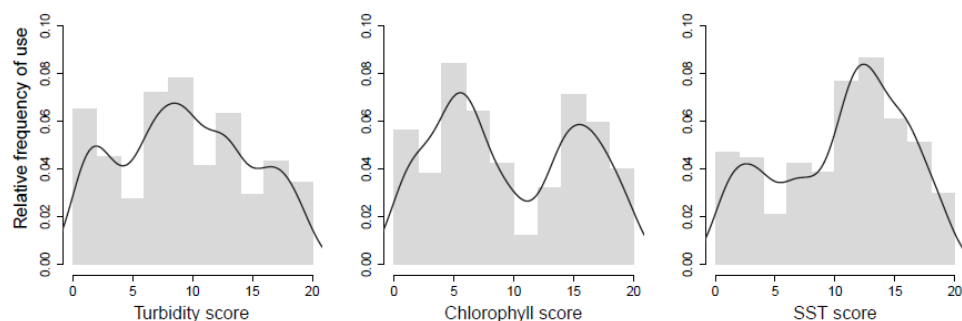


Figure 2. Selectivity of oceanographic conditions by white-tailed tropicbirds while flying over the sea (this includes travelling and searching for food). For each variable the score represents

the conditions chosen by the birds in relation to those available within the range of movement of the individuals tracked (see methods and Figure S2). Birds used areas of lower turbidity and higher SST than expected from the available conditions. Lines represent the density distribution and should be interpreted similarly to the bars distribution.

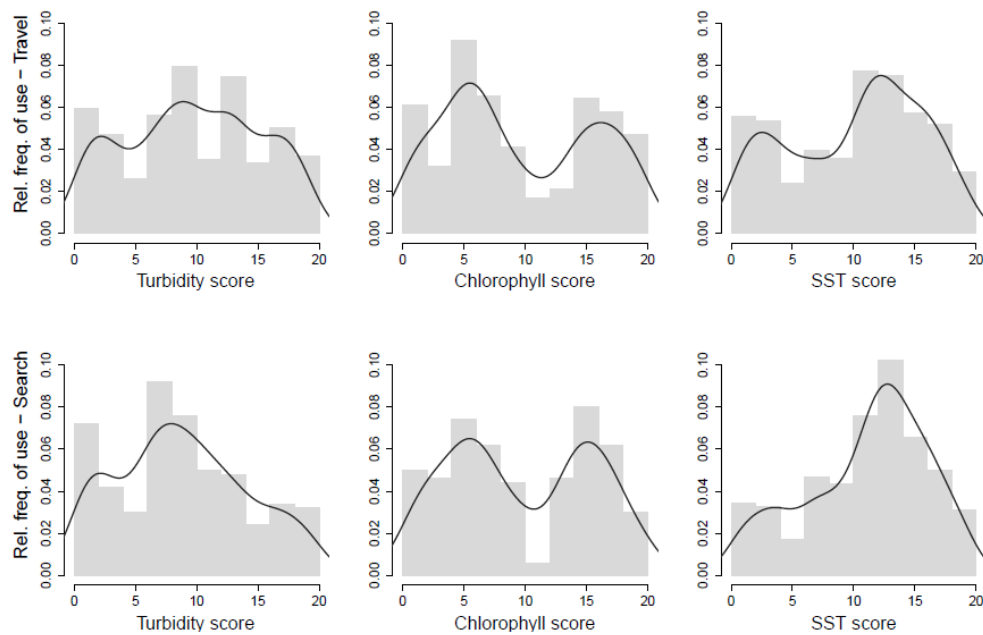
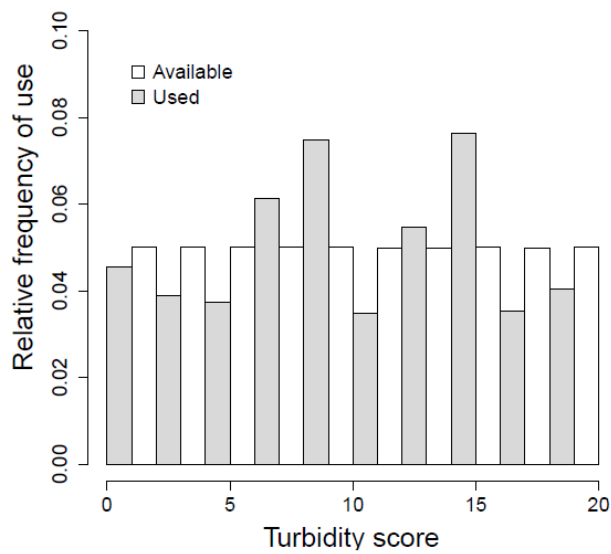
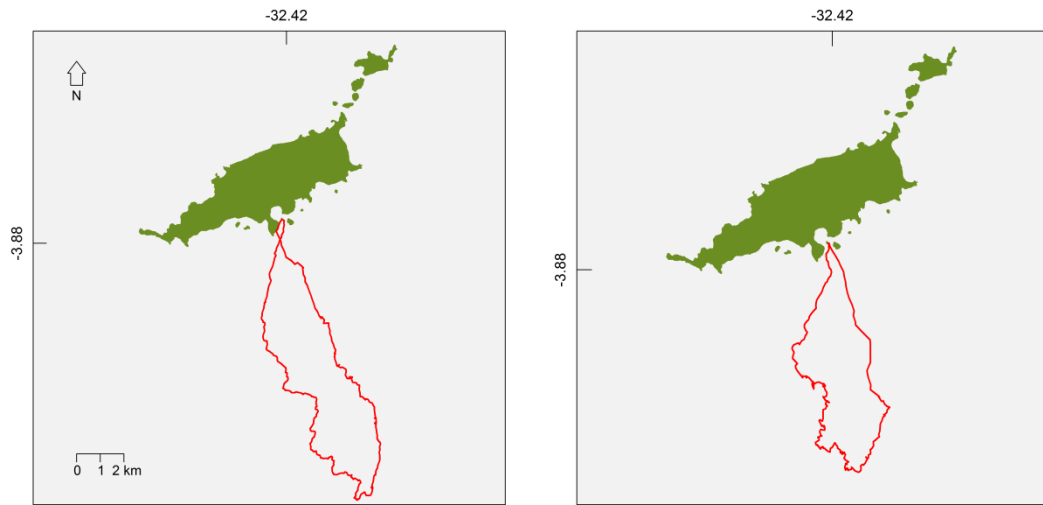


