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Foraging and migratory ecology of tropicbirds (Phaethontidae)

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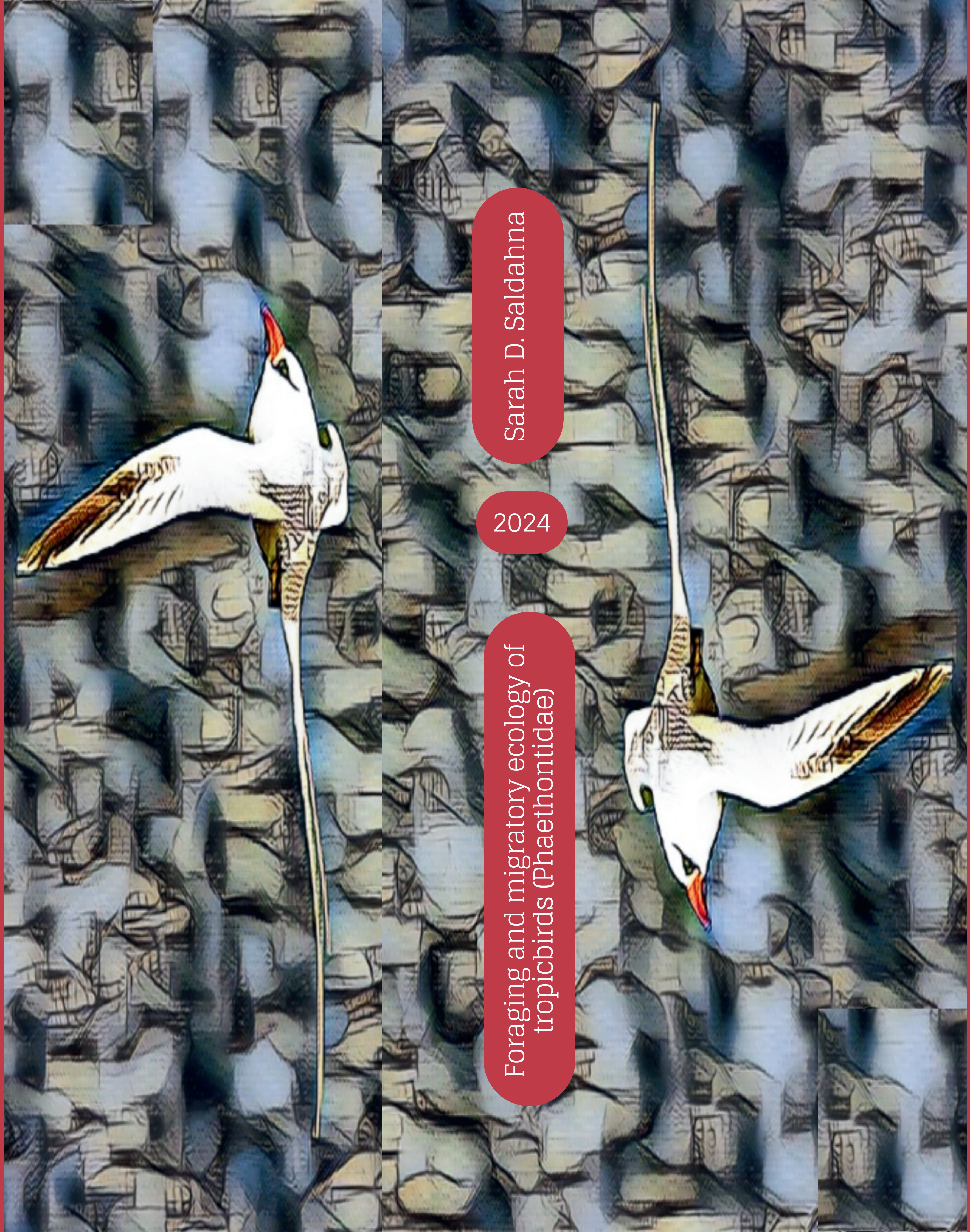

Sarah D. Saldahna

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Facultat de Biologia

Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals

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Foraging and migratory ecology of tropicbirds (Phaethontidae)

Memòria presentada per

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per optar al grau de doctor/a per la Universitat de Barcelona.

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Saldanha

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Abstract

In polar and temperate regions, strong seasonality in environmental conditions often drives animal phenology, resulting in population-wide synchrony in the timing of critical biological events such as breeding and migration. The association between phenology and seasonality is less pronounced in tropical systems, where environmental conditions remain relatively constant throughout the year. As a result, many species exhibit asynchronous or year-round breeding patterns. This leads to the question of whether these species respond to seasonal changes, which may remain present albeit to a lesser extent, and what shapes their phenology. To assess the effects of seasonality on tropical species, we investigated the foraging and migratory ecology of the Red-billed Tropicbird (*Phaethon aethereus*), a poorly studied pantropical species that breed year-round in Cabo Verde, between 2017 and 2024. Along four chapters, this thesis presents novel insights into how tropicbirds cope with seasonal changes in resource availability and environmental conditions using a combination of biologging (GPS, GLS-immersion loggers, time-depth recorders (TDR), and accelerometry), nest monitoring, and diet analyses. In the first chapter, we used auxiliary biologging data from immersion loggers, TDR and accelerometry to evaluate and semi-supervise Hidden Markov Model to classify tropicbirds' behaviors at sea based on tropicbird GPS tracks. We found that although overall classification accuracy greatly improved with semi-supervision, these models failed to capture tropicbird the foraging state, and give a word of caution on using these models to classify behaviors in other opportunistic foragers. Building on the methodological insights of this first chapter, the second chapter of this thesis focuses on the effects of seasonality on the foraging behavior of tropicbirds during the breeding season. In this chapter, we found seasonal patterns in foraging behavior, occupancy, and diet, which affected fitness metrics. We relate these patterns to the increased availability of squid and nest site suitability at the end of the dry season and an increase in weather-related foraging costs in the wet season. In the third chapter, we investigated whether seasonal patterns persist during the non-breeding period and found individual and seasonal consistency in the areas used. We also found that seasonal shifts seem to be related to population-wide habitat preferences. In the fourth chapter, to decipher whether the observed seasonal patterns in foraging and migratory behavior reflect individual plasticity, or seasonal specialization we investigated the repeatability and heritability of tropicbird phenology. We found that individuals maintained remarkably consistent year-round phenology across subsequent years and that phenology appears heritable, with recruits returning to breed around the same time they fledged. Our results provide some of the first in-depth knowledge on the seasonal variation in the foraging behavior of a tropical seabird species, suggesting seasonality in tropical systems may be a stronger driver of the movements of top predators than previously thought. Moreover, we found strong individual repeatability and heritability of phenology, suggesting that these seasonal patterns remain consistent within generations. Therefore, we anticipate that, in changing environmental conditions, tropicbirds may have a restricted ability to modify their individual foraging and migratory strategies, rendering them more vulnerable to environmental change than previously anticipated.

Resum

En regions polars i temperades, la fenologia animal sol estar determinada per una forta estacionalitat de les condicions ambientals, cosa que dóna lloc a una sincronia en el calendari d'importants esdeveniments biològics, com la reproducció i la migració. En sistemes tropicals, on les condicions relativament constants al llarg de l'any, la relació entre fenologia i estacionalitat és menys pronunciada i, com a resultat, moltes espècies presenten patrons de reproducció asíncrons o es reprodueixen durant tot l'any. Això porta a la pregunta d' com s'adapten aquestes espècies als canvis estacionals, que segueixen presents, encara que en menor mesura. Per avaluar els efectes de l'estacionalitat en espècies tropicals, investiguem l'ecologia migratòria i d'alimentació del Cua de Jonc Bec-roig (*Phaethon aethereus*), una espècie pantropical poc estudiada que cria durant tot l'any a Cap Verd, amb dades preses entre el 2017 i el 2024. A al llarg de 4 capítols, aquesta tesi presenta nous coneixements sobre com els Cua de Joncs fan front als canvis estacionals en la disponibilitat de recursos i les condicions ambientals utilitzant una combinació de mètodes per estudiar la conducta, incloent GPS, registradors d'immersió GLS, registradors de profunditat temporal (TDR), accelerometria, seguiment de nius i anàlisi de dietes. Al primer capítol, utilitzem dades auxiliars de seguiment remot procedents de registradors d'immersió, TDR i accelerometria per avaluar i semisupervisar el Model d'Hidden Markov de comportament als Cua de Joncs al mar. Trobem que, encara que la precisió general de la classificació va millorar enormement amb la semisupervisió, aquests models van a fallar a l'hora de capturar el comportament de cerca d'aliment dels Cua de Joncs, i suggereixen precaució sobre l'ús d'aquests models a la classificació de comportaments en espècies que s'alimenten de manera oportunista. Partint dels coneixements metodològics d'aquest primer capítol, el segon capítol d'aquesta tesi se centra en els efectes de l'estacionalitat en el comportament de la recerca d'aliments dels Cua de Joncs durant l'època de cria. En aquest capítol trobem patrons estacionals en el comportament de cerca d'aliment, l'ocupació i la dieta, que van tenir conseqüències en alguns components de l'eficàcia biològica. Relacionem aquests patrons amb la disponibilitat de calamars i la idoneïtat dels llocs de nidificació al final de l'estació seca, i amb un augment dels costos de cerca d'aliment relacionats amb les condicions meteorològiques a l'estació humida. Al tercer capítol, investiguem si els patrons estacionals persisteixen també durant el període no reproductor i trobem coherència tant individual com estacional a les àrees utilitzades i que els canvis estacionals semblen estar relacionats amb el seguiment de nínxols. Al quart capítol, per desxifrar si els patrons estacionals observats en la recerca d'aliment i el comportament migratori reflecteixen plasticitat individual o especialització estacional, investiguem la repetibilitat i l'heretabilitat de la fenologia dels Cua de Joncs. Descobrim que els individus mantenen una fenologia notablement consistent al llarg de tot l'any els anys següents i que la fenologia sembla hereditària, amb reclutes que tornen per reproduir-se més o menys en la mateixa època en què van sortir del niu. Els nostres resultats proporcionen els primers coneixements en profunditat sobre la variació estacional en el comportament de cerca d'aliment d'un ocell marí tropical. Aquests resultats suggereixen que l'estacionalitat als sistemes tropicals pot ser un factor més determinant dels moviments dels depredadors superiors del que es pensava. A més, trobem una forta repetibilitat individual i heretabilitat de la fenologia, cosa que suggereix que aquests patrons estacionals romandran consistents dins de les generacions. Per tant, predim que les poblacions d'aus tropicals poden ser més vulnerables al canvi ambiental del que es pensava.

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General Introduction

Animal movement and biologging

Movement constitutes a fundamental aspect of species ecology, as it serves as the primary conduit through which animals engage and adapt to their surroundings. Through movement, animals can access resources, find mates, and avoid risks, such as inhospitable environmental conditions or interspecies interactions like predation and competition (Dingle et al., 1985). Since movement plays a vital role in the interface between individual animals and their environment, it impacts individual fitness and can affect how species respond to environmental change and, consequently, ecosystem structure (Hooten et al., 2017).

The where, when, and why of animal movement is governed by a combination of both extrinsic (e.g. environmental conditions, resource availability, and inter-species interactions) and intrinsic (e.g. individual physiological needs and preferences) drivers that, together, result in diverse array of movements across different spatiotemporal scales (Dingle et al., 1985). Although the spatiotemporal scales of animal movements are along a continuum, researchers tend to divide them between local and long-distance movements. Local movements, such as those undertaken within a home range or territory, may relate to immediate daily resource acquisition, territorial defense, and social interactions. In contrast, long-distance movements, such as migration or dispersal, can span thousands of kilometers and occur over weeks to months.

Given their ecological importance, predicting both local and long-distance animal movements has long been a focus of investigation. Since movement is an energetically costly state, animals can enhance individual fitness by minimizing the time and energetic expenses during displacement while maximizing their energetic gains. This principle forms the basis of the theoretical framework known as Optimal Foraging Theory (OFT), which predicts that animals will optimize their foraging efficiency by minimizing transit time to, from, and between foraging patches and selecting high-quality foods (Stephens & Krebs, 1986). Although OFT is focused on resource acquisition, it also encompasses other drivers of movements, such as risk avoidance and the evasion of inhospitable environmental conditions as costs to resource acquisition. Moreover, in a changing environment, OFT predicts that animals will change their behavior and habitat use in order to continue adapt to the availability of resources (Stephens & Krebs, 1986). As such, movement is not just a response to environmental change, but a testament to the adaptability of animals, with species adjusting their movements and foraging strategies in response to variations in the distribution, abundance, and quality of food resources as well as the ever-changing costs to acquire them.

Over the past three decades, the field of movement ecology has been revolutionized by advancements in biologging technology, particularly the development of small and lightweight devices incorporating Global Positioning Systems (GPS) and/or light-level geolocators (GLS). The innovation of GPS has not only enabled researchers to track a diverse range of terrestrial and aquatic species with high accuracy and at relatively low cost but has also provided unprecedented insights into how organisms navigate and interact with their environments over fine temporal and spatial scales (Carter et al., 2019; Dean et al., 2012; McClintock et al., 2017, 2020; Russell et al., 2015). In parallel, the innovation of the GLS devices, which use light records to collect coarse estimates of latitude and longitude on a daily basis, has opened up new possibilities for tracking year-round and migratory movements of a variety of species (Burger & Shaffer, 2008; Wilson & Vandenabeele, 2012). These technological advances have not only revolutionized the way we study animal movement, but have also sparked new avenues of research, both at local and long-distance scales.

In particular, the widespread use of high-accuracy GPS tracking devices has driven the development of statistical methods and modeling approaches to infer animal behaviors from trajectory data (Jonsen et al., 2013). Analyzing parameters such as speed, angle, and tortuosity allows for the automated identification of specific behaviors, aiding conservation efforts by allowing researchers to identify and protect key ecological areas like foraging or resting sites (Allen & Singh, 2016; Hance et al., 2021; Hays et al., 2019; Lascelles et al., 2016; Scales et al., 2016; Wakefield et al., 2009). In addition, auxiliary sensors such as wet-dry sensors (WD), which distinguish when an animal is immersed in salt water or not (Carneiro et al., 2022; Dean et al., 2012), Time Depth Recorders (TDR) which detect dives below a specific threshold (McClintock et al., 2013) and high-frequency tri-axial accelerometers which provide unprecedented information on fine-scale movements (Browning et al., 2018; Leos-Barajas et al., 2017; Schwarz et al., 2021; Viviant et al., 2010) have revolutionized the study of animal behavior, resulting in inferences that go as far as separating individual prey-capture attempts.

Seasonality

Seasonality, marked by predictable cyclical shifts in environmental conditions over the course of the year, plays a pivotal role in driving the timing and destination of animal movements (Dufour et al., 2020; Forrest & Miller-Rushing, 2010). This is primarily due to fluctuations in temperature, precipitation, and light levels, which impose energetic and thermoregulatory constraints and influence resource availability, including food and nesting sites, thereby impacting individual fitness (Ramírez et al., 2017). To navigate these seasonal changes, species employ various strategies, such as synchronizing reproduction with favorable conditions and avoiding unfavorable ones through migration, hibernation, or estivation. Alternatively, they may adapt through ecological plasticity, adjusting ecological traits like habitat use, foraging behavior and diet (van Beest & Milner, 2013; Varpe, 2017). As such, seasonality can influence animal movement on both local and long-distance scales.

In polar and temperate regions, population-wide synchrony reflects distinct breeding conditions coinciding with peaks in resource availability, such as spring green-up (Nemes et al., 2024). Conversely, in tropical regions where climatic conditions are generally more homogeneous, the association between phenology and seasonality weakens, leading to asynchronous or year-round breeding (Longhurst, 1995; Lundberg, 1988). However, although weakened, many tropical environments do exhibit at least some climatic seasonality, such as changes in precipitation (Vázquez & Stevens, 2004), which can result in fluctuations in breeding activity, foraging behavior, and diet, suggesting some population-level preferences for seasonal conditions even in tropical environments (Esparza et al., 2022; Keogan, Phillips, et al., 2018; Passuni et al., 2016; Schreiber & Ashmole, 1970; Villegas-Amtmann et al., 2011). These fluctuations can, in turn, impact the foraging efficiency, body condition, and survival of adults and offspring throughout the year (Esparza et al., 2022). Thus, understanding the drivers of seasonal changes in tropical systems is crucial for elucidating the evolutionary pressures acting on species throughout their annual cycle.

In marine environments, seabirds are one of the best-studied groups of higher trophic-level organisms and have often been proposed as ecosystem sentinels (e.g., Frederiksen et al., 2007; Furness & Camphuysen, 1997; Scopel et al., 2018). As highly mobile marine top predators, seabirds are sensitive to changes in lower trophic levels and are known to react to environmental variability and anthropogenic impacts on their ecosystems (e.g., Hazen et al., 2019; Sydeman et al., 2015). In addition, although they spend most of their time at sea, seabirds breed colonially on land, making them accessible for sampling and monitoring (Durant et al., 2009). As such, studying the movement ecology of seabirds can shed light on not only their ecology but also the general dynamics of marine ecosystems.

As ocean sentinels, changes in seabird spatial ecology and fitness are often considered to reflect ecosystem shifts. Given the ongoing threat of climate change, the urgency of investigating species' adaptability to environmental shifts and their repercussions on ecological dynamics cannot be overstated. However, with almost half of seabird species listed as globally threatened with extinction or near Threatened by the International Union for Conservation of Nature (IUCN), seabirds are one of the most threatened groups of vertebrates (Dias et al., 2019). A meta-analysis of worldwide seabird populations spanning from 1952 to 2015 revealed a lack of adjustments in breeding seasons over time or in response to sea surface temperature, highlighting the vulnerability of both seabirds and marine ecosystems to climate change (Keogan et al., 2018). This review also underscores the significant knowledge gaps regarding the adaptability of tropical species to environmental change, further emphasizing the need for immediate research in these systems.

Tropical seabirds

Tropical seabirds are a diverse group of birds that inhabit the tropical regions of the world's oceans. They comprise many species including various albatroses, shearwaters, petrels and storm-petrels (procelarifomes), terns (Laridae) and all noodies (Laridae), tropicbirds (Phaethontidae), frigatebirds (Fregatidae) and boobies (Sulidae; Ballance & Pitman, 1999). On a global scale, the tropical marine systems they inhabit are characterized by lower productivity compared to non-tropical systems, with the exception of the major central oceanic gyres and coastal upwelling systems. As such, phytoplankton production in tropical marine systems is limited, consequently affecting the total biomass at higher trophic levels, resulting in low prey abundance and patchy prey distribution (Ainley & Boekelheide, 1983; Ashmole, 1971). Consequently, tropical seabirds face selective pressure to maintain foraging success despite the reduced feeding opportunities compared to their non-tropical counterparts.

To find prey in these homogeneous environments, tropical seabirds tend to exhibit greater flexibility in their foraging behavior than their polar and temperate counterparts, often departing the colony in all directions on their foraging trips and showing low repeatability in their foraging movements (Lerma et al., 2020; Oppel et al., 2015; Soanes et al., 2021; Weimerskirch et al., 2005). Moreover, certain tropical seabird species, particularly tropical shearwaters, terns, and noddies, are frequently observed foraging in multispecies flocks alongside sub-surface predators like tuna or dolphins, which create feeding opportunities by driving prey closer to the surface (e.g., Ballance et al., 1997; Hebshi et al., 2008; Jaquemet et al., 2004; Miller et al., 2018; Spear et al., 2007; Weimerskirch et al., 2005). This strategy is particularly prevalent among fish-eating species that follow surface-dwelling tunas and dolphins in regions with pronounced vertical thermal gradients (Spear et al., 2001). Conversely, other tropical species, such as tropicbirds, are generally observed foraging alone (Jaquemet et al., 2004; Spear & Ainley, 2005), suggesting variability in the importance of heterospecific attraction and foraging strategies in these unpredictable environments.