Figure 3. Selectivity of oceanographic conditions by white-tailed tropicbirds while travelling (upper panels) and searching for food (lower panels). For each variable the score represents the conditions chosen by the birds in relation to those available within the range of movement of the individuals tracked (see methods and Figure S2). Birds while searching used areas of lower turbidity and higher SST than expected from the available conditions, but did not show clear preference for any oceanographic condition while travelling. Lines represent the density distribution and should be interpreted similarly to the bars distribution.

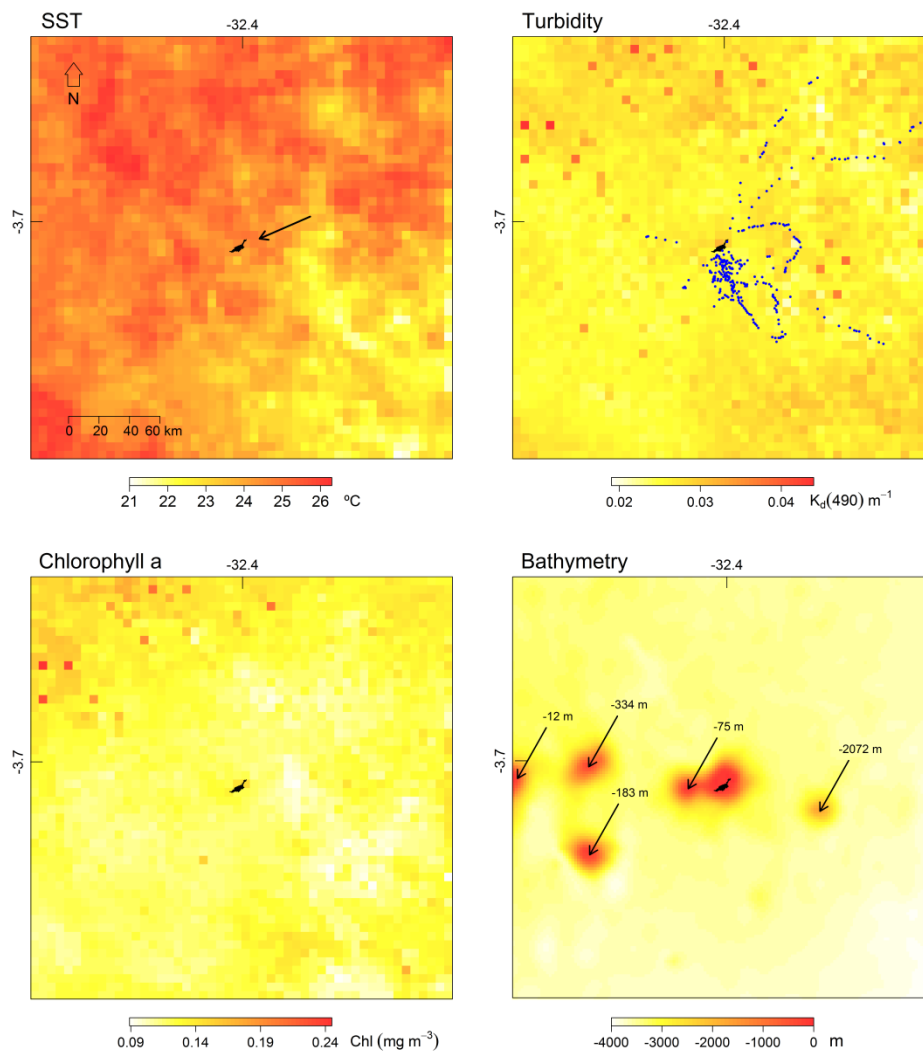


Supplementary Figure S1. Example of the analysis conducted to examine bird selectivity of oceanographic conditions (illustrated for Turbidity). This analysis is based on the comparison between of oceanographic conditions available within the range of movements of white-tailed tropicbirds and those used by them (see methods). Available conditions (white bars) show a uniform distribution centered at 10, while the conditions used by the birds (grey bars) represent selectivity if different from a uniform distribution. The distribution of conditions used by the birds alone is enough to make conclusions on selectivity, thus in Figures 2 and 3 we do not show the distribution of available conditions.

Figure S2



Supplementary Figure S2. General pattern of white-tailed tropicbirds foraging trips, illustrated by two tracks recorded with temporal resolution of 0.1 Hz.



Supplementary Figure S3. Spatial distribution of oceanographic variables within the range of movements of white-tailed tropicbirds. Geographical range was set by the longest movement in the tracking dataset. Images of SST, Turbidity and Chlorophyll-a represent average conditions for all tracking days. It should be noticed, however, that these conditions varied considerably within the sampling period. Average Pearson's correlation between images available for the sampling period was nearly zero for all variables. Original images were obtained from NASA's OceanColor Web (<http://oceancolor.gsfc.nasa.gov>). Bathymetry was obtained from ETOPO1 Global Topography distributed by NOAA (<https://maps.ngdc.noaa.gov>). Black arrow over the SST image identifies Fernando de Noronha archipelago; blue dots over the Turbidity image are sampling points where birds

were classified to be searching for food; arrows over the Bathymetry image identify seamounts, with depth above the surface annotated.

Discussão Geral

Os resultados apresentados nos capítulos anteriores compreendem detalhado estudo sobre a ecologia de forrageio de *Phaethon lepturus*, com informações sobre comportamento colonial, estratégias de forrageio, métricas de viagens, diferentes comportamentos de vôo e associação entre características oceanográficas e áreas escolhidas para alimentação.

Ciclo circadiano

O presente trabalho contou com aproximadamente seis meses de observação (divididos entre os anos de 2014 e 2015) de Rabos-de-junco-do-bico-laranja em sua colônia no Atlântico Equatorial, localizada em Fernando de Noronha, Brasil. O arquipélago vem passando por um grave processo de antropização e dentre os impactos da ocupação humana tem-se o aporte de espécies exóticas, como gatos domésticos, ratos e lagartos teiú, além da retirada de potenciais locais para nidificação de aves marinhas, notadamente na ilha principal (Catry *et al.* 2009a, Nunes *et al.* 2017). De fato, o relativo isolamento da Ilha Do Morro do Chapéu (área de difícil acesso e com fiscalização ICMBio/Econoronha) pode explicar o porquê deste local, atingido periodicamente por ondas fortes em eventos de *swell*, concentrar tantos ninhos de Rabos-de-junco em uma pequena área. Durante nosso período de estudo um número máximo de 66 ninhos ativos foi contabilizado, seguindo o padrão assincrônico (Ramos *et al.* 2005, Catry *et al.* 2009, Catry *et al.* 2013) de reprodução da espécie, com casais no período de incubação de ovos nidificando lado a lado a ninhos com filhotes de três a quatro semanas, bem como filhotes em fase de *fleeding*, ou seja, prestes a deixarem a colônia.

As aves saem da colônia ao amanhecer (<05h30 min a. m) para iniciar viagens curtas ou longas de forrageio, e os filhotes são deixados sem proteção durante boa parte do dia, independente de sua idade. A necessidade de viagens diárias às áreas de alimentação mesmo pelo membro do par que é responsável pelo cuidado parental naquele momento está relacionada à aquisição de um limite energético mínimo (*target payload mass*) obtido por aves adultas para provisão do filhote (Schaffner 1990), que costuma ser atingido em áreas próximas à colônia enquanto viagens para sítios alimentares mais distantes são realizadas para provisão própria (Weimerskirch *et al.* 1994, Congdon *et al.* 2005, Sommerfeld e Hennicke 2010).

Aves que retornam de viagens de alimentação costumam circundar a ilha por horas enquanto praticam várias tentativas de pouso, comportamento também descrito por Schaffner (1990) em Porto Rico. A alimentação de filhotes ocorre somente durante o dia (Diamond 1975, Schaffner 1990, Le Corre *et al.* 2003) e filhotes acima de três semanas são visitados por um membro do casal ou pelos dois pais a cada 72 horas em média, seguindo um padrão bimodal de intervalos de alimentação (Schaffner 1990, Shoji *et al.* 2015). Não há atividade de chegada e saída de aves na colônia após o entardecer e, portanto, é comum que filhotes passem a noite desassistidos. Essa característica pode facilitar o consumo de ovos por parte do caranguejo aratu (*Goniopsis cruentata*) e filhotes por parte de caranguejos-amarelos *Johngartia lagostroma*, nativos do arquipélago (Rodrigues 2016) ou lagartos teiu, uma hipótese levantada por Leal *et al.* (2016).

Nossas observações *in situ*, contudo, apontam que competição interespecífica pode ser um fator determinante no sucesso reprodutivo dos Rabos-de-junco, e documentamos disputas por ninhos, aves feridas e ao menos um caso de expulsão de um filhote (prestes a deixar o ninho) por um casal. Esse comportamento está relacionado à alta filopatria desta espécie, que parece ocupar anualmente as mesmas cavidades utilizadas como ninhos em temporadas reprodutivas passadas (Catry *et al.* 2009a).