Similarly, due to the lower seasonal fluctuations in marine productivity, tropical seabirds are not necessarily bound to breed exclusively during specific, highly productive periods of the year and exhibit various breeding and migratory behaviors. The breeding phenology of many tropical species is quite variable, with numerous species breeding synchronously (e.g., Surman et al., 2012), asynchronously (e.g., Medrano et al., 2022), or even year-round (e.g., Franklin et al., 2022a). In extreme cases, phenology and seasonality can be entirely decoupled, with individuals breeding sub-annually once a specific quorum is reached (e.g., Reynolds et al., 2014; Stonehouse, 1962). Moreover, this diversity of breeding strategies not only exists between different tropical seabird species but also between populations of the same species. For instance, White-tailed Tropicbirds generally breed sub-annually across their entire range, except in Bermuda, where they follow an annual breeding cycle (Prys-Jones & Peet, 1980). Moreover, tropical seabirds also exhibit a large diversity of migration strategies, with some species remaining resident year-round while others are partial or long-distance migrants. In some cases, species of largely asynchronous or year-round breeders are migrants (e.g., White-tailed Tropicbirds (Mejías, 2017) and gadfly petrels (Franklin et al., 2022a). In these cases, the specific drivers of migration are more ambiguous since the environmental conditions surrounding the breeding areas are presumably adequate for the species year-round (Lambert & Fort, 2022). This extensive variability in breeding and migration behaviors highlights the adaptability of tropical seabirds to the unpredictability of tropical oceans.

While the number of tracking studies on tropical seabird species has increased in recent years, it still falls behind that of temperate and polar regions (Mott & Clarke, 2018). Recent reviews on the repeatability of migrating phenology in tropical seabirds (Franklin et al., 2022b), the effects of climate change on seabirds (Keogan et al., 2018), and seabird foraging site fidelity and movements (Bernard et al., 2021; Weimerskirch, 2007) have all highlighted a significant knowledge gap regarding tropical seabird movements and phenology. Despite this knowledge gap, it is generally assumed that the broad flexibility observed in foraging, migratory ecology, and breeding phenology in tropical seabirds indicates their adaptability to environmental change (Chapman et al., 2011; Franklin et al., 2022b; Soanes et al., 2021). However, this assumption remains largely unsubstantiated, as it is unclear whether this population-wide flexibility results from individual plasticity, nor whether this plasticity is used to buffer carry-over effects or environmental change. Therefore, studies are needed to accurately predict how tropical species may respond to climate change-induced shifts in environmental conditions.

In this thesis, we examine the effects of seasonality on the foraging and migratory ecology of the Red-billed Tropicbird (*Phaethon aethereus*), a relatively understudied pantropical species that breed year-round in Cabo Verde. Over four chapters, this thesis provides new insights into how tropicbirds adapt to seasonal variations in resource availability and environmental conditions, utilizing a combination of biologging tools (GPS, GLS-immersion loggers, time-depth recorders (TDR), and accelerometry), nest monitoring, and diet analyses.

Study species

In this thesis, I focused on the Red-billed Tropicbird (*Phaeton aethereus*; Figure 1). The Red-billed Tropicbird is one of only three species in the poorly known family Phaethontidae, which also includes the White-tailed (*Phaethon lepturus*) and Red-tailed Tropicbirds (*Phaethon rubricauda*). Based on at-sea surveys, both Red-billed and Red-tailed Tropicbirds are generally solitary foragers that associate infrequently with sub-surface predators, in comparison with White-tailed Tropicbirds and other tropical seabird species (Jaquemet et al., 2004; Maxwell & Morgan, 2013; Spear & Ainley, 2005b; Vilchis et al., 2006). They generally have a flapping flight, although some thermal soaring has been recorded in Red-tailed Tropicbirds (Garde et al., 2023). Red-billed Tropicbird inhabit tropical and sub-tropical areas in the East Pacific, Atlantic and Indian Oceans (Orta et al., 2020). They breed asynchronously in scattered colonies and feed mainly on small epipelagic fish, such as needlefish, flying fish, and squid, forage by plunge diving (Castillo-Guerrero et al., 2011; Diop et al., 2018; Madden et al., 2022; Spear & Ainley, 2005). During the breeding season, they are central place foragers that may travel over 500 km from the colony in search of prey (Diop et al., 2018) and use a dual foraging strategy during chick-rearing in which they alternate between short trips to feed their young and long trips to feed themselves (Piña-Ortiz et al., 2024). This species is classified as Least Concern (BirdLife International, 2024). However, the Cabo Verde population is declining. The main threats described include introduced terrestrial predators, especially cats, and rats, although poaching is also an issue in Cabo Verde. The effects of other threats, such as the impact of fisheries or climate change, are unknown.

Figure 1. Nest of the species studied in this thesis, the Red-billed Tropicbird. Photography of Jacob González-Solís.

Study area

Cabo Verde is a volcanic archipelago ≈600 kilometers off Western Africa. It has ten islands and five islets (Figure 2). It is located within the southern limit of the Canary Current Large Marine Ecosystem (Valdés & Déniz-González, 2015), at the eastern boundary of the North Atlantic subtropical gyre (Fernandes et al., 2005). It is considered a hotspot of endemism for seabirds, with several species of petrels and shearwaters breeding only there (Howell & Zufelt, 2019). Breeding seabird species include Red-billed Tropicbird (*Phaethon aethereus*), Brown Boobies (*Sula leucogaster*), Cape Verde Shearwater (*Calonectris edwarsii*), Cape Verde Petrel (*Pterodroma feae*), Little Cape Verde Shearwater (*Puffinus boydi*), Bulwer's Petrel (Bulweria bulwerii), White-faced Storm Petrel (*Pelagodroma marina*), Cape Verde Storm Petrel (*Hydrobates jabejabe*) and, one locally extinct species, the Magnificent Frigatebird (*Fregata magnificens*; Semedo et al., 2020). Fieldwork took place at two colonies on Boavista Island, three on Sal Island, and one on Cima and Raso Islet in Cabo Verde between 2017 and 2024 (Figure 2, 3).

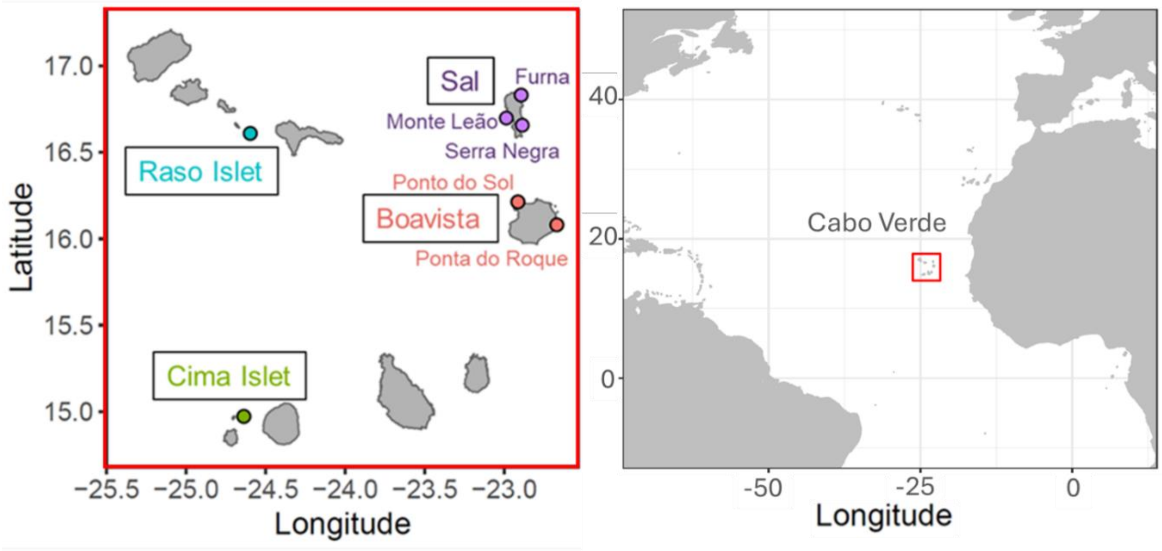

Figure 2. Location of the Cape Verde Archipelago, off western Africa and of Red-billed colonies on Sal and Boavista Islands and on Raso and Cima Islets.

Figure 3. Cima Islet, in Cabo Verde off Western Africa. Photography of Mónica de la Fuente.

Aims

General aim

The main aim of this thesis is to uncover the effects of seasonality on the foraging and migratory ecology of Red-billed Tropicbirds (*Phaethon aethereus*), a pantropical marine top predator that breeds year-round in Cabo Verde. Within this general aim, we pursued four specific objectives:

Specific objectives

1) Assess how tropicbirds respond to seasonal changes in oceanographic conditions and resource availability during the breeding season by studying tropicbird movement ecology, activity patterns, diet, and fitness metrics.
2) Assess how seasonal changes in oceanographic conditions affect the distribution and migratory ecology of tropicbirds during the non-breeding season.
3) Assess links between cyclical life history events and whether there are carry-over effects on phenology, spatial ecology, and breeding success.
4) Evaluate the potential evolutionary impact of seasonal patterns by determining whether the underlying mechanism driving phenological variability is individual adaptability or specialization in distribution and phenology and whether phenology is heritable.

In Chapter 1, we assessed whether semi-supervised Hidden Markov Models reliably classified tropicbird GPS tracks into behavioral states using auxiliary biologging data from immersion loggers, TDR, and accelerometry to both validate and semi-supervise the models. The methodological insights of this chapter helped fulfill the objective 1.

In Chapter 2, we assessed the effects of seasonality on the foraging behavior of tropicbirds during the breeding season. Here, we measured seasonal patterns in foraging areas, daily activity patterns, and diet and relate these to changes in oceanographic conditions and nest occupancy throughout the year. We also investigated the consequences of these seasonal patterns on fitness metrics and measured individual consistency in foraging areas used. This chapter fulfills the objectives 1 & 4.

In Chapter 3, we investigated whether seasonal patterns in tropicbird spatial ecology and daily activity patterns also persist during the non-breeding period and whether these patterns can be linked to individual or population-level niche tracking. Moreover, we assess the relationship between previous breeding success on the non-breeding distribution and individual consistency in non-breeding areas. This chapter fulfills objectives 2, 3 & 4.

In Chapter 4, we investigate the underlying mechanism of phenological variability in tropicbirds to understand how they may cope with future environmental change. Specifically, we investigated whether breeding and migratory phenology are 1) correlated between cyclical life-history events, 2) repeatable at the individual level, and 3) heritable. This Chapter fulfills objectives 3 and 4.

Overview of methods

Bird monitoring and sampling

Nest monitoring: To monitor adult body condition, breeding success, chick growth, and diet, nests were generally visited every 1-3 days, but some isolated nests (<5%) were only visited monthly, and Raso islet was only monitored in the winters of 2017 and 2018 (Figure 4, 5). At each nest visit, the contents of the nest were recorded (empty, chick/egg, and whether there was an adult or not), and if an adult or chick was present, we measured its morphometrics (weight, wing length, tarsus length, bill depth, culmen, and head-bill length).. All the birds captured were marked with stainless rings with a unique identifier code (Figure 6).

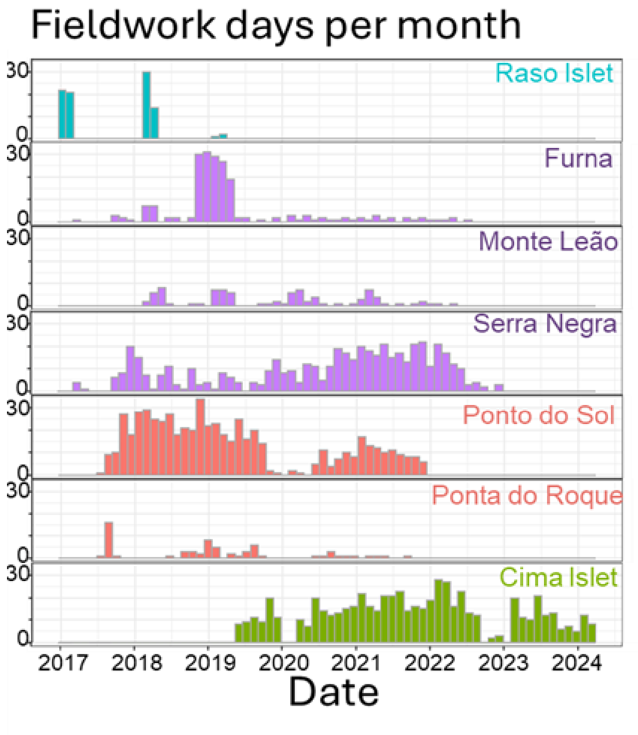

Figure 4. Histogram of the number of fieldwork days per month per colony as a metric of monitoring effort throughout the study period, coloured by Island.

Figure 5. Nest monitored in Cima Islet of a Red-billed Tropicbird. Photography of Projeto Vitó.

Figure 6. Red-billed Tropicbird banded with stainless rings. Photography of Projeto Vitó.

Biological samples: We collected regurgitates and whole blood samples for diet analysis (regurgitates and blood) and sexing (blood). Regurgitates from tropicbird adults were collected opportunistically during nest monitoring. Each sample was initially stored in plastic bags with ethanol and later frozen. In the lab, we first defrosted and cleaned the samples with distilled water over a 3mm sieve. Then, the identifiable prey items and otoliths in each sample were counted, measured, and classified to the lowest possible taxonomic level using morphological identification (Goyena & Fallis, 1988; Schneider, 1990). Additionally, prey-muscle samples were processed for stable isotope analyses (see laboratory analyses). Blood was also collected during nest monitoring upon retrieval of tracking devices. We collected ~1.5 ml of blood from the tarsal vein of breeding adults, which was stored in absolute ethanol and at -20°C after fieldwork for stable isotope analysis and molecular sexing.

Tracking devices

We used tracking devices to record the location and timing of tropicbird movements and to infer behavior and activity patterns while at sea. All tags deployed in this thesis represented less than 3% of the bird's body weight, as recommended in the literature (Phillips et al., 2003).

Geographic Positioning System (GPS): To obtain the accurate spatial during the breeding season, we deployed CatLog Gen2 GPS. The GPS loggers weighed 18g (2.9% of mean tropicbird weight; 630g±55, n=1,297 individuals) and were programmed to record GPS positions every 5 minutes. GPS were attached to the base of the six central tail feathers with Tesa® tape and Loctite® (see Figure 7).

Figure 7. Axy-Trek attached to the central tail feathers of Red-billed Tropicbird. Photography of Sarah Saldanha

Light-level geolocators: To collect spatial and activity data, especially during the non-breeding season, we deployed Migrate Technology C330 geolocators and Biotrack BAS_MK19 (GLS) with a wet-dry sensor (saltwater immersion logger). These geolocators, weighing 3.3g (0.5% of tropicbird weight), were attached to the bird’s metal ring using a zip tie (see Figure 12). Migrate Technology GLS recorded light intensities every minute, maximum light intensity every five minutes and conductivity (salt-water immersion data; wet-dry) every six seconds, while Biotrack GLS recorded both light intensity and wetness every 10 minutes. We used the light intensity data from GLS to estimate the location of animals based on the timing of sunrise and sunset respecting the Greenwich Meridian and the duration of the day. The timing of the sunrise and sunset provides information on the longitude, due to the rotation of the earth, while the duration of day provide information for calculating the latitude (with longer days in higher latitudes in summer and shorter days in lower latitudes in winter). Although these devices provide information for a large time span and are relatively lightweight and inexpensive, the spatial resolution has a large error (≈500 km for tropicbirds in Cabo Verde; Halpin et al., 2021). Moreover, the estimation of latitude is particularly low during the equinoxes, since day lengths are nearly equal across all latitudes. We also used the wet-dry data from GLS to infer activity patterns. Since geolocators were deployed on the tarsus, we inferred that if the tag is submerged, it means that the bird is resting on the water, while if the geolocator is "dry", it would mean that the bird is flying/inland.

Axy-Trek: We also deployed Axy-trek devices on tropicbirds. Axy-Trek loggers weighed 17g (2.6 % of tropicbird weight) and recorded GPS, acceleration, and pressure data at 5-minute, 25 Hz, and 1s intervals, respectively. The tri-axial accelerometer in the device recorded acceleration in the surge (X, forward/backward), heave (Z, dorso/ventral) and sway (Y, side to side). TDR sensor, which recorded pressure at a frequency of 1Hz. Axy-Trek was attached to the base of the six central tail feathers with Tesa® tape and Loctite®. With these devices, we extracted precise information on tropicbird behavior at sea.

Laboratory procedures

Molecular sexing: We sexed the birds by extracting 0.01 ml of blood from the tarsal vein and detecting the female-specific CHD1-W locus, using protocols from Fritlolfsson and Ellegren (1999). Hispalis Biolab from Sevilla, Spain conducted the analyses.

Stable isotopes: We analyzed the carbon (δ13C) and nitrogen (δ15N) isotopic values from tropicbird whole blood and prey-muscle samples from spontaneous regurgitates collected during the breeding period (Ramos & González-Solís, 2012).

The blood and muscle samples were analyzed through Elemental Analysis with the Isotopic Ratio Mass Spectrometer Flash EA1112, conducted at the Serveis Cientifics i Tècnics of the Universitat de Barcelona. We expressed the isotope ratios as δ values in part per mil (‰), according to the following equation:

$$\delta X=[(Rsample/Rstandard) – 1],$$

Where X is 13C or 15N and R is the 13C/12C or 15N/14N ratio for the sample and the standard respectively. International standards are Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric air (AIR) for nitrogen (Weiser and Powell, 2011). International laboratory (IAEA N1, IAEA N2, IAEA CH7, IAEA 600, USGS 40) and internal laboratory standards (Acetanilide, Fructose, UCGEMA P and Urea) were analyzed every 12 blood sampled to compensate for any drift over time and obtain the correct values of δX with an overall precision of 0.2‰.

Ethics statement

All procedures included in this thesis, involving animal manipulations were in accordance with required European legislation, and the local legislations of Cabo Verde (permissions from Direção Nacional do Ambiente from Cabo Verde "Autorização N.º91/2018; Autorização N.º107/2019; Autorização N.º016/DNA/2020"). Deployment and recovery of GPSs and geolocators, and associated sampling procedures, were accomplished in <10 minutes per bird in the nests and did not have any visible detrimental effects on individuals (e.g., external signs of panting or weakness).

Picture by Fernando Medrano Martinez

Chapter 1. Animal behavior on the move: the use of auxiliary information and semi-supervision to improve behavioral inferences from Hidden Markov Models applied to GPS tracking datasets

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ABSTRACT

State-space models, such as Hidden Markov Models (HMMs), are increasingly used to classify animal tracks into behavioral states. Typically, step length and turning angles of successive locations are used to infer where and when an animal is resting, foraging, or travelling. However, the accuracy of behavioral classifications is seldom validated, which may badly contaminate posterior analyses. In general, models appear to efficiently infer behavior in species with discrete foraging and travelling areas, but classification is challenging for species foraging opportunistically across homogenous environments, such as tropical seas. Here, we use a subset of GPS loggers deployed simultaneously with wet-dry data from geolocators, activity measurements from accelerometers, and dive events from Time Depth Recorders (TDR), to improve the classification of HMMs of a large GPS tracking dataset (478 deployments) of Red-billed Tropicbirds (*Phaethon aethereus*), a poorly studied pantropical seabird.We classified a subset of fixes as either resting, foraging or travelling based on the three auxiliary sensors and evaluated the increase in overall accuracy, sensitivity (true positive rate), specificity (true negative rate) and precision (positive predictive value) of the models in relation to the increasing inclusion of fixes with known behaviors. We demonstrate that even with a small informed sub-dataset (representing only 9% of the full dataset), we can significantly improve the overall behavioral classification of these models, increasing model accuracy from 0.77 ± 0.01 to 0.85 ± 0.01 (mean ± sd). Despite overall improvements, the sensitivity and precision of foraging behavior remained low (reaching 0.37 ± 0.06, and 0.06 ± 0.01, respectively). This study demonstrates that the use of a small subset of auxiliary data with known behaviors can both validate and notably improve behavioral classifications of state space models of opportunistic foragers. However, the

improvement is state-dependant and caution should be taken when interpreting inferences of foraging behavior from GPS data in species foraging on the go across homogenous environments.