Estratégia dual de forrageio

Rabos-de-junco apresentam estratégia dual de forrageio, quando adultos alteram viagens curtas para áreas próximas à colônia com viagens longas para áreas de alimentação mais distantes. Em adição, percebe-se coordenação entre pares, sendo a ocorrência simultânea do casal no ninho durante alguns minutos ou horas o gatilho para que um adulto cuide do filhote e o outro inicie uma viagem longa de alimentação, de acordo com o que é descrito em Tyson *et al.* (2017). Este comportamento foi previamente observado em rabos-de-palha-de-rabo-vermelho (Le Corre *et al.* 2003, Sommerfeld e Hennicke 2010) e indica que a disponibilidade de presas próxima à colônia pode não ser suficiente para alimentação do filhote e manutenção de necessidades energéticas do adulto (Granadeiro *et al.* 1998, Weimerskirch 1998, Congdon *et al.* 2005, McDuie *et a.* 2015, Shoji *et al.* 2015), fato comumente observado em oceanos tropicais oligotróficos (Schaffner 1990,

Granadeiro *et al.* 1998, Weimerskirch 1998, Congdon *et al.* 2005, Spear e Ainley 2005, Catry *et al.* 2009a, Fauchald 2009, McDuie *et al.* 2015).

Métricas de forrageio e atividade no mar

Nossos resultados corroboram estudos anteriores de métricas de movimento (distância total e máxima da viagem, duração, proporção de tempo em pouso e vôo) das espécies da família Phaethontidae. Em Fernando de Noronha, a duração de viagens curtas teve média de $3,9 \pm 5,3$ horas, enquanto viagens longas (considerando valores obtidos em aparelhos de GPS) tiveram duração média de $10,5 \pm 8,87$ horas. Observações *in situ*, contudo, apontam viagens longas com o mínimo de quatro, máximo de 11 e média de $6,83 \pm 2,63$ dias. No que diz respeito à distância total alcançada, viagens curtas atingiram média de $78,2 \pm 65,2$ km, enquanto viagens longas obtiveram distância total de $213,8 \pm 99,9$. A média de distância máxima em relação à colônia foi de $24,6 \pm 17,0$ km para curtas e $104,8 \pm 47,8$ km para viagens longas. Através dos aparelhos de GPS foi possível também acessar a velocidade das viagens. Viagens curtas apresentaram velocidade média de $31,22 \pm 15,45$ km/h⁻¹ enquanto viagens longas tiveram velocidade média igual a $34,13 \pm 17,01$ km/h⁻¹. Quando todas as viagens são contabilizadas, a velocidade média é de $32,58 \pm 16,26$ km/h⁻¹, abaixo do observado em estudos anteriores com a família Phaethontidae ($46,8$ km/h⁻¹ em Schaffner 1990, $44,28$ km/h⁻¹ em Pennycuick *et al.* 1990, $44,2$ km/h⁻¹ em Leal 2013).

Considerando as proporções de tempo gastas em cada comportamento é possível que a baixa velocidade média detectada nos rabos-de-junco de Fernando de Noronha esteja relacionada ao longo período que passam em comportamento de procura por manchas de alimentação, caracterizado por velocidade > 10 e < 40 km/h⁻¹. Além disso, é importante observar que estudos anteriores parecem não ter determinado um limiar máximo para velocidade, o que significa que pequenas falhas na precisão de posicionamento de equipamentos rastreadores podem ter induzido picos de altas velocidades no conjunto de dados e favorecido velocidades médias acima de 40 km/h⁻¹.

Através destas métricas, foi possível estabelecer o alcance teórico de forrageio (*Theoretical Foraging Radius*, Le Corre *et al.* 2003, Soanes *et al.* 2016), medida que avalia, através da duração das viagens, velocidade média e proporção de tempo

gasto em vôo, o quão distante da colônia aves podem ir em cada saída para alimentação. O valor encontrado para viagens curtas foi de 94,97 km, consistente com os valores reais de distância encontrados. Para viagens longas, o alcance encontrado certamente está subestimado, já que apenas uma pequena parte de cada viagem foi computada nos aparelhos de GPS. Entretanto, os dados obtidos mostram o valor de 279,52 km, também consistente com os resultados observados.

Este índice é utilizado pela *Birdlife International* para detectar áreas prioritárias para a conservação de aves, já que questões logísticas impedem o uso de *biologging* em boa parte das colônias reprodutivas de aves marinhas em nível global e fornecem subsídios para delimitação de polígono de proteção de fauna ameaçada (Soanes *et al.* 2016). Ressaltamos que em Fernando de Noronha o polígono atual de proteção do Parque Marinho restringe-se à área imediatamente circundante ao Arquipélago, não abrangendo as zonas de alimentação de rabos-de-junco (Figura 1), tanto em viagens longas quanto curtas. O conhecimento do comportamento de forrageio e associações entre as aves e características do oceano circundante pode ser usado, portanto, como ferramenta para ampliação do polígono protegido e consequente proteção dos sítios de alimentação desta espécie ameaçada nacionalmente.