INTRODUCTION

Inferring behavior from animal movements is crucial to understand relationships between species and their environments [1,2] or potential human-wildlife conflicts [3–5]. Over the last three decades, advances in biologging technology through the creation of smaller, cheaper and more sophisticated and accurate sensors, have facilitated rapid developments in the field of movement ecology, allowing for the study of movement in a wide array of species and environments (e.g. [6]). In tandem, several statistical methods and modelling approaches have been developed which mathematically analyse step length (the distance between consecutive positions), angle, tortuosity, and other traits of a trajectory to infer what segments of an animal’s track are spent in specific behaviors based on knowledge of their locomotion and ecology [7]. This can be particularly useful for conservation and management [8], enabling the identification and protection of areas important for animal ecology, such as those associated with foraging [9,10], and/or resting [11,12]. However, whilst the study of animal movement is progressing rapidly, transforming tracking data into meaningful behavioral states still remains a challenge for many species.

Typically, attempts to segment tracks into behavior use the step length and tortuosity of animal movements, acquired by transforming data from GPS/Argos loggers into a bivariate series of step lengths and turning angles [13]. Based on these values, tracks are then segmented into two or three behavioral states: foraging and travelling, and if anticipated, resting. To differentiate foraging from travelling, inference often relies on the concepts of Area Restricted Search (ARS) and Optimal Foraging Theory (OFT). ARS predicts that when resources are patchily distributed, foraging is concentrated in high density areas, within which there is a decrease in step length and an increase in turning angle rate [14]. Outside of these foraging patches, OFT predicts that animals will minimise time in transit to, from, and between foraging areas by taking the most direct route over unsuitable environments, resulting in fast, directed movements [15]. The identification of rest is often associated with a long period without movement in terrestrial environments or with movement associated with drift in aquatic environments [11,12]. However, while several methods are commonly used to infer behavior from GPS tracks, their results are rarely cross-validated, and when they are, show a disparate ability to correctly predict behavioral states (S1).

While some differences in model performance among studies can be attributed to the type of model and/or validation method [16–20], performance is highly dependant on how distinct behavior-specific movement patterns are [16,18,20–22]. For example, in heterogeneous systems, where resources are patchily distributed in space and time in a predictable manner, animals typically follow the concepts of ARS and OFT, using commuting trips to actively seek out rich foraging patches while quickly bypassing nutrient poor areas, resulting in a clear separation between the movement patterns of travelling and foraging [17,23]. However, in homogeneous systems, where resources are more evenly and often unpredictably distributed in space and time, species may adopt a more opportunistic approach and undertake looping trips, where foraging is sporadic and short-lived, termed foraging on the go [24–26]. In this case, models may struggle to separate foraging movements from travelling, resulting in high levels of misclassification. Difficulties in inference may be further exasperated when both resting and foraging take place at short step length or when the turning angle of resting is artificially high because of GPS error [27–29]. Limitations have been noted across a variety of modelling methods including Hidden Markov Models (HMMs) [28], Expectation-maximization binary clustering (EmbC) [26,28], Residence in

Space and Time (RST) [30], and First Passage Time (FPT) [29]. As a result, post-hoc adjustments are applied to improve model performance, either by pooling locations classified as resting and intensive search together [28], re-classifying foraging locations with step lengths representing speeds below those of local currents (1m/s) as resting [30] or eliminating locations with short step lengths altogether before running the analysis [29]. However, the predictions of these models, both pre- and post-adjustments, are usually evaluated visually, and without cross-validation with other datasets making it difficult to measure the benefits of these changes (S1).

Model performance can be improved by incorporating additional information on what an animal is doing from auxiliary sensors. For example, wet-dry sensors (WD) can distinguish when an animal is immersed in salt water [3,23], Time Depth Recorders (TDR) can be used to detect dives below a specific threshold [31] and high frequency tri-axial accelerometers can provide unprecedented information on fine-scale movements resulting in inferences that go as far as separating individual prey-capture attempts [17,32–34]. Data acquired from these sensors can be incorporated into behavioral models, allowing for more accurate classification. Although several modelling techniques can be used to incorporate these data, HMMs have drawn particular attention due to their relatively high accuracy [22,34], their robustness at lower GPS resolution [16,20,22], and the development of the flexible user-friendly R packages that can incorporate information from additional data streams, even when collected at different time resolutions (e.g. ‘moveHMM’ and ‘momentuHMM’; [33,35,36]). Nonetheless, the use of auxiliary sensors is often limited by their cost, size, and weight, and so they often only comprise a small fraction of a full GPS tracking dataset, and cannot easily be incorporated as additional datastreams [33]. For this reason, many studies limit their use to validate behaviors identified from GPS positions, instead of directly using these data to improve the model classifications themselves (e.g. [23,37]).

When a small auxiliary sensor dataset is present, one potential solution is manually setting associated positions to a given inferred behavior, and then use these positions to semi-supervise the model behavioral classification of the rest of the dataset, with an aim to improve the models' overall accuracy. In this study, we aim to assess whether the addition of information from auxiliary sensors can improve behavioral inference in animals mainly performing looping trips through relatively homogeneous environments, such as seabirds foraging in tropical waters. We use a large GPS tracking dataset of a tropical seabird species, the Red-billed Tropicbird (*Phaethon aethereus*), of which a subset was double tagged with a combination of accelerometers, wet-dry sensors, and/or TDR sensors. From these auxiliary sensors, we determine informed positions of resting, foraging, and travelling and use these to semi-supervise the fitting of an HMM predominantly based on movement metrics between GPS fixes. Specifically, by incorporating additional auxiliary sensors to GPS tracking, we assess whether (1) model accuracy in identifying behavioral states improves with an increasing percentage of supervision; (2) the improvement in the inference is homogeneous across the three basic behavioral states, i.e. resting, foraging and travelling, and (3) this improvement saturates or could theoretically achieve behavioral inference levels comparable to those obtained for species using commuting trips. It is hoped that outputs from this study can direct researchers in the deployment of specific tracking regimes to yield the most accurate identification of behavior from animal movement and to will limit errors that can contaminate future analyses, such as the identification of areas of ecological importance for species.

METHODS

Fieldwork

Fieldwork took place at 7 colonies dispersed across 2 islands (Boavista and Sal) and 2 islets (Cima and Raso) in Cabo Verde between 2017 and 2021. While fieldwork on Sal and Boavista islands was almost continuous during this time, work on the islets was restricted to campaigns of a few months each until 2020, after which work on Cima Islet was nearly continuous, and discontinued on Raso.

Red-billed Tropicbirds were captured on their nests during incubation or early chick-rearing, and equipped with a combination of CatLog Gen2 GPS, Axy-Trek loggers (which records GPS, tri-axial accelerometer, and time-depth information), and/or Migrate Technology geolocators (GLS) with a wet-dry sensor (salt water immersion logger). The GPS loggers used weighed 18g (2.9% of mean tropicbird weight (630g±55, n=1297 individuals) and were programmed to record GPS positions every 5 minutes. Axy-Treck loggers weighed 17g (2.6 % of tropicbird weight) and recorded GPS, acceleration and pressure data at 5-minute, 25 Hz and 1s intervals, respectively. The Migrate Technology C330 geolocators (GLS) with a wet-dry sensor weighed 3.3g (0.5% of tropicbird weight) and register if the bird was wet or dry every 6 seconds. GPS and Axy-Trek's were attached to the 6 central tail feathers with Tesa tape while GLS were attached to the tarsus, on the bird's metal ring with the help of a zip tie.

Data processing

To test whether adding data from auxiliary sensors improved the accuracy of HMM behavioral inferences, we first processed the wet-dry, accelerometry and TDR data separately before summarizing and matching the information to each GPS position (interpolated to 5-

minute intervals). We matched the data forwards (e.g. the value of the wet-dry, accelerometry, and TDR metrics at a GPS position at time t summarized the values of the period between t and t+1) to be consistent with the calculation of the step and turning angle by the prepData function of the ‘momentuHMM’ package [36]. From wet-dry loggers, we extracted the proportion of time wet between each GPS position. From the accelerometry data, we extracted the proportion of time resting on water, diving, and flapping between each GPS position. From the TDR data, we extracted the number of dives between each GPS position. Further details on device processing methods are in supplementary material S2.

Creation of informed dataset

To create an informed dataset of inferred bird behavior to both semi-supervise and validate the HMM, we combined the information from the wet-dry, accelerometer, and TDR data based on the following conditions to assign positions as foraging, resting, or travelling. These positions are referred to as having a known state.

1. Foraging: diving was identified one or more times in the accelerometer or TDR data stream.

2. Resting: the wet-dry sensor recorded a period as 100% wet, or the accelerometers recorded a period as over 50% on water. No dives were detected in either the accelerometer or TDR data stream.

3. Travelling: the wet-dry sensor recorded a period as 0% wet or the accelerometers recorded a period as 100% flapping. No dives were detected in either the accelerometer or TDR data stream.

HMMs

We ran two series of HMMs to determine if an increasing percentage of supervision can improve the accuracy of behavioral classifications. The first used only GPS tracks with auxiliary data (151 foraging trips) to determine whether accuracy at high porportions of supervision saturates, while the second used the complete GPS dataset (1084 foraging trips) within which only a small percentage (13.9%) of trips contained auxiliary data to test whether even small auxiliary datasets can improve model accuracy.

All HMMs were implemented in the R package 'momentuHMM'[36]. Although GPS loggers were programmed to record positions every 5 minutes, poor satellite reception resulted in gaps in the data (of 6-20 minutes between 1.5% of positions, and over 20 minutes between 0.4% of positions). Therefore, to satisfy model assumptions, GPS data were linearly interpolated to a regularised five-minute sampling frequency to have an equal time period between each position when the gaps were less than 20 minutes long. When gaps were over 20 minutes long, the periods before and after the gaps were handled discretely by the HMMs. HMMs function by identifying underlying latent processes based on the variation in the observed data while also calculating the probabilities of switching from one state to another. When inferring behavior from animal movement, these models use observed step length and turning angle to infer the underlying (or hidden) behavioral states that drive them [38]. The models separate the modes in a purely data-driven way, by defining the states that best capture the variability in the data. This leaves it to the observer to define a posteriori which state can be used as a proxy for each behavior based on the estimated movement characteristics (e.g., mean step length and turning angle) of each state. We chose a three-state HMM as a trade-off between model accuracy, interpretability of states, and biological knowledge of the species [39]. States were delineated by the HMM using step lengths and turning angles between positions, and then classified as resting (short step lengths and low turning angles), foraging (mid step lengths and high turning angles), and travelling (longs step lengths and low turning angles). To select appropriate starting values for the models, a k-means clustering algorithm (with k=3 for the number of states) was used for the state-dependent probability distribution parameters of each data stream [23]. We used a gamma distribution to describe step lengths, and a von Mises distribution with a mean of zero for turning angles. To reduce the risk of models converging at a local rather than global maxima for the maximum likelihood, we reran each model 10 times using a randomization starting values , before selecting the model with the highest maximum likelihood and lowest Akaike Information Criterion (AIC) [36].

Model validation

To measure how the use of informed data increases model accuracy, we used an iterative approach similar to a k-folds analysis, in which we left out 10 random samples of 10% of the known states to be used as testing datasets, while the remaining 90% of known states were used as training datasets. For the first series of HMMs using only the GPS tracks with auxiliary data, we created models with randomly selected subsets of the known states representing 0 to 75% of this dataset (75% representing the maximum number of known states available for our dataset after setting aside 10% as the testing dataset). For each increase of 5% percent of known states from 0 to 75%, we ran 10 models, using the 10 different random samples of test and training datasets to validate the models. For the second series of HMMs using the complete GPS dataset, we only tested the increase in accuracy between 0 and a maximum percentage of known states (9%) due to computational restrictions and therefore ran 10 models at each of these percentages using the 10 different random samples of test and training datasets.We then decoded the states of each model using the Viterbi algorithm.

For each model, we then generated the assigned state confusion matrix to assessoverall assignment accuracy using the confusionMatrix function in the ‘caret’ R package [40]. In addition to the overall accuracy we also extracted the class-wise sensitivity, specificity, and precision from the confusion matrices (Fig. 1). These metrics are complimentary and the importance of each will depend on the research questions at hand. Using foraging behavior as an example, high sensitivity of foraging would indicate that most known foraging positions are correctly classified as foraging by the model. However, this does not exclude the possibility of many resting and travelling positions being also misclassified as foraging. To measure this, one uses specificity, or the proportion of resting and travelling positions correctly classified as non-foraging. If there is an uneven number of known resting, foraging or travelling positions, even a small proportion of one behavior misclassified as another can dilute the proportion of correct classifications. Here is when precision is needed to determine the proportion of positions classified as foraging that are actually foraging, and not resulting from a misclassification of resting or travelling positions. To compensate for a lack of standardized practices in evaluating and reporting the performance of behavior classification models [18], we also calculated additional measures of model performance to make it possible to compare our results to as many previous studies as possible (S3).

Finally, to explore if the exclusion of positions with low state classification probabilities improved overall HMM behavioral classification, we used the stateProbs function from the ‘momentuHMM’ package [36] to extract the state classification probability of each position. We then removed all positions with a probability of classification of less than 90%, and evaluated whether this resulted in an increase in the model’s global accuracy and class-wise sensitivity, specificity, and precision.”

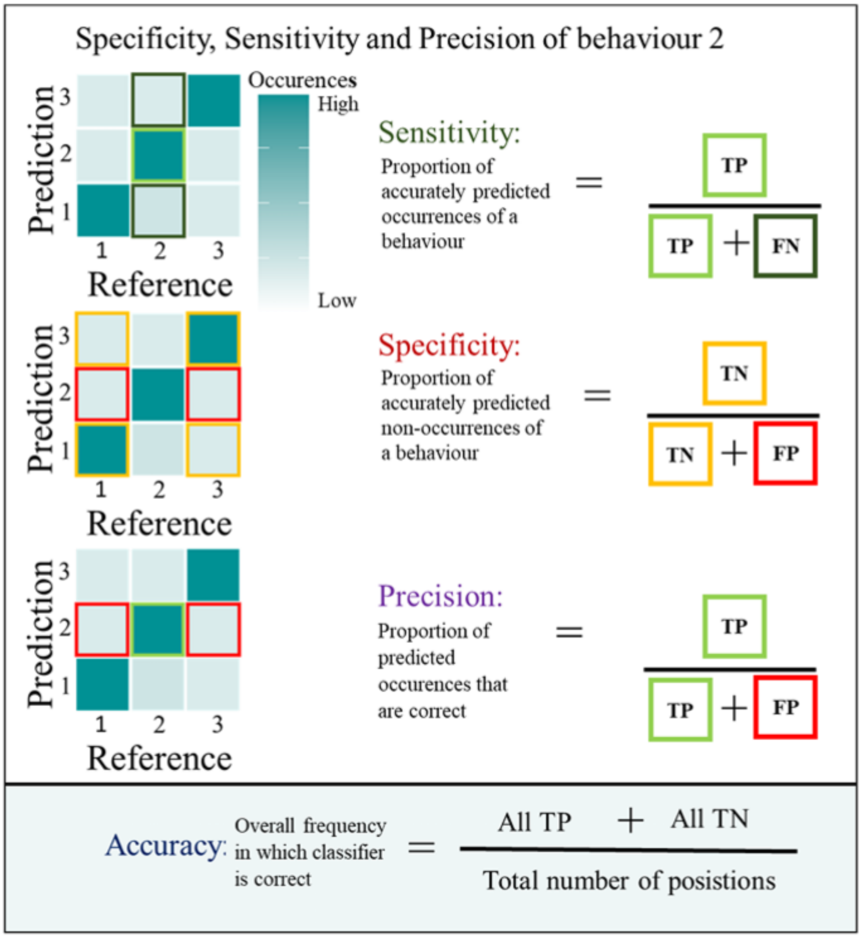

Figure 1. Example calucaltion of global accuracy, state-wise sensitivity, specificity, and precision using confusion matrices. Example calculation of state-wise sensitivity, specificity and precision for behavior 2 (in our case foraging) alongside global accuracy using confusion matrices. The confusion matrix colour fills indicate the idealized distribution of the data, with dark squares in the diagonal representing high concentrations of data correctly predicted and clear squares at the edge indicating low concentrations of incorrectly predicted data. TP (true positive – light green outline): number of predictions where the classifier correctly predicts the positive class as positive, TN (true negative – yellow outline): number of predictions where the classifier correctly predicts the negative class as negative, FP (false positive – red outline): number of predictions where the classifier incorrectly predicts the negative class as positive, FN (false negative – dark green outline): number of predictions where the classifier incorrectly predicts the positive class as negative.

RESULTS

We recovered a total of 151 Red-billed Tropicbird foraging trips with both GPS and auxiliary data, and another 933 trips with GPS data only (Table 1). Within the dataset informed by auxiliary sensors, we were able to classify 83.7% of the GPS positions to either resting, foraging or travelling, representing 10.4% of the complete dataset (including birds equipped only with GPS loggers). After leaving out 10% of positions with known behaviors for model validation, the maximum percentage of supervision within the informed and complete GPS datasets were 75% and 9%, respectively.

Table 1. Sensor sample sizes and inferred behavioral states. From left to right, auxillary sensor set-up, total number of tracked birds with specified auxillary sensor set-up alongside total sensor set-up deployments, total number of foraging trips, total number of registered GPS positions registered, and the number and percentage of GPS positions with known resting, foraging, and travelling states based on the combination of sensors used. ACC indicates accelerometer, TDR indicates Time Depth Recorder, and WD indicates wet-dry data.

Auxiliary Sensor(s)	Birds	Deployments	Trips	GPS positions	Known resting	Known foraging	Known travel
None	345	420	933	447346	0	0	0
ACC + TDR	20	20	44	23555	15642 (66%)	826 (4%)	3743 (16%)
WD	26	31	91	31389	18767 (60%)	0 (0%)	5973 (19%)
ACC + TDR + WD	6	7	16	8539	5850 (69%)	390 (5%)	1962 (23%)
Total	**397**	**478**	**1084**	**510829**	**40259(8%)**	**1216 (<1%)**	**11678 (2%)**

Since tropicbirds were simultaneously tagged with up to 3 auxiliary sensors (across 2 devices), the behaviors of some positions were informed by multiple sensors (Table 2). Using our conservative classification criterion resulted in only 15 positions (out of 8539 positions defined simultaneously by multiple sensors) with incoherent information coming from different sensors (e.g. the accelerometer identified that the bird was resting while the wet-dry sensors identified the bird as flying), therefore the behavior of this position was left as unknown for the models. We extracted the highest percentage of GPS positions with known states when animals were tagged with all 3 sensors (wet-dry, accelerometry, and TDR). Accelerometers detected more foraging positions than TDR, recording dives that were shallow (0.78±0.36 m) and short (1.41±0.55 s) (Table 1,2). Wet-dry loggers detected the most resting and travelling positions (Table 1,2). Given the conditions for known states used, we did not predict foraging based on wet-dry data alone nor did we predict resting or travelling based on the TDR data alone (Table 2).

Table 2. Total number, percentage, and number of unique positions with behaviors inferred by each auxiliary sensor. The total number, percentage, and the number of positions uniquely identified as known resting, foraging, and travelling based on accelerometry (ACC), wet-dry state (WD) and time depth recorders (TDR). Percentages were calculated based on the total number of GPS positions with each sensor type. The unique number of positions indicates the number of positions that were uniquely identified as a given behavior by each sensor type given that some positions were informed by more than one sensor simultaneously.