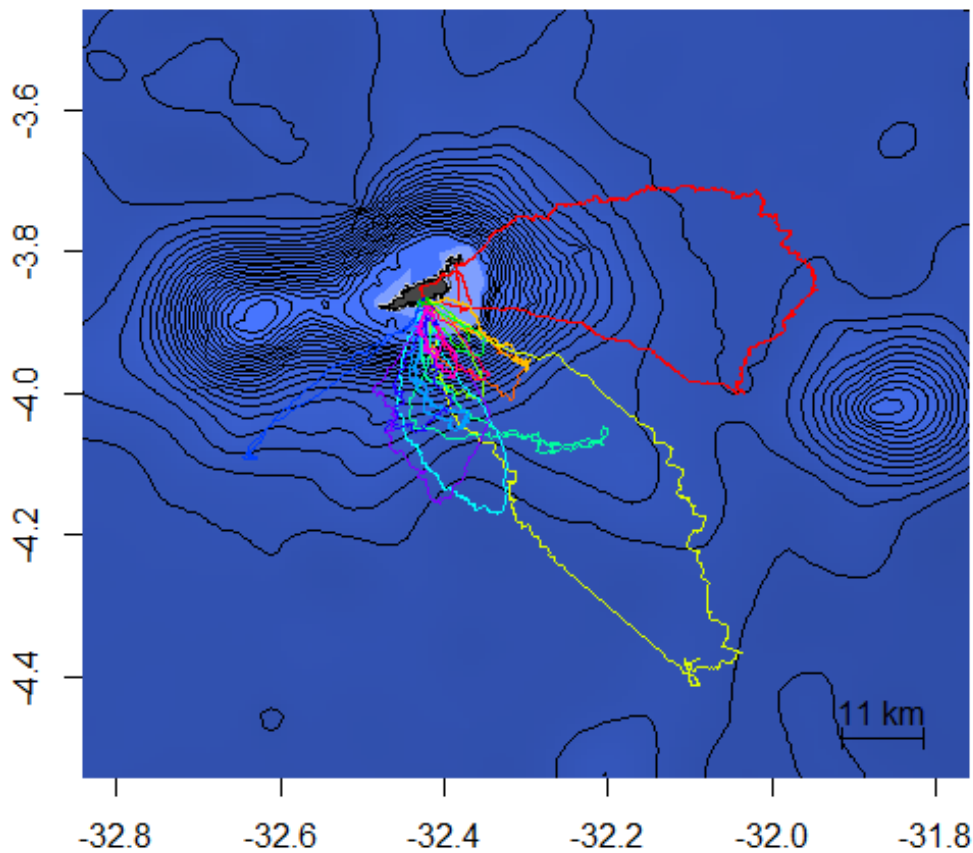


Figura 1- Representação de todas as viagens curtas de forrageio de *Phaethon lepturus* acessadas. O polígono de proteção do Parque Nacional Marinho de Fernando de Noronha (em volta do Arquipélago, em cinza claro) não contém as áreas de alimentação escolhidas pelas aves da colônia do Morro do Chapéu.

Associação com características oceanográficas

Processos oceanográficos são de grande importância para a ocorrência de manchas de presas e sua disponibilidade para aves marinhas (Bertrand *et al.* 2014, Garthe *et al.* 2017). Em oceanos tropicais, contudo, processos físicos são eclipsados pela importância de fatores biológicos, como a utilização de alimentação facilitada por predadores de sub-superfície por aves marinhas (Ballance e Pitman 1999, Jaquemet *et al.* 2004, Spear e Ainley 2005). Em Fernando de Noronha a presença de grandes grupos de cetáceos (notadamente do Golfinho-rotador *Stenella longirostris*) (Silva-Júnior 1996) e atuns (Lessa 1997, Dominguez *et al.* 2016) fornece disponibilidade de

presas às aves, fenômeno conhecido na região como “comidinha” e utilizado por pescadores para localizar grandes cardumes de peixes-alvo da pesca.

Informações coletadas via aparelhos de GPS e junto a pescadores e pesquisadores de predadores de sub superfície parecem indicar que Rabos-de-junco não utilizam esta estratégia de forrageio, ao contrário das espécies de Atobás e Trinta-réis do arquipélago (Travassos *com. pess.*). De fato, em escala local características comportamentais da espécie, como aprendizado de áreas de alimentação, amplitude de forrageio, comportamento social e necessidade de alimentar filhotes influenciam a distribuição dos animais no mar enquanto fatores oceanográficos costumam ser responsáveis por esta distribuição em média e larga escala (Garthe *et al.* 2017). Dentre os fatores físicos que influenciam a distribuição no mar de aves marinhas a Clorofila *a* é o mais utilizado como *proxy* de produtividade primária (Grémillet *et al.* 2008, Monticelli *et al.* 2014, Grécian *et al.* 2016, Rayner *et al.* 2016), assim como a Temperatura da Superfície Marinha (SST) e, em menor escala, ventos, salinidade e batimetria (montes submarinos, *wakes*, zonas de ressurgência, frentes oceânicas (Thiers *et al.* 2014, Grecian *et al.* 2016, Carroll *et al.* 2017).

Em nosso estudo, a distribuição de rabos-de-junco foi nitidamente associada a áreas do mar com baixa turbidez e altos valores de SST durante comportamento de procura por manchas de alimentação, enquanto valores de Clorofila *a* não foram significantes para o uso da área. A ausência de associação entre as aves e valores de clorofila é condizente com Grémillet *et al.* (2008), que explica que ao utilizar valores de Clorofila *a* e demais características, obtidos *in situ* ou via imagens de satélite, pesquisadores tendem a condicionar altos valores dessas variáveis à respostas positivas de predadores de topo, ignorando o desequilíbrio espaço-temporal existente entre alta produtividade primária e real disponibilidade e consumo de presas. É possível que efeitos *bottom-up* relacionados à produtividade ocorram em escala distinta da avaliada em nosso recorte temporal e, portanto, não aparente no presente estudo.

A associação entre rabos-de-junco e áreas com baixa turbidez era esperada, já que essa espécie utiliza *plunge diving* (mergulho feito em alta velocidade, a partir do ar), *surface* e *aerial feeding* (alimentam-se de presas a centímetros de profundidade ou mesmo fora d’água, no caso de peixes-voadores, Haney e Stone 1988, Pennycuick

1990, Ballance e Pitman 1999, Catry *et al.* 2009a), sendo necessário, portanto, local com boas condições de iluminação e clareza da água (Ainley 1977, Henkel 2006, Baptiste e Leopold 2010). Estudos anteriores corroboram a associação entre rabos-de-junco e SST (Pocklington 1979, Le Corre *et al.* 2003, Mejías *et al.* 2017). Nosso estudo hipotetiza que a ocorrência de sua presa preferencial, peixes da família Exocoatidae, (Diamond 1975, Le Corre *et al.* 2003, Catry *et al.* 2009b) em áreas de temperatura oceânica elevada (Zainuddin 2011, Lewallen *et al.* 2017) parece ser o fator responsável pela relação.

O ambiente oceânico de Fernando de Noronha é influenciado por ventos predominantes de sudeste (Becker 2001) e por duas correntes oceânicas: As águas claras e quentes da corrente Equatorial Superficial nas camadas superiores e a Central do Atlântico Sul na zona mais profunda, esta última contendo estoque de nutrientes. A rígida estratificação térmica entre essas camadas, com formação de termoclina entre 70 e 170 metros de profundidade, dificulta a ocorrência de ressurgências impedindo a ascensão de nutrientes à zona eufótica e maior produtividade oceânica (Souza *et al.* 2013). A temperatura e a salinidade da água da zona eufótica nesta região mantém-se $> 20\text{ }^{\circ}\text{C}$ e > 35.5 , respectivamente (Cordeiro *et al.* 2013), e os valores de clorofila *a* variam de 0.46 a $1.65\mu\text{g L}^{-1}$, caracterizando águas oligotróficas (Souza *et al.* 2013).

Estudos realizados na região apontam manchas imprevisíveis de produtividade acentuada, próximas às ilhas e montes submarinos, principalmente na região oeste do arquipélago (*downstream* ou *wake* da ilha) e não atingindo a superfície (Cordeiro *et al.* 2013, Tchmabi *et al.* 2017). Nossos resultados, contudo, apontam viagens de forrageio atingindo a região contrária a esta, ou seja, sudeste. Esta aparente contrariedade entre probabilidade de maior produtividade primária e escolha de habitat pode ser explicada por quatro fatores: Inicialmente, a escala temporal de produtividade é diferente daquela observada na ocorrência de presas para predadores de topo, ou seja, existe incompatibilidade temporal de alguns níveis tróficos entre as escassas oportunidades de maior produtividade primária e disponibilidade de presas (Grémillet *et al.* 2008). Em adição, a disponibilidade de Exocoatidae pode determinar a escolha de sítios com características contrárias às encontradas no *downstream* do arquipélago. A ocorrência de presas não determina necessariamente sua disponibilidade para predadores, podendo haver

incompatibilidade espacial entre locais com maior aporte de presas e áreas nas quais os predadores de fato forrageiam, visto que a escolha de hábitat para alimentação perpassa desde características oceanográficas até condições individuais, como sucesso prévio, comportamento colonial e estágio reprodutivo (Weimerskirch 2007, Grémillet *et al.* 2008, Carroll *et al.* 2017); Aves prestes a sair da colônia também podem utilizar, em larga escala, a direção em que aves vindas de viagens bem sucedidas de alimentação retornam à colônia (Boyd *et al.* 2016). Por fim, a escolha por áreas de forrageio a sudeste pode ser relacionada ao posicionamento da Ilha do Chapéu (na face sul do Arquipélago), evitando que Rabos-de-junco em retorno de alimentação voem por cima da ilha principal e tenham maiores chances de contato com Fragatas (*Fregata magnificens*) e seu comportamento de cleptoparasitismo (Duffy 2015). De fato, nenhum Rabo-de-junco em viagem curta sobrevoou a ilha principal em seu retorno à colônia, embora o tenham feito durante a partida.

Pesquisas futuras na região são necessárias para determinar a escala espaço-temporal e qual a influência de cada um destes fatores na escolha por área de forrageio de *Phaethon lepturus* e demais aves marinhas, indicando, por exemplo, a persistência direcional destas aves a uma determinada área oceânica e a sobreposição de ocorrência e disponibilidade de presas em volta do arquipélago. O conhecimento sobre as estratégias de forrageio, padrões de vôo e escolha de hábitat podem favorecer mudanças no polígono de proteção do Parque Nacional Marinho de Fernando de Noronha, que embora atualmente proteja as colônias reprodutivas, não abrange as zonas de alimentação, seja em viagens curtas ou longas.