Auxiliary Data	**Known resting**	**Known foraging**	**Known travel**
ACC	21490 (67%), unique 16264	1132 (4%), unique 107	5268 (16%), unique 3761
WD	23995 (60%), unique 18769	-	7917 (20%), unique 6410
TDR	-	1109 (3%), unique 0	-
Total	**40259**	**1216**	**11678**

As in the auxiliary datasets, the HMM results of all models consistently suggest that tropicbirds spend most of their time resting on water, followed by travelling and foraging (Fig. 2, S6). The transition probabilities between behavioral states also indicate that the probability of remaining in resting from one position to another (0.82±0.05) is much higher than remaining as travelling (0.76±0.05) and foraging (0.59±0.09), and this relationship becomes even stronger with the inclusion of known states (leading to 0.90±0.02, 0.79±0.05, 0.47±0.16 for resting, travelling and foraging respectively with the inclusion of 75% known states, S6). While the turning angle distribution remains similar for the three states with increasing semi-supervision, the distribution of step lengths for the foraging state changed, becoming more overlapped with that of travelling (Fig. 3). This suggests that step length may not be an appropriate metric for separating the behavior of travelling and foraging.

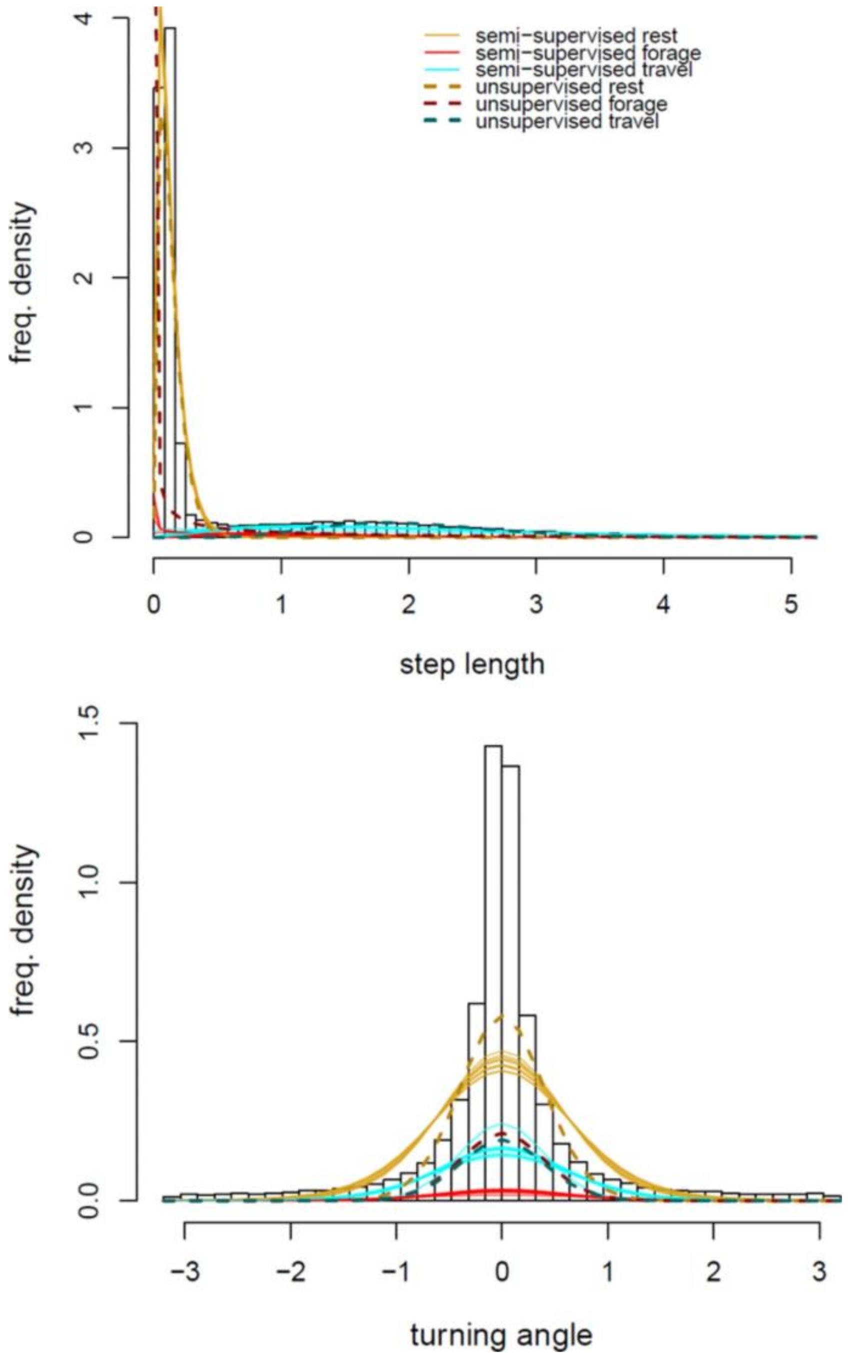

Figure 2. Confusion matrices of auxiliary data only models. Confusion matrices showing the mean and standard deviation in the number of reference behaviors against model predictions for iterations of the auxiliary data only models with no supervision (left) and with the highest amount of supervision (75%, right). Top row shows all positions while the bottom row shows positions with a classification probability over 0.9.

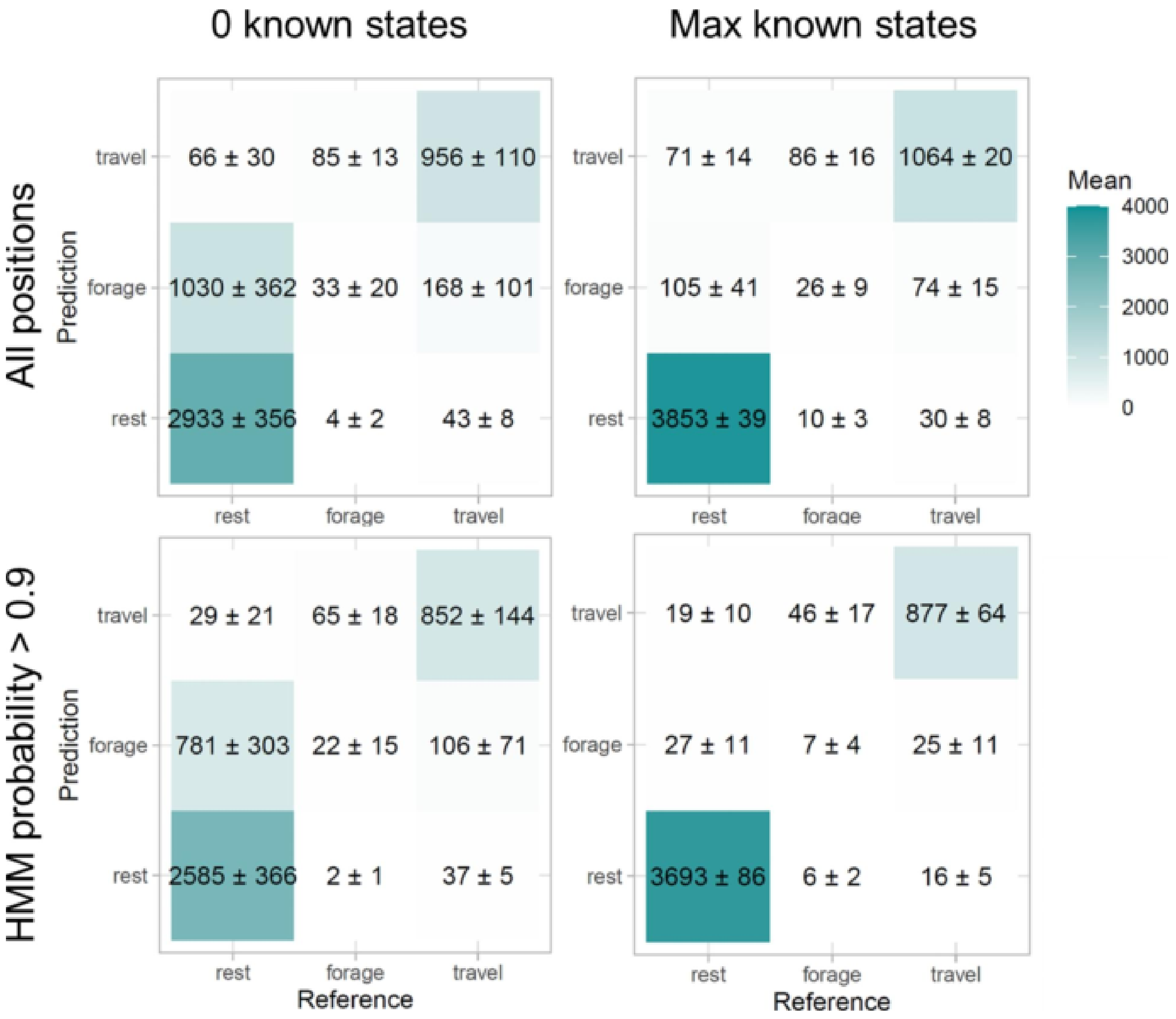

Figure 3. State-wise distributions of step and turning angle from HMMs without supervision and with maximum supervision (75%). State-wise distribution of the step length (top) and turning andgle (bottom) of resting (yellow), foraging (red) and travelling (cyan). Dashed lines indicate the model with no supervision while solid lines represent each of the 10 itterations of the model with maximum supervision (75%).

In the first series of models using only the data with auxiliary sensors, overall accuracy increased from 0.74±0.07 to 0.93±0.01 when the proportion of included known states increased from 0 to 0.75 (Figs 2, 4-5). This increase in model accuracy was mainly driven by the increase of sensitivity of resting (the proportion of resting correctly identified as such; from 0.73±0.03 to 0.96±0.01) and specificity of foraging (the proportion of non-foraging positions identified as such; from 0.77±0.08 to 0.97±0.01) with a small increase in the sensitivity of travel (from 0.82±0.09 to 0.91±0.01). The specificity of rest and travel of foraging remained relatively stable (going from 0.96± 0.01 to 0.97±0.01, and remaining at 0.96± 0.01), while the sensitivity of foraging decreased (from 0.26±0.14 to 0.21 ±0.08). However, these values of sensitivity and specificity were influenced by an uneven number of known resting, foraging and travelling positions, with far more resting and travelling positions than foraging. Therefore, despite the overall improvements to the model, the precision of foraging (the proportion of correctly identified foraging positions) remained low (increasing from 0.03±0.01 to 0.13±0.05), with a high number of resting or travelling positions misclassified as foraging (86±16 and 10±3 respectively) in comparison to the percentage of positions correctly classified (26±9%).

Restricting the dataset with HMM classification probability resulted in an increase in model accuracy (Fig. 6), although at the cost of reduced GPS positions for specific behavioral classifications (S7). Foraging positions had the lowest state-wise HMM probability values followed by travelling, and finally resting, resulting in an uneven loss of positions (S7). Moreover, even when reducing the probability of classification to only positions above 0.9, the overall precision of foraging still remained low (0 known states: 0.02±0.02, 0.75 known states: 0.12±0.07) (Fig. 3), suggesting that the number of correctly identified foraging positions was low in comparison to the misclassified resting and travelling positions.

In the second series of HMMs built using the complete GPS dataset, overall model accuracy increased from 0.77±0.01 to 0.85±0.01 when the inclusion of known states increased from 0% to 9% (Fig. 7, S8). This increase in accuracy was mainly driven by the increase of sensitivity of resting and foraging (from 0.76±0.01 to 0.86±0.01, and from 0.26±0.03 to 0.37±0.06, respectively) and specificity of foraging and travel (from 0.80±0.00 to 0.87±0.01, and from 0.82±0.01 to 0.87±0.01). The specificity of travel and of resting remained relatively stable (from 0.96±0.00 to 0.98 ±0.00, and from 0.96±0.01 to 0.98±0.00). As in the auxiliary data only model, the precision of foraging, increased with the inclusion of known states but remained low (from 0.03±0.01 to 0.06±0.01), and in comparison to the number of positions correctly classified (44±8), many resting or travelling positions were left misclassified as foraging (5±1 and 71±15, respectively; S8).

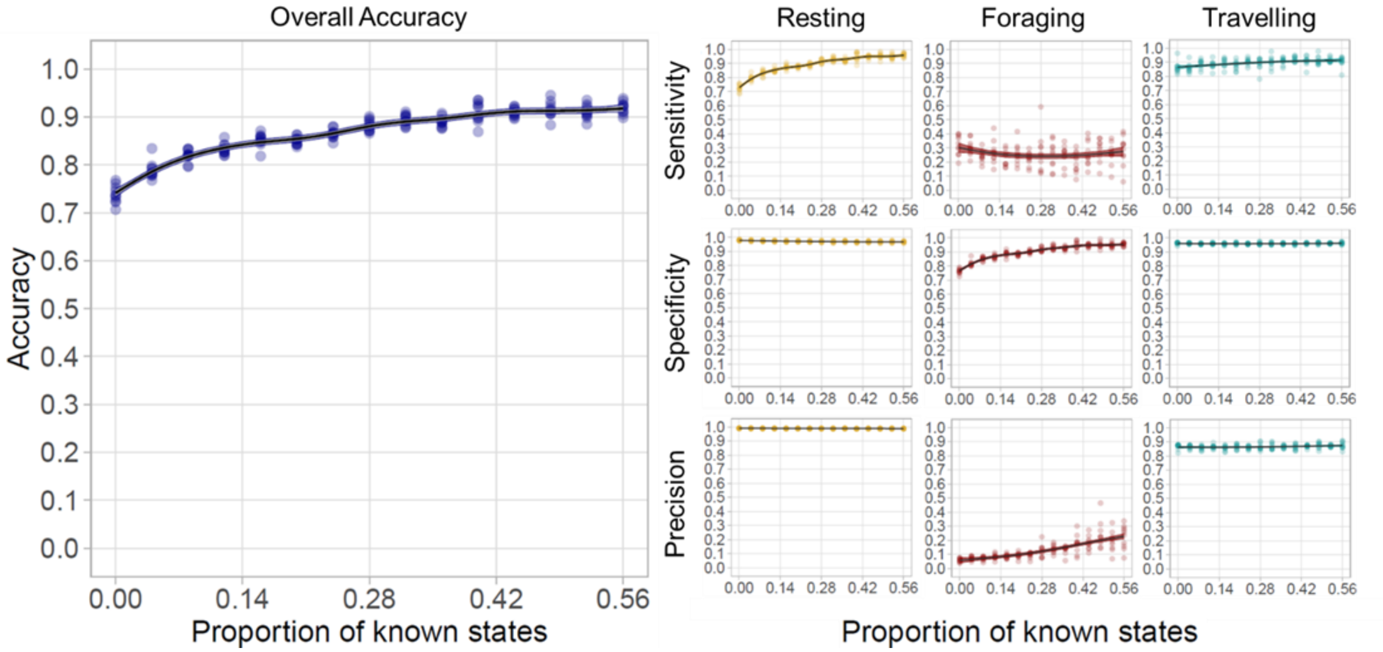

Figure 4. Accuracy, specificity, sensitivity and precision with incearing known states in the auxiliary data only models. Increase in global accuracy (blue, first column on left), as well as state-wise specificity, sensitivity and precision of resting (yellow; second column), foraging (dark red; third column) and travelling (cyan; forth column, on right) with an increasing proportion of known states included in the auxiliary data only model.

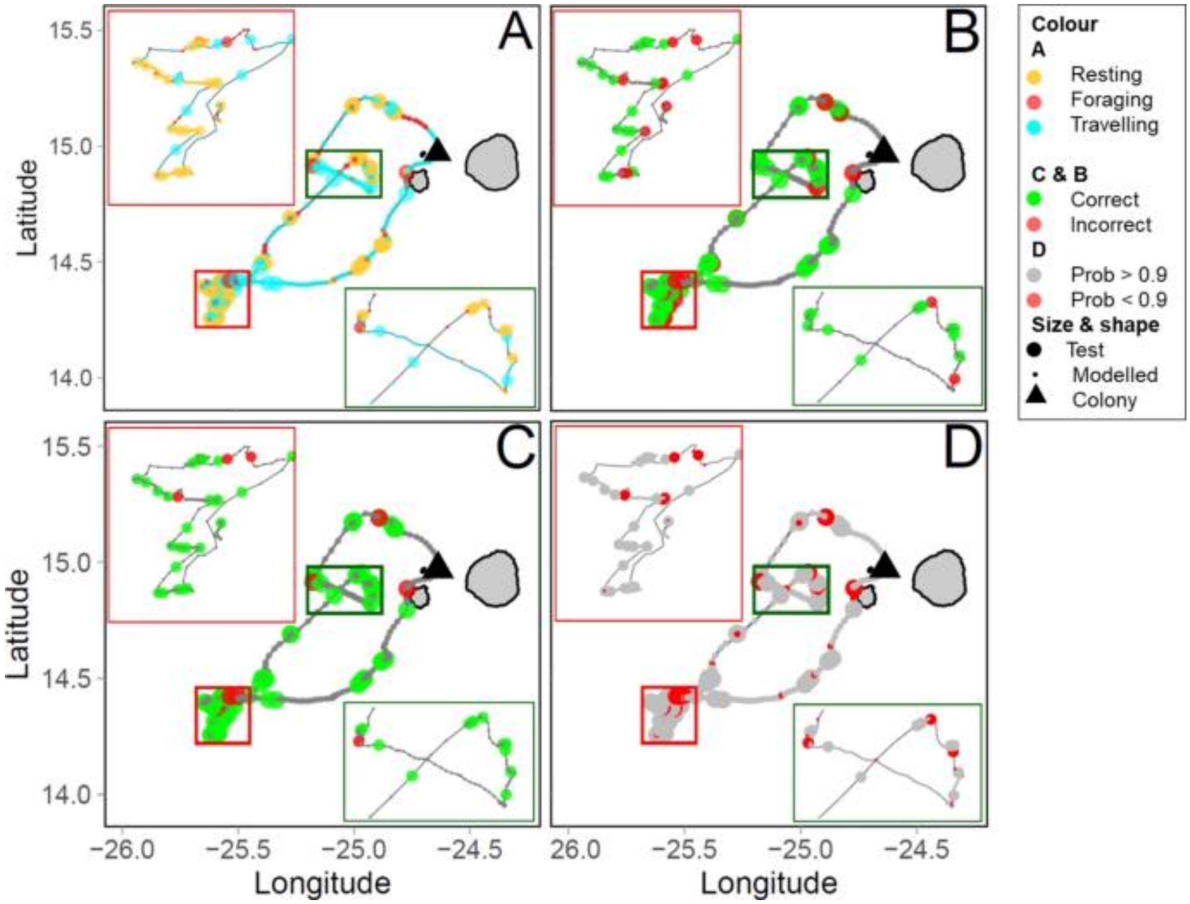

Figure 5. Example of a foraging trip from the dataset informed with auxiliary data. Large circles indicate positions used as test states to measure accuracy, while small circles represent those included in the model as known states. A) Positions colored by known states (yellow=resting, red=foraging, cyan=travelling). B) Positions coloured by correct (green) or incorrect (red) classification by a HMM with no known states (0%) informed by auxiliary data. C) Positions coloured by correct (green) or incorrect (red) classification by a HMM in which we included 75% known states informed by auxiliary data. D) Positions coloured by the HMM probability of classification, red points have a probability <0.9 while grey points have a probability > 0.9.

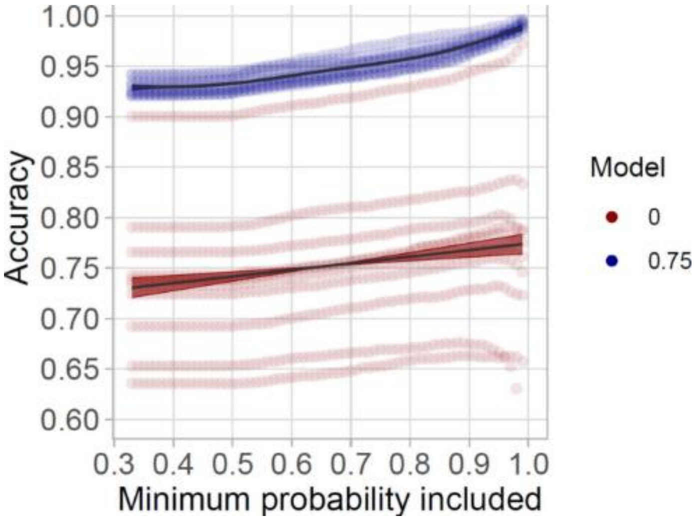

Figure 6. Increase in model accuracy with the removal of positions with low HMM probability. Increase in model accuracy upon the removal of positions with increasing minimum HMM probability values for behavioral classification. Blue: models with the highest percentage of supervision (75%), red: models without supervision (0%).

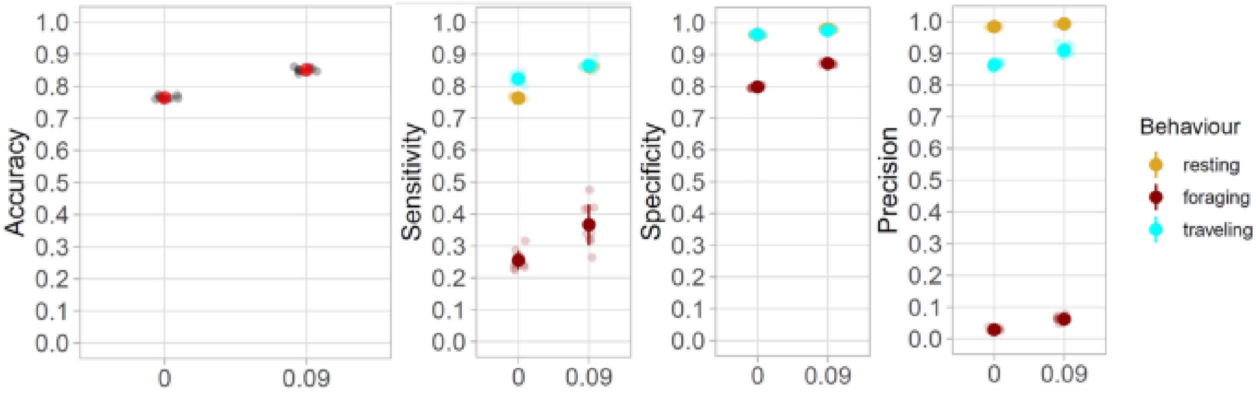

Figure 7. Increase in global accuracy and state-wise sensitivity, specificity and precision in complete dataset. From left to right, increase in global accuracy (A), and state-wise sensitivity (B), specificity (C), and precision (D), of resting (yellow), foraging (dark red) and travelling (cyan) states without and with the maximum proportion of known states in the complete GPS dataset.

DISCUSSION

We show that semi-supervising HMMs with data from auxiliary sensors, such as accelerometer, TDR, and wet-dry sensors can dramatically improve a state-space model's global accuracy and state-wise sensitivity and specificity in the classification of GPS tracking data into behavioral states, signifying that the proportion of both true positive and true negative behavioral classification increased. We found that even at small proportions, semi-supervision improved behavioral annotation, although high accuracy (> 0.90) was only reliably achieved with over 32% of known states. Despite this overall increase in accuracy, the foraging behaviors were poorly identified, with state classifications having low sensitivity (0.24±0.17) and precision (0.13±0.05), even with the highest percentage of supervision (75%), indicating a high misclassification rate such that many positions classified as foraging were actually resting or travelling. This suggests that tropicbirds may not use ARS while foraging, but rather forage opportunistically throughout their trips. The exclusion of positions with low HMM probability (<0.90) alone was not sufficient to improve the classification of the foraging behaviors, further underlining the difficulties in the classification of this behavior without auxiliary data in species where decision-making is on the go.

Overall model accuracy

With semi-supervision, the models reached overall accuracy levels similar to previous studies on species with commuting trips (e.g. [17,41], S1, S3). The overall accuracy was especially high with both semi-supervision and the exclusion of positions with HMM state classification probabilities of <0.90 (reaching 0.98±0.01), suggesting that combined use of semi-supervision with auxiliary data and thresholds on HMM state classification probability can significantly improve behavioral classification. However, high global accuracy was biased by the correct classification of resting behavior, which was overly-represented in both the supervised and validation datasets, underlining the importance of state-wise performance measures.

Behavioral classification and inference

Although semi-supervision improved the overall accuracy of the models, the improvement in the inference was not equal between the three basic behavioral states. While there were strong increases in the sensitivity of resting and the specificity of foraging, the inference of travelling only improved slightly. There was a much steeper decrease of resting positions misclassified as foraging (from 1030±362 to 105±41 with 75% supervision) compared to travelling positions misclassified as foraging (from 168±101 to 74±15 with 75% supervision). This suggests that model semi-supervision mainly helped distinguish between resting and foraging, while confusion between foraging and travelling remained. This is also apparent in the changes of the state-wise distributions of step length with the increase of semi-supervision, with a separation in the distributions of resting and foraging while the distribution of foraging and travelling continued to highly overlap. Without the use of other movement metrics, these overlapping or 'noisy' labels essentially cannot be distinguished with HMMs [42]. This suggests that step length is not a good movement metric for separating foraging and travelling behavior in this species, and highlights the challenges associated with delineating opportunistic feeding events in seabirds foraging on the wing.

Despite improvements to overall accuracy, we found much lower sensitivity and precision of foraging than what was previously reported from studies using HMMs to classify the foraging behavior of other seabirds [17,23,41]. The sensitivity of foraging for the semi-supervised models was low and was not improved by semi-supervision, declining from from 0.26±0.14 to 0.21 ±0.08 with the highest percentage of supervision (75%), suggesting that many foraging positions were undetected and that this number is not reduced by semi-supervision. Moreover, the precision of foraging behavior increased from 0.03±0.01 to 0.13±0.05 with the highest percentage of supervision (75%), but did not saturate, indicating that this level of semi-supervision was insufficient to prevent erroneous inference of foraging states.

Difficulty in correctly classifying foraging positions may can be discussed at both model and ecological levels. At the model level, this was caused by a large overlap between the state-wise distribution of foraging and that of the other behaviors, signifying that, based on step length and turning angle alone, HMMs were unsuccessful at distinguishing the signal of foraging from the other behaviors[42]. At the ecological level, this overlap between behavioral signals may stem from the distribution of tropicbird's prey and foraging strategy compared to other non-tropical seabirds, such as large shearwaters, auks or gannets [17,23,41]. Tropicbirds are offshore specialists that mainly forage on flying fish [28], in waters of low-productivity [43,44], making their distribution highly unpredictable both in time and space. Such patterns are possibly driven by the low predictability of prey distributions in tropical oceans, resulting in low foraging site fidelity and a prominence of looping trips, as observed in many other tropical species [24,25,45–47]. This contrasts with the commuting trips of non-tropical seabirds who concentrate foraging in predictable areas associated with high productivity [48]. Some tropical species often forage opportunistically, with prey-capture attempts occurring within directional transit [24,49], making it difficult for behavioral models to differentiate foraging from travelling locations. Although opportunistic foraging appears to cause a higher classification error for foraging compared to other behaviors in tropical sulids [16,26,37], the error rate in tropicbirds is particularly high, suggesting that this species may use opportunistic foraging more frequently than other tropical species.

If not addressed, the low sensitivity and precision of foraging in these models can have important implications in conservation and management decisions. Foraging areas are often the target of spatial management plans because of their ecological importance for species, and therefore their correct identification is critical [1,9,10]. In models with low foraging sensitivity, many foraging positions are going undetected, suggesting that in theory these models may underestimate total foraging ranges. However, previous studies with high misclasssification rates have demonstrated strong spatial overlap between true foraging positions extracted from TDRs and modelled foraging areas [37,41], suggesting this may not be an issue in practical terms. This may be because opportunistic foraging positions are well dispersed throughout trips, resulting in a higher than usual overlap between foraging and home range areas [25]. More importantly, in this study the precision of foraging also remained low, leaving a high percentage of resting and travelling positions erroneously identified as foraging. This may have important implications for habitat modelling studies, since resting and travelling positions misclassified as foraging may be obscuring important behavior-specific habitat relationships [50] and potentially time-activity budgets [51].

Improving behavioral classification for opportunistic foragers

Whilst semi-supervised learning can improve association between observed movement metrics and desired behavioral states, limitations exist. In such instances, the inclusion of additional auxiliary sensors, such as TDR, accelerometers, and/or cameras, may be necessary across the full dataset to identify less frequent behaviors such as prey-capture attempts, and achieve satifcatory model performance. If the sampling resolution of the GPS positions is greater than the duration of certain behaviors, the signal of these behaviors may be obscured by others associated to the same GPS fix, and thus the application of auxiliary sensors may need to be coupled to increases in the temporal resolution of GPS locations. Although HMMs have been shown to be relatively robust against reductions in resolution in comparison to other methods, such as deep learning [16,17], the infrequency of diving behavior may make it especially difficult for the models to correctly identify [52]. In our study, dives only lasted 1.4±0.6 s seconds and were infrequent and dispersed (just 1.2±1.3 dives per GPS position, and only 22% of dives were recorded within the same or in adjacent GPS positions), suggesting that foraging may be obscured by resting and travelling if dive-specific auxiliary data is not available. Similar observations have been made in the attempt to distinguish mating behavior in GPS-tracked deer [53] or in the differentiation of natural and non-natural foraging in seabirds [3]. In these cases, the addition of more complexe auxiliary sensors (such as cameras, TDRs, and accelerometers etc) may be needed to truly identify these particular behaviors. Auxiliary devices have been used in combination with GPS data to identify foraging behaviors in many seabirds and seals, which may otherwise be impossible [3,32,54,55].

In the case of opportunistic foragers, such as Red-billed Tropicbirds, the identification of foraging habitat based solely on dives may underestimate the foraging area used by these species. If prey-capture attempts occur opportunistically within directional transit, it may be ineffective to separate directional movements from foraging. This is reflected by the proportionally small improvement of model classification when it came to separating foraging from travelling with semi-supervision. The relative homogeneity of tropical oceans may render the identification of foraging behavior meaningless, since birds actually seem to search for prey over the entire looping trips. In this regard, teasing apart resting from non-resting behavior may be enough for subsequent analyses of foraging habitat use and preferences in opportunistic foragers.

Guidance for the implementation of semi-supervised behavioral classification

Foremost, semi-supervised learning can improve associations of observed movement metrics with desired behavioral states, but, only if the chosen metrics are distinct for each of the states. If the metrics highly overlap (as the step lengths of foraging and travelling did in our study), overall improvements will be limited. Therefore, it is important to choose the right sensors, recording frequency, and movement metrics to answer specific research questions a priori to undertaking the research in question. This, of course, is easier said than done, since the choice of such metrics will also depend on the ecology and behavior of the species in question, which may be unknown to the researcher before the commencement of the study. Therefore, we suggest combining both semi-supervision and model validation when possible, to make sure that the assumptions of the ecology of the species made at the beginning of the study are correct, and that movement metrics are accurately identifying the chosen behaviors.

Although all auxiliary sensors helped improve model accuracy, each sensor came with its own advantages and disadvantages, which vary with the specific study question and ecology of study species. Here, wet-dry loggers generated the largest number of positions with known behaviors alone, primarily because tropicbirds spend the majority of time resting on water

[28]. In seabird species that spend more time on the wing, wet-dry sensors may detect fewer resting positions, but can still be used to identify potential prey capture attempts within foraging [3,23]. TDR loggers, on the other hand, gave accurate measures of foraging attempts but could not detect when the bird was resting or travelling, and recorded fewer overall dives than accelerometers, possibly because of missed shallow dives [56] or the capture of flying fish in air [30]. In species with deeper and more complex dives, TDR devices can greatly improve behavioral classifications [57].

Accelerometers where the only auxiliary sensor that allowed for the detection of all three behavioral states. However, the complexity of processing accelerometer data is much higher than wet-dry loggers and TDRs. Transforming accelerometer data into behavioral states required the additional step of extracting periods of flapping, diving, and resting from the accelerometer signals, a process which in our case, was semi-supervised by both WD and TDR data. This added an additional layer of complexity and potential error to modelling the raw accelerometry data while also highlighting the importance of WD and TDR devices in identifying behavior. Therefore, the selection of auxiliary sensors to use for a given study should consider both the complexity of the study question, and the ecology of the study species.

Future research

In the present study, we highlight the benefits of semi-supervision in HMMs while creating awareness of possible misclassifications and the importance of cross validation. Whilst using real world tracking data allowed us to demonstrate the applied ramifications of this in a biological context, we were unable to measure the absolute increase in accuracy related to semi-supervision and suggest that a follow-up simulation study could greatly improve our overall understanding of limitations of HMMs. Such a study would comprise of creating datasets with increasing levels of overlap between state distributions, and measuring how HMMs of these datasets react to increasing semi-supervision. This would allow researchers to create guidelines based on the initial distribution of data to understand if, and/or how much semi-supervision is needed to improve the overall classification. Since data would be simulated, issues relating to uneven datasets and possible introduced errors from inferring the known behaviors from auxiliary datasets would be eliminated. Such an analysis could also be used to make inferences on the limitations of HMMs in situations beyond movement ecology, and we recommend this as a more generalised future study.

CONCLUSIONS

Semi-supervision increased model accuracy, even when positions with inferred behaviors represented a small proportion of the dataset. This increase was uneven among the three basic behavioralstates, with stronger increases in the sensitivity of resting and the specificity and precision of foraging, while travelling remained relatively stable. Despite these improvements, the behavioral inference levels of foraging remained low compared to those of species using commuting foraging trips and may not be enough for the analysis of foraging habitat use and preferences. Precaution should be taken in the identification and use of foraging behavior states in opportunistic foragers, such as species searching for prey across a homogeneous environment. The nature of the foraging behavior of species foraging on the go may lead to an over-fitted identification of foraging behavior. Indeed, we suggest that in this type of species, distinguishing resting from non-resting behaviors should be enough for subsequent analyses of foraging habitat use and preferences. However, even in these cases, the use of semi-supervision can greatly improve behavioral inferences and the choice of auxiliary sensor(s) will depend on the specific ecology of species, deployment logistics, processing time, and costs.

LIST OF ABBREVIATIONS

HMM : Hidden Markov Models

TDR : Time Depth Recorders

GPS: Global Positioning System

ARS: Area Restricted Search

OFT: Optimal Foraging Theory

EmbC: Expectation-maximization Binary Clustering

RST: Residence in Space and Time

FPT: First Passage Time

TP: True Positive

TN : True Negative

FP: False Positive

FN: False Negative

ACC: Accelerometry

WD: Wet-dry

ETHICS APPROVAL

All procedures involving animal manipulations were in accordance with required European legislation. All research and monitoring was conducted under permission from the Direção Nacional do Ambiente from Cabo Verde "Autorização N.º91/2018; Autorização N.º107/2019; Autorização N.º016/DNA/2020".

DATA AVAILABILITY

GPS Tracking data is available in the Seabird Tracking Database of Birdlife International. All the R workflow is available at:

https://github.com/SarahSaldanha/Semi_supervised_HMM

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AUTHOR’S CONTRIBUTIONS

SS, SC and JGS conceived the ideas and designed methodology; SS, TM and SC collected the data; SS analysed the data; SS led the writing of the manuscript. JGS and SC supervised the research. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

S1. Review table of behavioral validation

Article	Loc	Behaviors	Resolution	Cross-validation	Species	Model	Overall	Foraging/Active										
								AUC (%)	Sensitivity (%)	Specificity (%)	Precision %	Negative Predictive Value %	False Positive Rate	False Negative Rate	FI	Kappa	Mean Levenshtein distance	Balanced Accuracy
Dean et al. 2012	Britain and Ireland	Resting, foraging, travelling	5-10 min interpolated to 1 min	TDR	Manx Shearwater (*Puffinus puffinus*)	HMM			96									
Browning et al. 2018	UK and Ireland	Diving or non-diving	100 s	TDR	Common Guillemot (*Uria aalge*)	Supervised deep learning (best model)		0.92 (training), 0.90 (validation)	68	92	67	93						
						HMM			67 (2 states), 84 (3 states)	53 (2 states), 42 (3 states)	87 (2 states) , 87 (3 states)	28 (2 states), 32 (3 states)						
						Speed and tortuosity thresholds			0-2	77-81	0-47	17-19						
					European Shag (*Phalacocorax aristotelis*)	Supervised deep learning (best model)		0.95 (training), 0.91 (validation)	67	94	64	95						
						HMM			57 (2 states), 81 (3 states)	78 (2 states), 60 (3 states)	95(2 states), 93 (3 states)	32 (2 states), 34 (3 states)						
						Speed and tortuosity thresholds			0-29	78- 86	13-19	14-Oct						
					Razorbill (*Alca torda*)	Supervised deep learning (best model)		0.89 (training), 0.86 (validation)	55	91	51	92						
						HMM			57 (2 states), 75 (3 states)	62 (2 states), 46 (3 states)	87 (2 states), 88 (3-states)	87 (2 states), 88 (3 states)						
						Speed and tortuosity thresholds			0-5	72-86	0-45	14-Oct						
Bennison et al. 2018	Ireland	Resting, foraging, travelling	2 min	TDR	Northern Gannet (*Morus bassanus*)	First passage time			31				57	69				
						K- Means Clustering			38				74	62				

Article	Loc	Behaviors	Resolution	Cross-validation	Species	Model	Overall	Foraging/Active										
								AUC (%)	Sensitivity (%)	Specificity (%)	Precision %	Negative Predictive Value %	False Positive Rate	False Negative Rate	FI	Kappa	Mean Levenshtein distance	Balanced Accuracy
						Speed and tortuosity thresholds			77				68	23				
						HMM			81				63	19				
						EMbC			51				74	49				
						KUD												
						Machine learning			22	95	46	87						
Adams et al. 2020	Hawaii	Resting, foraging, travelling	2 min	TDR	Brown Booby (*Sula Leucogaster*)	Residence in space and time			~ 60					~ 40				
			2 min		Red-footed Booby (*Sula sula*)	Residence in space and time			~ 80					~ 20				
			3 min	Non-validated	Red-tailed Tropicbird (Phaethon aethereus)													
			15 min		Laysan Albatross *(Phoebastria immutabilis*)													
			3 min		Wedge-tailed Shearwater (*Ardenna pacifica*)													
Austin et al. 2021	Cayman Islands	Resting, foraging, travelling	30 s or 2 min (interpolated to 2 min)	TDR and WD	Red-footed Booby (Sula sula)	HMM			77					23				
					Brown Booby (Sula Leucogaster)	HMM			80					20				
Torres et al. 2013	New Zealand	Resting, foraging, travelling	2 min	immersion (resting only)	Buller's Albatross (*Thalassarche bulleri*)	Speed and tortuosity thresholds												
Ironside et al. 2017	US	Food caching or not (directed movements and search)		Video footage	Cougar (*Puma concolor*)	Path Identification Index	81				75	97						
Roy et al., 2022	Peru and Brazil	Resting, foraging, travelling	1, 15, 30s	TDR	Peruvian Booby (*Sula variegata*)	FPT		62(1s), 73(30s)										
						HMM		86(1s), 84(30s)										

Article	Loc	Behaviors	Resolution	Cross-validation	Species	Model	Overall	Foraging/Active										
								AUC (%)	Sensitivity (%)	Specificity (%)	Precision %	Negative Predictive Value %	False Positive Rate	False Negative Rate	FI	Kappa	Mean Levenshtein distance	Balanced Accuracy
						FCNet		89(1s), 82(30s)										
						CNNet		94(1s), 85(30s)										
						UNet		96(1s), 91(30s)										
					Guanay Cormorant (*Leucocarbo bougainvilli*)	FPT		61(1s), 56(30s)										
						HMM		78(1s), 75(30s)										
						FCNet		87(1s), 65(30s)										
						CNNet		92(1s), 74(30s)										
						UNet		93 (1s) 88 (30s)										
Dragon et al. 2012	Kerguelen Island	Foraging and not foraging	6 h argos	TDR	Southern Elephant Seal (*Mirounga leonina*)	FPT											40	
						HMM											56	
			20 min			FPT											~ 65	
						HMM											71	
Hurme et al. 2019	Gulf of California, Mexico	Foraging and travelling	15s	Biosonar calls	Mexican Fish-Eating Bats (*Myotis vivesi*)	K- Means clustering												63
						First-passage time												62
						EMbC												63
						HMM												67
						Change point analysis												64
Carter et al. 2016	UK Ireland	Active and inactive	1 min	TDR	Northern Gannet (*Morus bassanus*)	Speed and tortuosity thresholds					49			51				
Lerma et al. 2020	Rapa Nui	Resting, intensive foraging, extensive foraging, travelling	4 min	TDR	Masked Booby (*Sula dactylatra*)	EMbC			53		53							

Article	Loc	Behaviors	Resolution	Cross-validation	Species	Model	Overall	**Foraging/Active**										
								AUC (%)	**Sensitivity (%)**	**Specificity (%)**	**Precision %**	**Negative Predictive Value %**	**False Positive Rate**	**False Negative Rate**	**FI**	**Kappa**	**Mean Levenshtein distance**	**Balanced Accuracy**
Dragon et al., 2012	Kerguelen Island	Intensive foraging and extensive foraging	20 min	TDR	Southern Elephant Seal (*Mirounga leonina*)	State-space model												
Torres et al. 2017	NewZealand	Resting, foraging, transit	5 min	Observation-based classification from 3 researchers.	Grey-headed Albatross (*Thalassarche chrysostoma*)	Residence in space and time												
de Weerd et al. 2015	Netherlands	Foraging, lying, standing, walking	1 min, 12 s and 2 s intervals	Direct observation	Cow (*Bos taurus*)	Classification and regression trees												
Hance et al. 2021	US	Active inactive	15 min	VHF Tracking and direct observation of resting	Fisher (*Pekania pennanti*)	HMM					83							
Beyer et al. 2013	Canada	Encamped or exploratory	2 h	Simulation analysis	Moose (*Alces alces*)	Bayesian state-space models										0.49 to 0.72 (mean 0.61)		
Jonsen et al. 2016	-	Foraging and travelling	3 h	Simulation analysis	Weddell seals (*Leptonychotes weddellii*)	Hierarchical and non hierarchical state space models												
Gurarie et al. 2009	Kuril Islands	-	variable interval (Argos)	Non-validated (for the norther seals), simulation analysis	Northern fur seal (*Callorhinus ursinus*)	Change point analysis												

S2. Data Processing

GPS

We processed and standardised GPS tracks from 397 breeding Red-billed Tropicbirds. The GPS tracks were cleaned of erroneous positions using a speed filter (30m/s) and split into discrete foraging trips with periods in the nest between trips omitted. Incomplete trips were also included in the analysis if they were over 30 minutes long. Although GPS tracks were set to record positions every 5 minutes, poor satellite reception resulted in gaps in the data. Therefore, we used linear interpolation to regularise the data to a common time interval of 5 minutes for every segment of data with gaps less than 20 minutes before fitting the behavioral models.