Considerando o alcance teórico de forrageio estimado e os dados de métricas de forrageio obtidos nesse trabalho têm-se ferramentas para a discussão de novos limites de proteção do Parque Nacional Marinho de Fernando de Noronha e da criação de uma *Marine Protected Area*, ou Área Marinha Protegida, que englobe mais do que as águas circundantes ao Arquipélago (Ronconi *et al.* 2012, Krüger *et al.* 2017) e proteja também as áreas de alimentação das aves marinhas que nidificam em Fernando de Noronha. De fato, um crescente número de estudos por pesquisadores brasileiros e de instituições estrangeiras vem sendo feitos na região, possibilitando maior conhecimento sobre a ecologia de movimento, padrões

evolutivos e posição trófica das aves (como exemplo temos Leal 2013, Leal *et al.* 2016, Nunes *et al.* 2017ab, Ramos *et al.* 2017, Projeto Mafalda), fornecendo arcabouço teórico robusto para a tomada de decisões por autoridades competentes. O estudo dessas aves em seu período não reprodutivo também é importante, pois elucidaria questões como relacionadas ao tempo que aves marinhas tropicais se comportam como *central place foragers*, se o oceano equatorial do nordeste brasileiro suporta estas aves durante todo o ano, ao uso de áreas costeiras por subpopulações vindas de Fernando de Noronha no período pós-reprodução e, mais importante no aspecto da conservação: Como proteger aves marinhas ameaçadas de interações com a indústria pesqueira e a ocupação humana em áreas de ocorrência?

Tendo em vista o advento de novas tecnologias de marcação e rastreamento de aves a cada ano, espera-se que estas questões sejam em breve sanadas e possam favorecer a manutenção das populações de aves marinhas no Arquipélago de Fernando de Noronha.

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Conclusão

Neste estudo foi comprovado que Rabos-de-junco de Fernando de Noronha exibem estratégia dual de forrageio. Em adição, percebe-se, principalmente nas duas primeiras semanas de vida do filhote, uma coordenação entre pares, indicando que há mecanismos que regulam o tipo de estratégia (viagem curta ou longa) que cada membro de um par realizará a seguir. A utilização de diferentes recursos para lidar com o ambiente e a restrição espacial imposta pelo período reprodutivo causa também distintos padrões de atividade no mar, com diferenças significativas entre procura e vôo direto em viagens curtas e longas.

Além disso, ao sobrepor viagens de Rabos-de-junco e características oceanográficas comumente utilizadas como *proxy* de produtividade primária e ocorrência de presas, viu-se que o ambiente disponível para forrageio desta espécie é altamente oligotrófico, impondo às aves a necessidade de constante procura por manchas de alimentação em oceano aberto. De fato, embora outras espécies de aves marinhas de Fernando de Noronha utilizem as pequenas zonas de ressurgência na plataforma do Arquipélago (< 8 km) e associem-se com predadores de sub superfície (notadamente atuns), Rabos-de-junco buscam alimento em áreas mais distantes, tanto em viagens curtas diárias para alimentar o filhote quanto em viagens longas para provisão própria.

Esta estratégia pode estar relacionada à preferência da espécie por altas temperaturas superficiais do mar, propícias à ocorrência de peixes-voadores, principal presa de Rabos-de-junco. É interessante notar que embora as aves pareçam conhecer a direção em larga escala onde manchas de alimentação estão (talvez por observarem grupos de indivíduos que acabaram de voltar de viagens de alimentação bem sucedidas ou mesmo através de uma memória compartilhada pela colônia), mais da metade do tempo gasto em viagens é de atividade de procura por presas, ou *area restricted search*. Isto indica a imprevisibilidade do alimento em curta escala espaço-temporal e evidencia a necessidade de alternar seus padrões de atividade a fim de adquirir alimento o suficiente para suprir sua demanda energética e a do filhote.

Novos estudos na área devem focar no comportamento de coordenação entre pares, distinguindo que mecanismo (hormonal, demanda do filhote, vocalização, encontro

na colônia, encontro na toca ou no mar) desencadeia a alternância de estratégias de forrageio e diferentes atividades no oceano. Além disso, o rastreamento de determinados indivíduos durante vários períodos reprodutivos, a inserção de acelerômetros e o uso de GLS em adultos e juvenis podem enriquecer o conhecimento sobre Rabos-de-junco em sua maior colônia brasileira. De fato, o rastreamento de aves marinhas ameaçadas tem grande potencial para elucidação de questões relacionadas ao seu comportamento colonial, reprodutivo e de forrageio, bem como fomenta ações de conservação como extensão de áreas protegidas ou mesmo a criação de novas áreas de conservação ambiental.

Em face dos desafios impostos por mudanças climáticas, uso insustentável de recursos pesqueiros e ocupação humana em áreas historicamente mantenedoras de colônias reprodutivas, iniciativas globais para compreensão dos padrões de forrageio e áreas de ocupação de aves marinhas tem sido recorrentes, notadamente as capitaneadas por organizações como *Seabird Tracking Database* e MoveBank. Sendo assim, a identificação de áreas de forrageio, padrões de movimento de *Phaethon lepturus* e inferências sobre causas destes padrões na zona oceânica brasileira, reconhecida internacionalmente como importante área de proteção às aves marinhas, é peça importante para a compreensão da interação entre aves ameaçadas e seu ambiente circundante.