Accelerometers

We recovered 27 axy-trek devices from 26 individuals and split these into 60 foraging trips based on the GPS positions (Table 1). These devices contained both a tri-axial accelerometer which recorded acceleration in the surge (X, forwards/backwards), heave (Z, dorso/ventral) and sway (Y, side to side) axis at a frequency of 25 Hz and a TDR sensor which recorded pressure at a frequency of 1Hz.

We classified the accelerometery signals into behavioral states with a random forest model (RF) using the ‘randomForest’ package in R (Liaw & Wiener, 2002). To build the RF model, we used a training dataset with supervised behavioral classifications to predict the behaviors of the complete accelerometer dataset. To create the training dataset, we used a subset of 16 trips from 6 individuals which had wet-dry data in addition to accelerometery and TDR data (Table 1). Using the wet-dry and TDR data to validate our classifications, we manually classified each signal into 3 behaviors in the software Framework4 (Walker et al., 2015): flying (dry, high acceleration in X and Z), on water (wet, low acceleration in X and Z) and diving (wet, high acceleration in X and Z and high pressure) based on the patterns in static acceleration for X, Y and Z as well as their derived variables pitch and roll, and, finally, the wet-dry and TDR pressure data.

Since the device was deployed on the tail of the bird and not in the back, the pitch and roll, which usually indicate whether the bird was standing vertically or horizontally and whether the bird was positioned with its dorsal side up or down, respectively, more likely indicated strong halting or turning. Pitch and Roll were calculated based on the following equations:

$$Pitch = Arctan\sqrt{\frac{X}{Y^2 + Z^2}} * \frac{180}{\pi}$$

$$Roll = Arctan\sqrt{\frac{Y}{X^2 + Z^2}} * \frac{180}{\pi}$$

To reduce the number of false positives in the random forest model, we only manually annotated dives when there was a visual change in pressure recorded by the TDRs and a change from dry to wet. However, shallow dives are underestimated by TDR (Cianchetti-Benedetti et al., 2017) and wet-dry data was recorded at relatively coarse intervals (6s), therefore we expected more dives to be predicted by the model than those identified manually.

Next, we segmented both the training dataset and the complete dataset into variable segment lengths using a change point model using the R package ‘cpm’ (Ross & Gordon, 2020) following the methods described in Born et al. 2014. We chose to use variable-time and not fixed-time segments to assign boundaries between behavioral classes since variable-time segments have been shown to improve the classification of some behaviors (Born et al. 2014).

For each of these segments, we then calculated various metrics to be fed into a RF model. We calculated the mean, standard deviation, maximum, minimum, cumulative positive, cumulative negative and cumulative absolute values of the X, Y, Z, pitch, roll and depth signals of the accelerometer data. In addition, we calculated two measures of dynamic body acceleration (DBA) for each of the sections: the overall dynamic body acceleration (ODBA) and vectorial dynamic body acceleration (VeDBA). These were calculated by taking a running mean of the raw data from each accelerometer axis across a 2-sec period to calculate the static acceleration, and then subtracting the static acceleration values from the raw acceleration values for that time period. ODBA and VeDBA were then calculated as follows:

$$VeDBA = \sqrt{(a_X^2 + a_Y^2 + a_Z^2}$$

$$ODBA = a_X + a_Y + a_Z$$

We then matched the behavioral classifications of the training dataset to each of the segments and ran a RF model to predict the behaviors of the unclassified accelerometer data. We used 1000 trees and optimized the number of predictor variables that were randomly selected at each node using the function ‘mtry’ from the ‘randomForest’ package in R (Liaw & Wiener, 2002). This function ran separate models with 0 to 15 predictor variables/node, allowing us to select the number of predictor variables which resulted in the lowest out of the bag (OOB) error. The OOB error is a built-in test of accuracy, in which bootstrapping is used to calculate classification errors within the RF models and estimates the overall accuracy of the model by holding back and comparing the classification of random subsets of the training dataset, selected with replacement. We also estimated the importance of the predictor variables using the function 'varImpPlot' from the 'randomForest' package in R (Liaw & Wiener, 2002) which measures the mean decrease in accuracy based on the change in the prediction error when the OOB data for that variable are re-arranged and all other variables are left unaffected. We classified the behaviors of the complete accelerometery dataset using the 'predict' function. To reduce the amount of misclassification, we only assigned the behaviors to a segment when the probability of said behavior was over 0.65. This threshold was selected as a trade-off between accuracy and the proportion of unclassified segments.

We then matched the accelerometery data to each GPS position by summarizing the proportion of time flying, on water and the total number of dives for each time period between interpolated GPS positions.

TDR

The time-depth recorder (TDR) data of the 27 Axy-treck tags were also used to identify diving identify dives based on the pressure sensor alone. Since the tags were deployed over a long period, the atmospheric pressure at sea-surface (Pm in mBar) was expected to vary greatly between trips. Therefore, we estimated Pm for each trip as the mode [pressure] and calculated depth (D in m) using the relationship: $D = 0.01 \times (Pm - Pa)$, where 1 mBar pressure difference corresponds to 0.01 m depth difference. We corrected for surface drift using the zero-offset correction of the diveMove package in R (Luque & Fried, 2011). The pressure sensors were very sensitive and small differences in depth may result from preening, fast turns, and takeoff instead of dives. Therefore, only dives ≥0.2 m were considered.

We then matched the TDR data to each GPS position by counting the total number of dives for each time period between the interpolated GPS positions.

Wet-dry

Twenty-five individuals with GPS tracks were outfitted with Migrate GLS, resulting in 107 foraging trips with at least both types of data. Using conductivity, these devices detect whether they are in water or not every 6 seconds and record the timing of transitions from wet to dry or from dry to wet. We matched the wet-dry data to each GPS position by summarizing the proportion of time wet (PropWet) for the periods of time between each interpolated GPS position. We then eliminated PropWet data when the time gap from one point to the next was over 5 minutes (caused by gaps in the GPS data) (0.5% of the positions).

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S3. Additional validation metrics

Model	Accuracy	Sensitivity_Rest	Specificity_Rest	PosPredValue_Rest	NegPredValue_Rest	Precision_Rest	Recall_Rest	F1_Rest	Prevalence_Rest	DetectionRate_Rest
Full unsupervised	0.77± 0.01	0.76± 0.01	0.96± 0.01	0.98± 0.00	0.57± 0.01	0.98± 0.00	0.76± 0.01	0.86± 0.00	0.76± 0.00	0.58± 0.00
Full max. supervision (9%)	0.85± 0.01	0.86± 0.01	0.98± 0.00	0.99± 0.00	0.70± 0.01	0.99± 0.00	0.86± 0.01	0.92± 0.00	0.76± 0.00	0.65± 0.00
Informed unsupervised	0.74± 0.07	0.73± 0.09	0.96± 0.01	0.98± 0.00	0.54± 0.09	0.98± 0.00	0.73± 0.09	0.83± 0.06	0.76± 0.00	0.55± 0.07
Informed max. supervision (75%)	0.93± 0.01	0.96± 0.01	0.97± 0.01	0.99± 0.00	0.88± 0.02	0.99± 0.00	0.96± 0.01	0.97± 0.00	0.76± 0.00	0.72± 0.01

Model	DetectionPrevalence_Rest	BalancedAccuracy_Rest	Sensitivity_Forage	Specificity_Forage	PosPredValue_Forage	NegPredValue_Forage	Precision_Forage	Recall_Forage
Full unsupervised	0.59± 0.01	0.86± 0.00	0.26± 0.03	0.80± 0.00	0.03± 0.01	0.98± 0.00	0.03± 0.01	0.26± 0.03
Full max. supervision (9%)	0.66± 0.00	0.92± 0.00	0.37± 0.06	0.87± 0.01	0.06± 0.01	0.98± 0.00	0.06± 0.01	0.37± 0.06
Informed unsupervised	0.56± 0.07	0.85± 0.04	0.26± 0.14	0.77± 0.08	0.03± 0.01	0.98± 0.00	0.03± 0.01	0.26± 0.14
Informed max. supervision (75%)	0.73± 0.01	0.96± 0.00	0.21± 0.08	0.97± 0.01	0.13± 0.05	0.98± 0.00	0.13± 0.05	0.21± 0.08

Model	F1_Forage	Prevalence_Forage	DetectionRate_Forage	DetectionPrevalence_Forage	BalancedAccuracy_Forage	Sensitivity_Travel	Specificity_Travel	PosPredValue_Travel
Full unsupervised	0.05± 0.01	0.02± 0.00	0.01± 0.00	0.20± 0.00	0.53± 0.01	0.82± 0.01	0.96± 0.00	0.86± 0.01
Full max. supervision (9%)	0.11± 0.02	0.02± 0.00	0.01± 0.00	0.13± 0.01	0.62± 0.03	0.87± 0.01	0.98± 0.00	0.91± 0.02
Informed unsupervised	0.05± 0.02	0.02± 0.00	0.01± 0.00	0.23± 0.08	0.51± 0.06	0.82± 0.09	0.96± 0.01	0.87± 0.02
Informed max. supervision (75%)	0.16± 0.06	0.02± 0.00	0.00± 0.00	0.04± 0.01	0.59± 0.04	0.91± 0.01	0.96± 0.01	0.87± 0.02

Model	NegPredValue_Travel	Precision_Travel	Recall_Travel	F1_Travel	Prevalence_Travel	DetectionRate_Travel	DetectionPrevalence_Travel	BalancedAccuracy_Travel
Full unsupervised	0.95± 0.00	0.86± 0.01	0.82± 0.01	0.84± 0.01	0.22± 0.00	0.18± 0.00	0.21± 0.00	0.89± 0.01
Full max. supervision (9%)	0.96± 0.00	0.91± 0.02	0.87± 0.01	0.89± 0.01	0.22± 0.00	0.19± 0.00	0.21± 0.00	0.92± 0.01
Informed unsupervised	0.95± 0.02	0.87± 0.02	0.82± 0.09	0.84± 0.04	0.22± 0.00	0.18± 0.02	0.21± 0.03	0.89± 0.04
Informed max. supervision (75%)	0.97± 0.00	0.87± 0.02	0.91± 0.01	0.89± 0.01	0.22± 0.00	0.20± 0.00	0.23± 0.01	0.94± 0.01

Model	VUS	weighed_F1	averaged_F1	multiclass_AUC	pairwise_AUC_RestForage	pairwise_AUC_RestTravel	pairwise_AUC_ForageTravel	AUC_Rest_all	AUC_Forage_all
Full unsupervised	0.16± 0.02	0.84± 0.00	0.86± 0.00	0.78± 0.01	0.77± 0.01	0.93± 0.00	0.63± 0.03	0.86± 0.00	0.53± 0.01
Full max. supervision (9%)	0.27± 0.05	0.90± 0.01	0.92± 0.00	0.86± 0.01	0.88± 0.01	0.97± 0.00	0.74± 0.03	0.92± 0.00	0.62± 0.03
Informed unsupervised	0.15± 0.07	0.82± 0.05	0.83± 0.06	0.76± 0.04	0.73± 0.09	0.93± 0.02	0.64± 0.03	0.85± 0.04	0.51± 0.06
Informed max. supervision (75%)	0.19± 0.07	0.94± 0.01	0.97± 0.00	0.89± 0.02	0.95± 0.02	0.99± 0.00	0.75± 0.04	0.96± 0.00	0.59± 0.04

Model	AUC_Travel_all
Full unsupervised	0.89± 0.01
Full max. supervision (9%)	0.92± 0.01
Informed unsupervised	0.89± 0.04
Informed max. supervision (75%)	0.94± 0.01

S4. Random Forest Results

Within the training dataset, we classified 1663, 6076 and 19332 segments as dives, flapping and on water, respectively based on the wet-dry and TDR data. A preliminary inspection of the mean and standard deviation of all 46 of the random forest coefficients suggested differences in the metrics of segments classified with different behaviors (S5).

The OOB error for the random forest created from the training dataset was lowest with 7 variables tried at each split and therefore this model was used to predict the behaviors of the full dataset. The OOB error was 18% with the highest class error associated with diving behavior (42%) followed by flapping (0.5%) and finally on water (0.06%). The most important predictors of behavior in this model were the maximum heave, minimum depth, and mean depth of the segments (Figure 1).

After predicting the behaviors of the full dataset and removing classifications with a probability of less than 0.65, 58% of the accelerometery dataset was classified as either dive, flapping or on water (Table 1).

Table 1. The total and per trip mean and standard deviation of the number of segments and proportion of time spent in each of the behaviors classified by the Random Forest model.

Behaviour	Total Segments	Total Proportion	Segments per trip	Proportion per trip
Dive	160782	0.01	2915 ± 9438	0.03 ± 0.08
Flapping	707043	0.20	13988 ± 19292	0.30 ± 0.25
Water	4769718	0.37	94465 ± 137771	0.35 ± 0.24
Unclassified	4052001	0.42	80632 ± 146194	0.33 ± 0.27

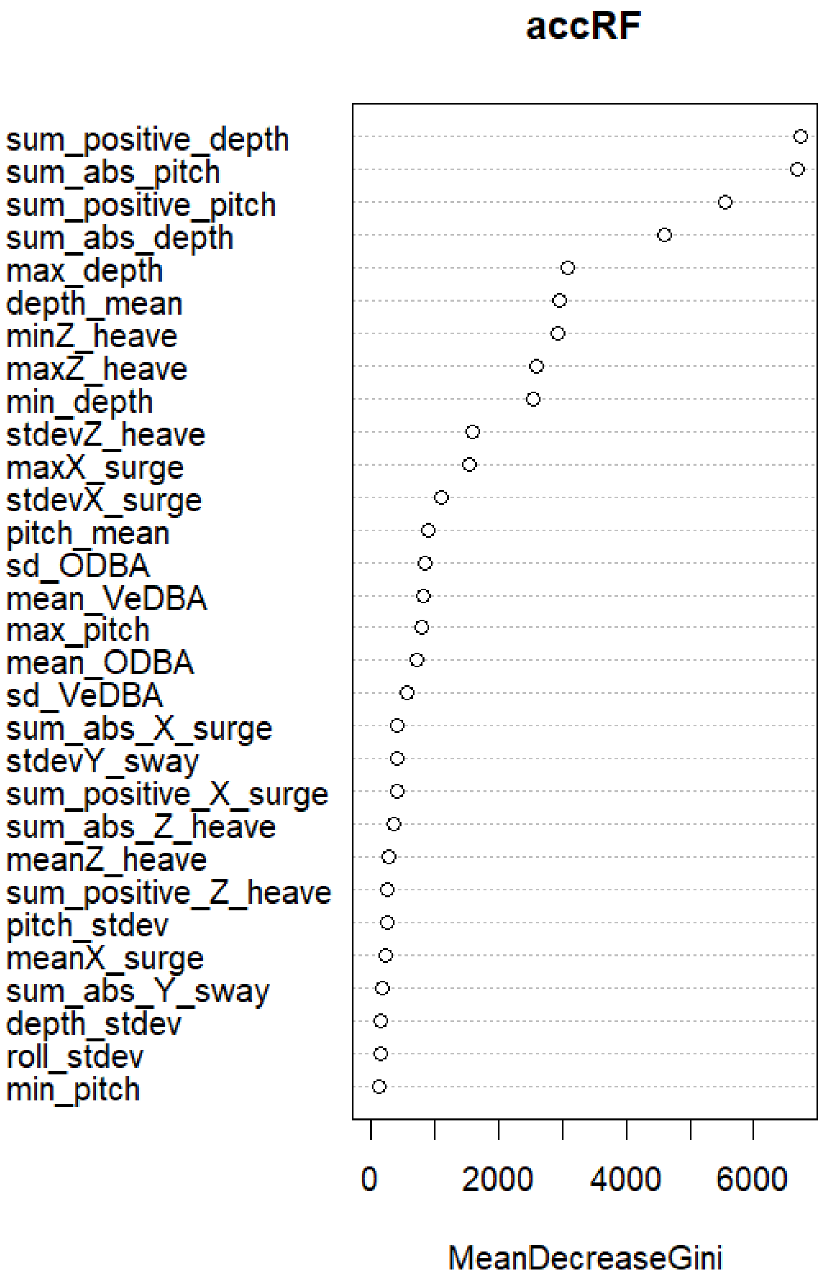


Figure 1. Results of the varImpPlot showing the importance of each variable in the random forest model

S5. Random forest segment summary

Behavior	mean_seg_length	sd_seg_length	mean_ODBA	sd_ODBA	mean_VeDBA	sd_VeDBA	mean_sd_ODBA	mean_sd_VeDBA
Dive	0.914972917	2.057358426	7.471565903	58.98429559	5.211490202	41.03694491	58.98429559	41.03694491
Flapping	2.06816623	4.323165355	28.55558907	117.3309097	20.08226899	82.3278591	117.3309097	82.3278591
Water	0.600526043	0.821167112	1.858442283	16.60633224	1.332505924	11.37814708	16.60633224	11.37814708

Behavior	mean_meanX_surge	sd_meanX_surge	mean_stdevX_surge	sd_stdevX_surge	mean_minX_surge	sd_minX_surge	mean_maxX_surge	sd_maxX_surge
Dive	0.185735229	0.679436355	0.246186981	0.503757741	-0.260813043	1.458838869	0.576634203	0.656742599
Flapping	0.454394595	0.323062801	0.120497157	0.191729202	0.240872848	0.305768818	0.712797775	0.635770069
Water	0.262248725	0.152002799	0.034125189	0.06943132	0.20156961	0.158418447	0.326028224	0.243030636

Behavior	mean_sum_positive_X_surge	sd_sum_positive_X_surge	mean_sum_negative_X_surge	sd_sum_negative_X_surge	mean_meanY_sway	sd_meanY_sway
Dive	10.23417584	40.45752872	-2.202266693	6.448451996	-0.008280901	0.355537541
Flapping	27.15749485	63.43315424	-0.061156927	0.319006492	0.008280542	0.150353622
Water	4.186772762	11.01105496	-0.061887112	0.48559032	-0.118615199	0.188975334

Behavior	mean_stdevY_sway	sd_stdevY_sway	mean_minY_sway	sd_minY_sway	mean_sum_positive_Y_sway	sd_sum_positive_Y_sway	mean_maxY_sway	sd_maxY_sway
Dive	0.274248897	0.434966349	-0.505286723	0.976042885	2.958369886	6.884727691	0.476714817	0.835268987
Flapping	0.094494824	0.18411441	-0.196463331	0.473277594	2.300476611	5.300333055	0.224641512	0.47891287
Water	0.055543166	0.12708909	-0.212934674	0.311123499	0.605453604	2.411684312	-0.022751412	0.335572118

Behavior	mean_sum_negative_Y_sway	sd_sum_negative_Y_sway	mean_meanZ_heave	sd_meanZ_heave	mean_stdevZ_heave	sd_stdevZ_heave	mean_minZ_heave	sd_minZ_heave
Dive	-3.043505063	5.387564792	0.773078338	0.469270599	0.322551535	0.494041607	0.173115683	1.257783942
Flapping	-3.752402204	8.769633475	0.884676234	0.296757759	0.230386355	0.253761232	0.51933248	0.518401901
Water	-2.234553609	3.693833287	0.904815415	0.134816337	0.074807981	0.080493652	0.783081815	0.230605511

Behavior	mean_maxZ_heave	sd_maxZ_heave	mean_sum_positive_Z_heave	sd_sum_positive_Z_heave	mean_sum_negative_Z_heave	sd_sum_negative_Z_heave
Dive	1.281587456	0.787143417	19.03563039	40.75857647	-1.247594738	4.009618954
Flapping	1.32263628	0.658669266	44.78037579	90.91950969	-0.228931637	1.669260075
Water	1.017595399	0.17931868	13.45529676	17.3666105	-0.022185319	0.455196068

Behavior	mean_pitch_mean	sd_pitch_mean	mean_pitch_stdev	sd_pitch_stdev	mean_min_pitch	sd_min_pitch	mean_max_pitch	sd_max_pitch	mean_sum_positive_pitch
Dive	15.13120942	19.57302606	8.193638218	9.347275947	0.450981902	30.05804926	30.19754486	20.75651432	553.5936702
Flapping	24.87286639	10.47244302	5.122586766	5.530224985	11.59094047	19.6093466	34.81101144	19.34799694	1555.603137
Water	15.47438642	7.819926614	2.160407894	3.204821651	11.85596551	9.057036361	19.38210571	10.94445834	248.5880453

Behavior	sd_sum_positive_pitch	mean_sum_negative_pitch	sd_sum_negative_pitch	mean_roll_mean	sd_roll_mean	mean_roll_stdev	sd_roll_stdev	mean_min_roll
Dive	2186.28688	-62.54019854	150.1843273	0.441467597	14.6907035	10.73145598	12.64896875	-18.29098658
Flapping	3820.764642	-10.36736503	49.09231986	0.754499487	8.805273506	5.696024408	6.876225662	-12.77354574
Water	682.5925009	-3.69358878	29.14355042	-7.04313628	11.19990107	2.962588849	5.005423499	-12.00037175

Behavior	sd_min_roll	mean_max_roll	sd_max_roll	mean_sum_positive_roll	sd_sum_positive_roll	mean_sum_negative_roll	sd_sum_negative_roll
Dive	27.75553021	19.45998164	25.53140161	148.7984738	317.5679513	-148.4229335	273.8061099
Flapping	22.86545769	15.22669209	21.32378431	167.6335639	391.0585512	-227.9307151	534.1978608
Water	14.32006368	-2.024843196	15.33787732	34.53319377	134.6580517	-132.049501	220.1495131

Behavior	mean_depth_mean	sd_depth_mean	mean_depth_stdev	sd_depth_stdev	mean_min_depth	sd_min_depth	mean_max_depth	sd_max_depth
Dive	-0.146788269	0.285085851	0.037863831	0.06396195	-0.20996819	0.36005729	-0.09169453	0.222891787
Flapping	0.026592897	0.065185762	0.001474607	0.001864611	0.02407326	0.064970458	0.029213352	0.06558152
Water	-0.00390129	0.074415024	0.000961538	0.002137202	-0.005384367	0.07483524	-0.002425867	0.07414535

Behavior	mean_sum_positive_depth	sd_sum_positive_depth	mean_sum_negative_depth	sd_sum_negative_depth	mean_sum_abs_depth	sd_sum_abs_depth
Dive	0.594812248	4.217005618	-2.583271115	4.983316817	3.178083363	6.292680046
Flapping	2.591071583	14.66043915	-0.230665668	1.083692262	2.82173725	14.66017833
Water	0.333790631	1.730512784	-0.336621334	0.580331014	0.670411965	1.762645696

Behavior	mean_sum_abs_X_surge	sd_sum_abs_X_surge	mean_sum_abs_Y_sway	sd_sum_abs_Y_sway	mean_sum_abs_pitch	sd_sum_abs_pitch	mean_sum_abs_roll	sd_sum_abs_roll
Dive	12.43644253	40.63474465	6.001874949	9.802989545	616.1338688	2190.111643	297.2214073	483.4804531
Flapping	27.21865178	63.48374756	6.052878815	11.89808969	1565.970502	3830.275742	395.564279	824.6593821
Water	4.248659874	11.01371797	2.840007213	4.482651846	252.281634	682.7357513	166.5826948	256.4730865

S6. Transition probability matrix

Table 1. Mean and standard deviation of HMM transition probabilities between resting, foraging and travelling from the 10 iterations of models with 0 known states

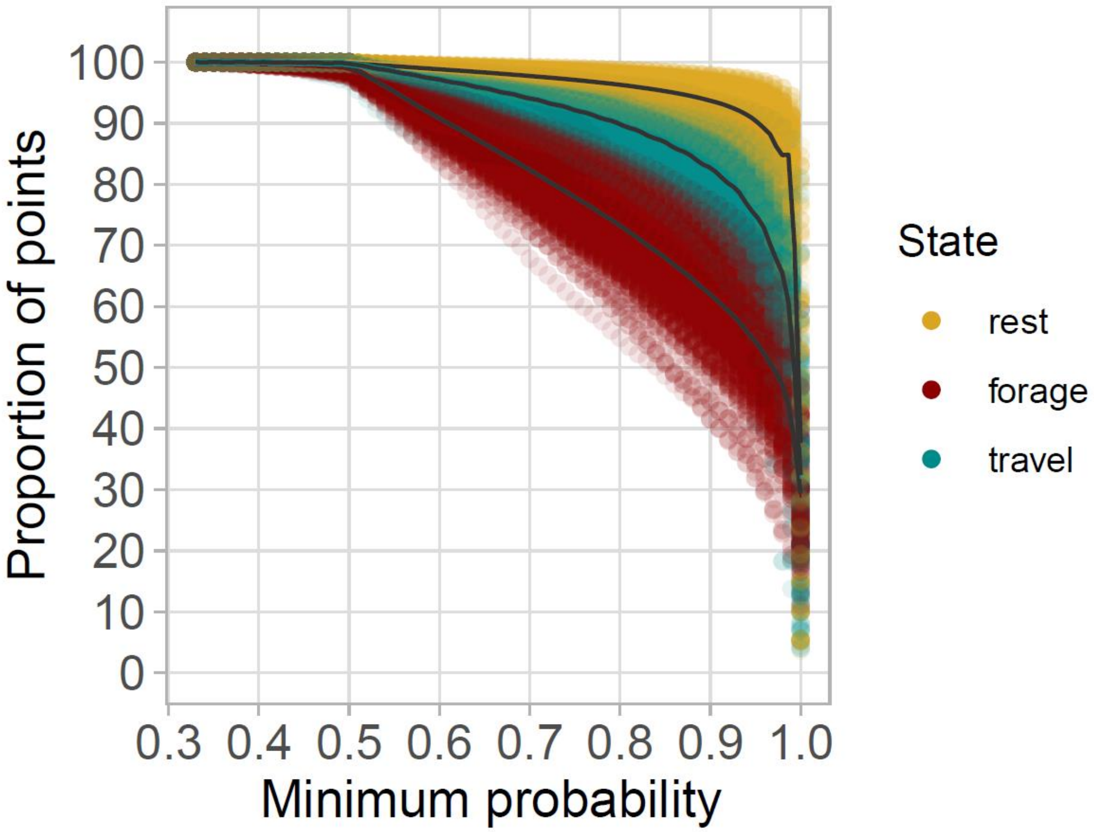
	rest	forage	travel
rest	0.82±0.05	0.12±0.03	0.05±0.02
forage	0.23±0.05	0.59±0.09	0.15±0.05
travel	0.099±0.05	0.14±0.06	0.76±0.05

Table 2. Mean and standard deviation of HMM transition probabilities between resting, foraging and travelling from the 10 iterations of models with a maximum proportion of known states (0.75)

	rest	forage	travel
rest	0.90±0.02	0.05±0.01	0.05±0.01
forage	0.22±0.17	0.47±0.16	0.23±0.14
travel	0.12±0.03	0.10±0.04	0.79±0.05

S7. Sample loss with removal of positions with low HMM probability

Proportion of GPS positions remaining in the dataset upon removal of positions with increasing minimum HMM probability values for behavioral classification.



S8: Confusion matrices of complete GPS HMMs

Confusion matrices showing the mean and standard deviation of the number of reference behaviors against model predictions for iterations of the complete GPS HMMs with no supervision (left) and with the highest amount of supervision (9%, right).

Picture by Marcos Hernández-Montero

Chapter 2. The effect of seasonality on the foraging behavior and breeding success of a tropical marine top predator.

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ABSTRACT

In polar and temperate regions, seasonality in environmental conditions is an important driver of animal phenology. In tropical systems, where the environment is relatively homogeneous year-round, the link between phenology and seasonality is weakened, and many species breed asynchronously or even year-round. This leads to the question of how these species adapt to seasonal changes, which remain present, albeit to a lesser extent. To assess relationships between foraging plasticity and seasonal changes in oceanographic conditions and resource availability, we investigated the foraging ecology of the Red-billed Tropicbird (*Phaethon aethereus*), a poorly studied pantropical species that breeds year-round in Cabo Verde. From 2017 to 2022, we monitored tropicbird nests at three islands (Boavista, Sal, and the Cima Islet) and GPS tracked 907 foraging trips from 329 adults to evaluate seasonality in nest occupancy, foraging patterns and efficiency, chick growth, chick and adult body condition, and breeding success, alongside links to seasonal changes in resource availability and environmental conditions. We found seasonal patterns in foraging behavior, with individuals taking more distant and less sinuous foraging trips, using a larger core foraging area, spending more time foraging during twilight, and consuming more squid in the dry season (December-June) than in the wet season (July-November). Moreover, nest occupancy, chick body condition, and breeding success were higher in the dry season. We suggest that the observed seasonal patterns are related to an increase in the availability of squid at the end of the dry season, a decrease in the nest-site suitability, and an increase in weather-related foraging costs in the wet season. Our results provide some of the first in-depth knowledge on the seasonal variation in foraging behavior of a tropical seabird species, suggesting

seasonality in tropical systems may be a stronger driver of the movements of top predators than previously thought.

INTRODUCTION

Seasonality, characterized by periodic changes in environmental conditions throughout the year, serves as a significant driver of animal phenology (Dufour et al., 2020; Forrest & Miller-Rushing, 2010). This is because of variation in environmental conditions such as temperature, precipitation, and light level (e.g. through energetic and thermoregulatory restraints), as well as resource availability, including food and suitable nesting sites (Ramírez et al., 2017), on individual fitness. To cope with seasonal changes, species may synchronize reproduction with periods of favorable conditions and avoid unfavorable ones through migration, hibernation, or estivation. Conversely, they can adapt to these seasonal changes through ecological plasticity, by modifying and balancing ecological traits, such as foraging behavior and diet (van Beest & Milner, 2013; Varpe, 2017).

In polar and temperate regions, population-wide synchrony reflects distinct seasonality in suitable breeding conditions alongside peaks in favorable resource availability (e.g. timing of spring bloom; Frederiksen et al., 2006). Conversely, in tropical regions where the marine environment is relatively nutrient-poor and homogeneous, the link between phenology and seasonality is weakened, and many species breed asynchronously or even year-round (Longhurst, 1995; Lundberg, 1988). According to standard bet-hedging theory, we can then expect more phenological variability at individual and population levels (Smetzer et al., 2021). Moreover, asynchronous breeding in these oligotrophic waters may result in higher individual fitness because of lower intra-specific competition (Ashmole, 1971). When this is the case, it may benefit different individuals within populations to specialize in a narrow foraging strategy to avoid competition (Cleasby et al., 2015; Votier et al., 2010; Wakefield et al., 2015). Despite weakened seasonality in tropical systems, the persistence of this phenomenon is evidenced by seasonal fluctuations in the numbers of active breeders and/or foraging behavior, reflecting population-level preferences for specific environmental conditions, resource availability, and/or interspecies interactions (Keogan et al., 2018; Passuni et al., 2016; Schreiber & Ashmole, 1970; Villegas-Amtmann et al., 2011). These fluctuations may, in turn, influence the foraging efficiency of the adults and impact the body condition and survival of adults and chicks throughout the year (Esparza et al., 2022).

Understanding the drivers of seasonal changes in tropical oceans can shed light on the evolutionary constraints acting upon species in these poorly studied systems. In the face of climate change, investigating species' adaptability to environmental change and its cascading effects on ecological interactions is essential for evaluating threats and developing management strategies. In a meta-analysis of the phenology of worldwide seabird populations between 1952 and 2015, seabirds had not adjusted their breeding seasons over time or in response to sea surface temperature, suggesting a particular vulnerability to climate change impacts (Keogan et al., 2018). This same meta-analysis underlines significant knowledge gaps about the adaptability of tropical species to environmental change.

We aim to identify how an asynchronous tropical species adapts to seasonality and to determine whether these changes are driven by seasonal variability in environmental conditions and/or resource availability. To achieve this, we focused on Red-billed Tropicbirds (*Phaethon aethereus*), a poorly studied pantropical species that breeds year-round. Our study was conducted on five breeding colonies on two islands and one islet in Cabo Verde, where we monitored tropicbird nests and tracked 907 foraging trips using GPS loggers on 329 adults from 2017 to 2022. Like many other medium-size seabirds, Red-billed Tropicbirds have few natural predators, making them an excellent model species for investigating how environmental conditions and resource availability influence foraging efficiency, diet and fitness, and ultimately reproductive phenology. Specifically, we focused on (i) identifying seasonal patterns in nest occupancy, foraging patterns, and diet; (ii) assessing seasonality in a suite of efficiency and fitness components, including foraging efficiency, adult and chick body condition, and breeding success; and (iii) assessing how these seasonal patterns relate to seasonality in environment conditions (bottom-up processes) and density dependence at colonies (top-down processes), and the relative importance of these two contrasting processes.

METHODS

Study species and field site

The Red-billed Tropicbird is a widespread marine predator, present in small numbers throughout the tropical Atlantic Ocean, in the east tropical Pacific and west tropical Indian Ocean. This species breeds asynchronously in scattered colonies and feeds mainly on small epipelagic fish such as flying fish, needlefish, and some squid (Castillo-Guerrero et al., 2011; Diop et al., 2018; Madden et al., 2022). During the breeding season, they are central place foragers that may travel over 500 km from the colony in search of prey (Diop et al., 2018). During chick-rearing, they use a dual foraging strategy in which they alternate between short trips to feed their young and long trips to feed themselves (Piña-Ortiz et al., 2024).

Fieldwork took place at two colonies on Boavista and three on Sal islands, and one colony on Cima Islet in Cabo Verde between 2017 and 2022. Cabo Verde lies 600 to 850 km west of Senegal, Africa. It is located within the southern limit of the Canary Current Large Marine Ecosystem (Valdés & Déniz-González, 2015), at the eastern boundary of the North Atlantic subtropical gyre (Fernandes et al., 2005). The ocean surrounding Cabo Verde is characterized by consistent North Easterly winds, which are stronger in the winter months. Although within the upwelling system, waters surrounding Cabo Verde are relatively oligotrophic, but there is a peak in productivity in February-March, reaching on average less than 20 mg·C per m3 (Medrano et al., 2022). Climatically, Cabo Verde is arid from December to June, with a wet season from July to November (Neto et al., 2020) with a peak in precipitation from August to October (Neves et al., 2017). While fieldwork on Boavista and Sal islands was mostly continuous during the study period, work on Cima islet was continuous only after mid-2019 (Figure 1).

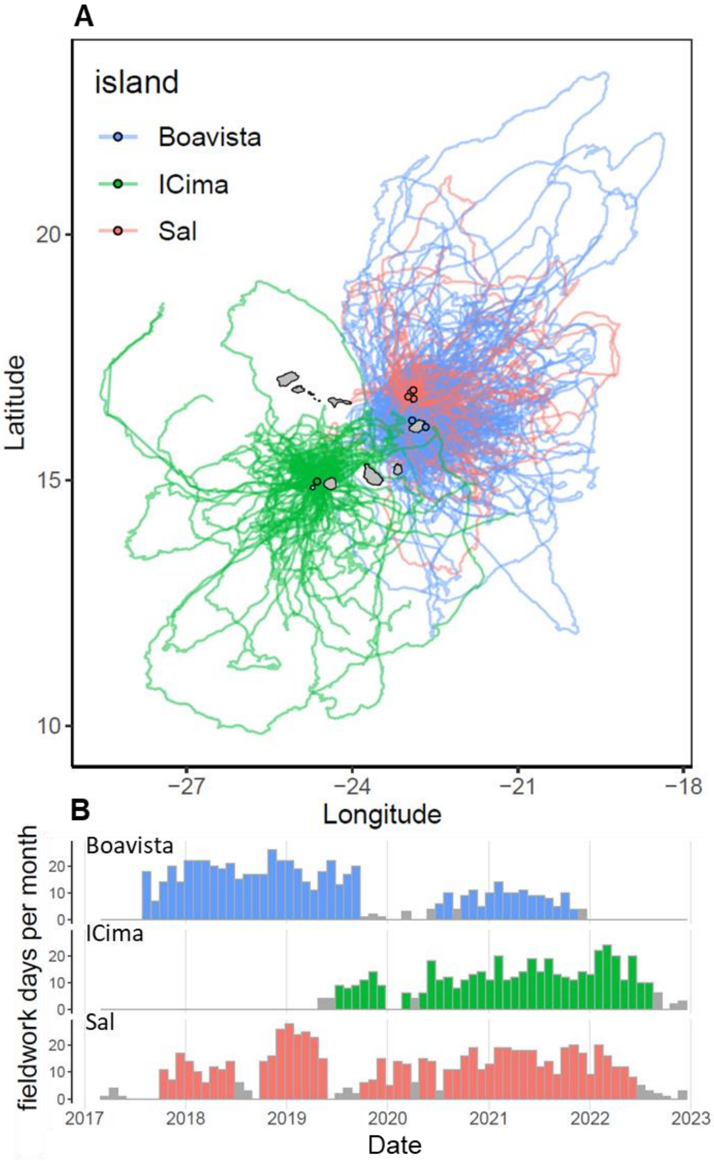


Figure 1. Red-billed Tropicbird foraging trips and monitoring effort in Cabo Verde. A) Map of tropicbird foraging trips coloured by their breeding islands with colony locations indicated by points. B) Number of fieldwork days per month per island. Bars in grey indicate months considered to have discontinuous effort (<5 fieldwork days) and were excluded from the analysis of seasonality in nest occupancy.