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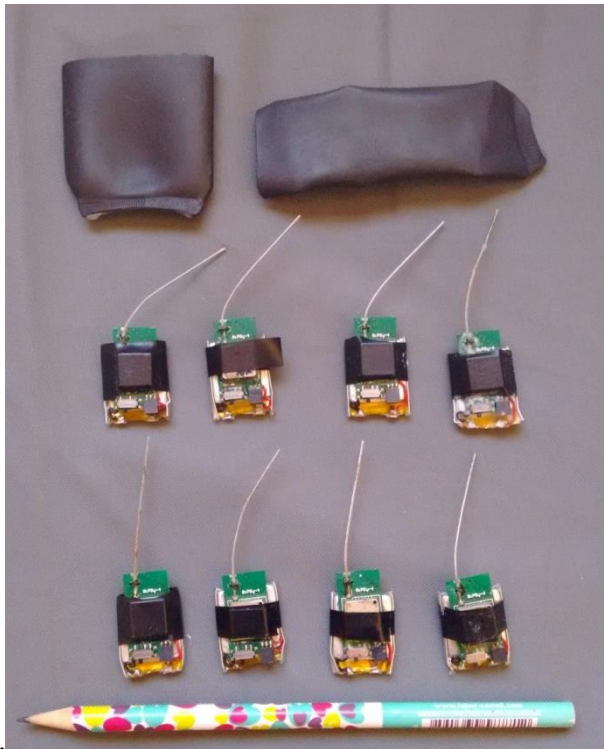


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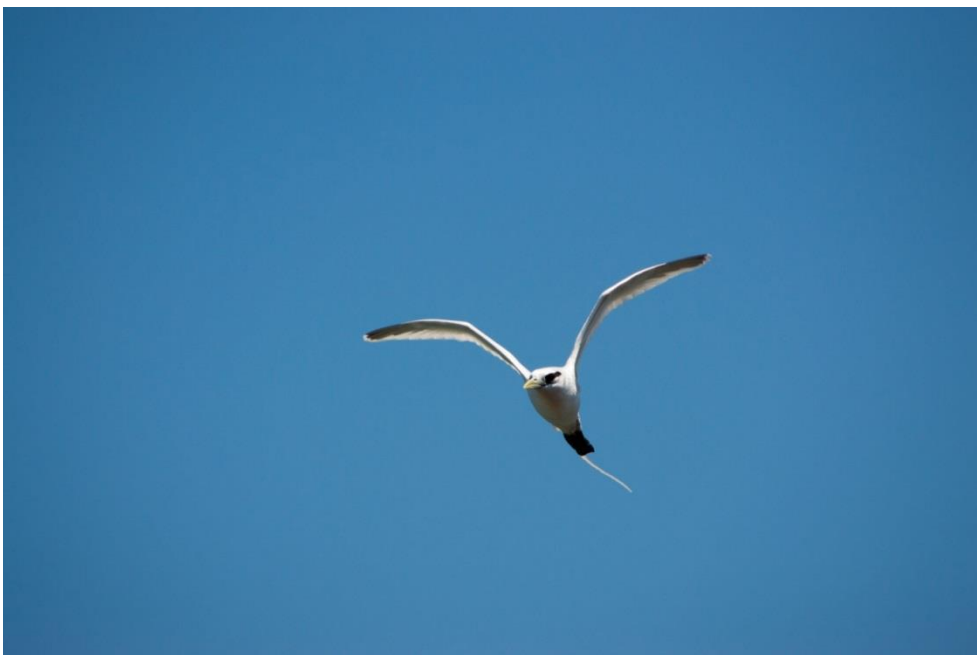


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Figura 10- Casal de *Phaethon lepturus*. Fonte: Arthur Barbosa.

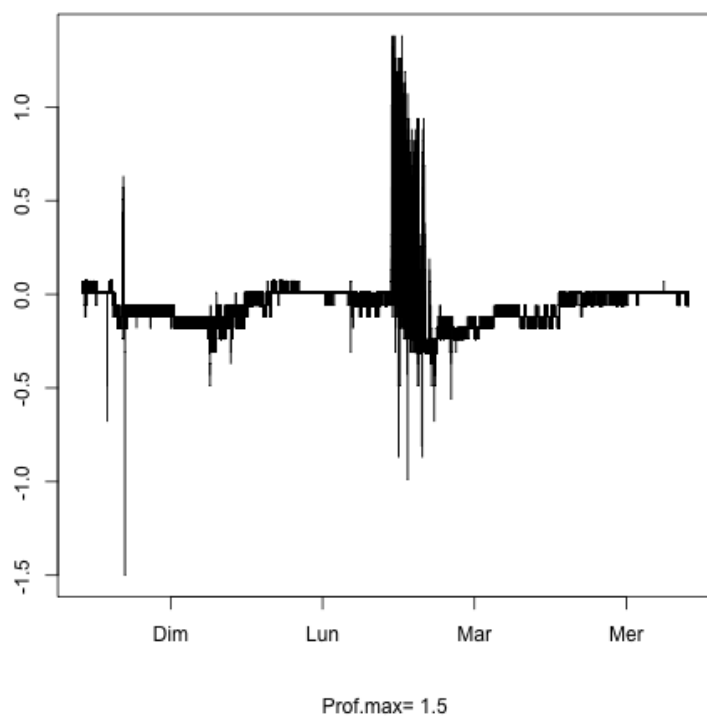


Figura 11- Resultado de acoplagem-teste de *Time Depth Recorder* (TDR) em *Phaethon lepturus*. Fonte: Sophie Bertrand.