Nest monitoring

To monitor adult body condition, breeding success, chick growth, and diet, nests were generally visited every 1-3 days, but some isolated nests (<5%) were only visited monthly. At each nest visit, the contents of the nest were recorded (empty, chick/egg, and whether there was an adult or not) and, if an adult or chick was present, we measured its morphometrics (weight, wing length, tarsus length, bill depth, culmen and head-bill length). Since monitoring was inconsistent at certain times of the year and at more isolated nests, data on breeding phenology (laying, hatching and fledging date) and success (hatching success and fledging success) were only used in analysis when the window of uncertainty for these data was less than 15 days. When only one or two of the three breeding phenology dates were known, the unknown date(s) was(were) estimated based on adding/ subtracting the population means of incubation (41±5 days, n=27) or chick-rearing period (84±5 days, n=25) of nests with no uncertainty to/from the known phenological date with the smallest window of uncertainty.

Logger deployments and processing

Red-billed Tropicbirds were captured on their nests during incubation or early chick-rearing and equipped with CatLog Gen2 GPS. The GPS loggers weighed 18g (2.9% of mean tropicbird weight; 630g±55, n=1,297 individuals) and were programmed to record GPS positions every 5 minutes. The GPS tracks were cleaned of erroneous positions using a speed filter (30m/s) and split into discrete foraging trips with periods in the nest between trips omitted. As in Saldanha et al., 2023, a sub-sample of tropicbirds were also equipped with Axy-Trek loggers (which record GPS, tri-axial accelerometer, and time-depth information;

33 foraging trips from 14 individuals), Migrate Technology C330 geolocators (GLS) with a wet-dry sensor (salt water immersion logger; 74 foraging trips from 19 individuals) or both (16 trips from 6 individuals) to semi-supervise Hidden Markov Models for the classification of GPS positions into behavior states. Axy-Trek loggers weighed 17g (2.7 % of tropicbird weight) and recorded GPS, acceleration, and pressure data at 5-minute, 25 Hz and 1s intervals, respectively. The Migrate Technology geolocators (GLS) with a wet-dry sensor weighed 3.3g (0.5% of tropicbird weight) and registered if the bird was wet or dry every 6 seconds. GPS and Axy-Trek were attached to the 6 central tail feathers with Tesa tape while GLS were attached to the tarsus, on the bird's metal ring with the help of a zip tie. All tracking data was processed as in (Saldanha et al., 2023), however, we followed the authors' suggestion to classify GPS positions into two instead of three discrete behavioral states. Small step lengths and low turning angles were inferred as inactive (i.e. resting on water), and large steps with a large variety of turning angles were inferred as active (foraging/flight) states. Since tropicbirds mainly forage on the go (Saldanha et al., 2023), we hereafter refer to the active state as foraging.

We tested for potential impacts of GPS deployments by assessing difference in breeding success and adult body condition between tagged and non-tagged individuals (see analysis section).

Analysis

Assessing seasonal patterns in nest occupancy, foraging patterns, and diet

Nest occupancy

To estimate seasonal changes in nest occupancy and determine whether density dependence was driving seasonal patterns of tropicbird foraging ecology, we used the hatch date or estimated hatch date of each nest (see nest monitoring). In the case when nests failed during incubation, to have comparable phenological dates, we estimated the hatch by adding the population mean of incubation to the laying date. Since not all tropicbird colonies were simultaneously monitored in Cabo Verde and colonies varied in size, we represented changes in nest occupancy as the proportion of recorded nests that hatched per month for each year and island. Moreover, to control for monitoring bias, we only included months with over 5 days of fieldwork per island and year (Figure 1). To determine whether nest occupancy varied seasonally, we modelled it in a Generalized Additive Mixed Models (GAMM) against a cyclic cubic regression spline of Julian date while controlling for differences between years and islands as random intercepts (Table 2).

Foraging patterns

Using only complete trips (without battery failure), we calculated the following metrics: trip duration, maximum distance from the colony, distance travelled, sinuosity (McLean & Skowron Volponi, 2018), and whether the trip was a day (short trip during daylight hours) or overnight trip (with at least one night period). Then, using GAMMs, we assessed whether there were seasonal trends in these metrics by modelling them against a cyclic cubic regression spline of Julian date with random intercepts for individual ID, breeding phase, island, and year (Table 3).

Home range of each animal was estimated as the area of 95% of the Kernel Density Estimate (KDE; Calenge C., 2006) of the positions classified as foraging within each trip, using Lambert equal-area projection. To identify seasonal changes in individual home ranges, using a GAMM, we modelled home range against a cyclic cubic regression spline of Julian date of the start of the trip, along with random intercepts for individual ID, breeding phase, island, and year (Table 3).

To identify seasonal shifts in main foraging areas, we calculated the spatial overlap (Bhattacharyya's Affinity, BA) between all kernels from trips of the same island and breeding phase. Then, using the calculated overlap, we assessed: 1) seasonal patterns in overlap, and 2) relationships between overlap and the difference in days between the beginning of trips. In the first model, we assessed seasonal changes in overlap by comparing the overlap between pairs of trips that occurred in the same month using a GAMM with separate cyclic cubic regression splines of Julian date for trips of the same vs different individuals. In addition, this model included parametric coefficients for whether the home ranges were from the same individual or not, from the same year or not, and the absolute difference in days between the two trips, along with random intercepts for individual ID, breeding phase, and island (Table 3). In the second model, we assessed whether the home ranges of individuals foraging during the same time of year overlapped more than those breeding at different times. To do this, we modelled the overlap between home ranges against a non-linear relationship with the absolute difference in days between the beginning of each overlapped trip, along with parametric coefficients for whether the home ranges were from the same individual or not, from the same year or not, along with random effects for both individual IDs, breeding phase, and island (Table 3).

To determine whether there are seasonal patterns in the proportion of time foraging, we calculated the proportion of time birds spent foraging during day, night, and twilight, separately. We limited our analysis to days and nights with at least 4 hours of GPS data, and twilight periods with at least 1 hour of data. We then used a GAMM to model the relationship between the proportion of time foraging against a cyclic cubic regression spline of Julian date. This model also included categorical variables for day, night, and twilight along with random intercepts for individual ID, breeding phase, island, and year (Table 3).

Diet

To determine whether there were seasonal patterns in tropicbird diet, 73 spontaneous regurgitates from 69 incubating adults breeding in Sal and Boavista were collected opportunistically during nest monitoring. From these samples, we classified every prey item to the lowest possible taxonomic level using morphological identification. Due to the small number of prey that we were able to identify at a species or family level, we gathered prey items by ecological prey group (carnivorous fish, zooplanktivorous fish, and cephalopods) to test for the frequency of these groups within samples. Stable isotope analyses were undertaken on muscle tissue samples from 110 prey items and 64 blood samples from adult tropicbirds to identify seasonal patterns in nitrogen ($\delta 15N$) and carbon ($\delta 13C$) stable isotope values. Additional information on these analyses is described in A1.

To assess whether there were seasonal trends in ecological prey group frequency in tropicbird regurgitates, we initially modelled all prey items collected and included individual ID as random intercepts. However, this resulted in an overly complex model for the size of our dataset (more coefficients than data). Therefore, we randomly selected only one prey item per regurgitate and bird to be included in the model (leaving 66 prey samples to be modelled as regurgitates from 3 adults did not have any identifiable prey). We modelled whether each of these prey items was carnivorous fish, zooplanktivorous fish, and cephalopods in a series of three binomial GAMMs against a non-linear relationship with a cyclic cubic regression spline of Julian date. These models also included random effects for breeding phase, island, and year (Table 3).

To assess whether there were seasonal trends in tropicbird blood stable isotopes, we modelled the nitrogen and carbon stable isotope values against a cyclic cubic regression spline of Julian date using GAMMs. Since we only had one blood sample per individual, these models only included random intercepts for breeding phase, island, and year (Table 3).

Assessing seasonality in efficiency and fitness

Foraging efficiency

As a measure of foraging efficiency, we calculated relative weight gain after a foraging trip by incubating tropicbirds, as well as per km, and hour at sea. Since tropicbirds sometimes remained in their nest for several days before departure or returned to the colony undetected, we subtracted/added the mean weight loss per day at the colony (19.2 g/day, n=142) and limited the analysis to weights that corresponded to complete incubation trips with birds weighted fewer than 3 days before and 3 days after spent at the nest and for which the sex of the individual was known (resulting in 62 trips from different incubating individuals). We modelled the seasonality of these three measures of efficiency while also considering differences between sexes, years, and islands as random intercepts in GAMMs (Table 4).

Adult body condition

To calculate an index of body condition (BCI) for breeding tropicbirds to assess how it changed among seasons, we collected weight and biometric measurements (wing length, tarsus length, bill depth, culmen and head-bill length; A2) opportunistically during nest monitoring, (measurements of 328 individuals by 39 samplers). We then normalized the biometric measurements and conducted a principal component analysis (PCA) to generate a composite measure of skeletal size (e.g., Benson, Suryan, & Piatt, 2003). The first principal component explained 40.0 % of the variance and was negatively related to all individual loadings of biometric measurements (wing: -0.28, culmen: -0.61, bill height; -0.29, head-bill: -0.61 and tarsus -0.31). To facilitate interpretation, we inverted the factor of body size by multiplying it by -1, so that higher values represent larger birds. Then we fit a non-linear relationship between the first principal component and adult weight to predict the median weight per body size and used the residuals of this model to calculate the BCI, with positive values representing birds with larger weights for their body size, and negative values representing the contrary. Finally, to measure the seasonal trends in adult BCI, we ran a GAMM with BCI as the response variable and as explanatory variables: a non-linear relationship with Julian date, and the random effects of sex, year, island, and breeding phase. Furthermore, to test whether there was a negative consequence of GPS deployment on BC1, we also included a categorical variable indicating whether the weight measurement was taken directly after a foraging trip with a GPS or not (Table 4).

Chick growth and body condition

To determine whether chick growth changed seasonally, we used 87 measurements of relative weight gain over a 5-day period collected from 51 15-30 days old chicks with known hatching dates (certainty of <7 days) and for which the weight was measured by the same sampler on both occasions (a total of 15 different samplers collected the data). This analysis was restricted to chicks between 15-30 days old, since growth is linear during this period (Beard et al., 2023). To model seasonal changes in relative weight gain, we modelled it in a GAMM against a cyclic cubic regression spline of Julian date, while considering differences between individuals, island, year, and sampler as random intercepts (Table 4).

We also modelled the seasonality of the chick BCI based on biometric measurements and weight recorded during monitoring. To calculate chick body condition, we used a similar approach as in measuring adult body condition. However, in this case, the first principal component (representing body size) explained 78.4% of the variance, and all individual loadings of the body size variables were positively correlated with the first principal component (wing: 0.47, culmen: 0.49, bill height; 0.46, head-bill: 0.48 and tarsus: 0.31). Then, using a subset of the data of chicks that were known to have successfully fledged (475 samples from 68 individuals), we used a GAM with the response variable weight and a tensor interaction between the first principal component from the PCA (representing body size) and age, to predict the median weight per body size and age for the complete dataset (936 measures of body morphology from 172 chicks collected by 34 samplers). Finally, we used the residuals of this model as the body condition index (BCI), with positive values representing birds with larger weights for their age and body size, and negative values representing the contrary. To measure whether there are seasonal trends in chick body condition, we then ran a GAMM of the BCI in relation to a cyclic cubic regression spline of Julian date with random intercepts for individual ID, sampler ID, island, and year (Table 4). Age was not included in this model since its effects were considered while calculating the BCI.

Assessing the relative ecological importance of density dependence and environment conditions as drivers of seasonal patterns in tropicbird foraging ecology

To determine whether resource availability and environmental conditions are related to seasonal patterns in foraging behavior, we first tested for seasonal trends in top-down (tropicbird nest occupancy) and bottom-up (environmental conditions) variables that may affect tropicbird phenology and foraging behavior. Then, using only those variables which showed seasonality, we tested their relative importance to predict seasonal trends in foraging behavior and fitness metrics.

Seasonality of environmental variables

To determine whether environmental conditions are driving seasonal patterns of tropicbird foraging ecology and nest occupancy, we extracted a series of environmental variables that were expected to affect resource availability, foraging efficiency (through visual impairment and/or increased flight costs) and breeding success (Table 1). To be comparable between months, variables hypothesized to affect resource availability and foraging efficiency were extracted within the smallest monthly foraging home range kernel based on at least 10 foraging trips per island and breeding phase, as this was assumed to represent the minimum foraging area (figures representing the selection of the minimum foraging areas for each colony and breeding phase can be found in A3). Variables hypothesized to affect breeding success were extracted at colony locations. To determine how environmental conditions varied seasonally, we used GAMMs to model each of the variables extracted within the minimum foraging range and at colony locations against a cyclic cubic regression spline of Julian date while controlling for differences between breeding phases, years, and islands as random intercept effects (Table 5).

Assessing the relative ecological importance of top-down and bottom-up drivers

To relate environmental conditions to tropicbird foraging behavior and fitness, we considered the timeframe in which different variables were expected to affect each biological outcome separately. For environmental variables that were considered to affect foraging patterns in-situ by causing reduced visibility and increased flight costs, we related the trip metric to the mean of the environmental variables within the minimum foraging area (described above) for the duration of each trip. Since we identified strong positive collinearity (>0.7) between trip metrics (cumulative distance travelled, duration of the trip, maximum distance from the colony and home range area), we used cumulative distance travelled to represent the suite of collinear trip metrics. Therefore, models were limited to response variables cumulative distance travelled, sinuosity and the proportion of time foraging during the day, twilight and night.

For environmental variables that were either considered to affect foraging patterns by indirect trophic links (primary productivity) or to have cumulative effects on tropicbird breeding success and body condition, we used the R package ClimWin (Bailey & De Pol, 2016) to search for critical windows, i.e. the time period of the environmental variable that best predicts biological outcomes, such as foraging metrics (primary productivity only), blood stable isotopes, adult body condition, chick body condition, hatching success, and fledging success (A4).

We then investigated whether seasonal patterns in trip metrics, proportion of time foraging, adult and chick body condition, and breeding success could directly (without Julian date) be explained by variables measuring intra-specific competition (nest occupancy), and/or environmental variables that may affect tropicbird foraging through flight costs (wind speed and air density), visibility (cloud cover, wave and swell height), and prey availability (primary productivity), and/or offspring survival (temperature and precipitation at the colony site). Here we limited our analysis to variables that were found to have a significant seasonal pattern (significant effect of Julian date) and for which we had sufficient sample sizes (diet from regurgitates were not analyzed here for this reason). Given the limited time range of the dataset, Secchi-disk depth was not included in this analysis. Since strong collinearity (>0.7) occurred between some environmental variables both in situ and during the significant windows, we performed a PCA to objectively transform the multicollinear environmental variables into a reduced set of new uncorrelated features. For each biological outcome, we ran the PCA over the specific set of environmental conditions in situ or within the significant windows (Table 7). We retained a subset of the PCs, by selecting the PCs where variance (expressed by the unscaled eigenvalue) was greater than 1 (latent root criterion) and interpreted each PC based on their eigenvector loadings using a cut-off value of ±0.4 (Budaev, 2010). Then, we modelled the trip metrics, the proportion of time foraging trip during the day, night or twilight period, blood stable isotopes, adult and chick body condition, and breeding success against the environmental components, along with nest occupancy, random intercepts for individual IDs, breeding phase, island, and year when applicable. Then, we used the 'dredge' function from the package MuMIn (Burnham & Anderson, 2002), to generate models containing all combinations (subsets) of the fixed effects, and selected the best model based on the lowest Akaike Information Criterion (AIC, A6).

Table 1. Source, resolution (spatial & temporal), aggregating metric and time window of environmental variables.

Type	Variable	Units	Metric	Temporal Res.	Spatial Res.	Years available	Source
Foraging costs: visibility	Secchi disk depth	m	mean	monthly	0.25	2017-2018	Pitarch et al., 2021
	Cloud Cover	Prop 0-1	mean	hourly	0.25	2017-2022	Copernicus-ERA5 Reanalysis
	Wave & swell	m	mean	hourly	0.50	2017-2022	Copernicus-ERA5 Reanalysis
Foraging costs: flight	Wind Speed	m s-1	mean	hourly	0.25	2017-2022	Copernicus-ERA5 Reanalysis
	Air density	kg m-3	mean	hourly	0.50	2017-2022	Copernicus-ERA5 Reanalysis
Resource availability	Primary productivity	mg m-2 day-1	mean	daily	0.08	2017-2020	Copernicus-Global Ocean low and mid trophic levels biomass content hindcast
Breeding success	Temperature	Kelvin	mean	hourly	0.25	2017-2022	Copernicus-ERA5 Reanalysis
	Precipitation	m day-1	sum	daily	0.25	2017-2022	Copernicus-ERA5 Reanalysis

All GAMMs were run with the function "gam" of the "mgcv" package of R, and gamma, gaussian and binomial link functions were assigned based on each model's residual distribution. All PCA's were run with the functions "prcomp" function from the "stats" package of the R Core Team (2020).

RESULTS

Seasonal patterns in nest occupancy, foraging patterns and diet.

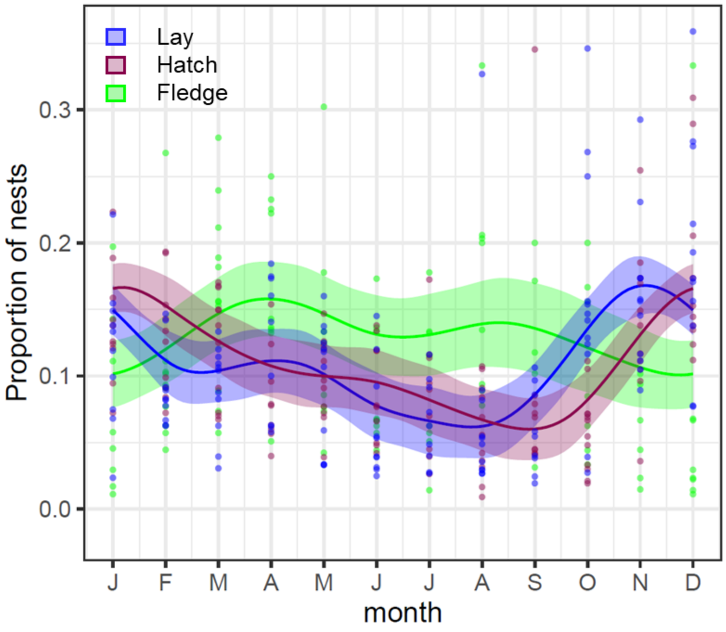
Nest occupancy

We found seasonal differences in the number of nests occupied at the colony, with a peak in laying in November, hatching in December and fledging in April (Figure 2, Table 2, 6)

Table 2: Models of seasonal patterns in tropicbird nest occupancy based on the proportion of eggs laid, hatched and chicks fledged per month, island, and year. P-values of non-linear relationships (effective degree of freedom, edf) and of parametric coefficients in parentheses. Significant values are in bold.

Response	**Intercept**	**Non-Linear**	**Random effects**		**Deviance Explained (%)**
		month	**year**	**island**	
Proportion Lay	**0.12 (<0.01)**	**4.64 (<0.01)**	**4.52 (<0.01)**	0.00 (0.80)	45.6
Proportion Hatch	**-0.13 (<0.01)**	**4.23 (<0.01)**	**4.63 (<0.01)**	0.00 (0.75)	45.9
Proportion Fledge	0.26 (0.06)	2.90 (0.20)	**4.94 (<0.01)**	0.06 (0.58)	57.7

Figure 2. The proportion of Red-billed Tropicbird nests with eggs laid, hatched, and chicks fledged per month, with each point representing these proportions per island and year. For each island and year, months were only included when at least 5 days of fieldwork took place per month.



Foraging patterns

From the 907 foraging trips recovered, 673 were complete (185 from incubating and 488 from chick rearing periods). Trip durations varied from less than one hour to over 9 days (mean 30.12±sd 41.93 hours), with tropicbirds travelling up to 803 km from their colonies (mean 66.67±sd 88.85 km). Both incubating and chick-rearing tropicbirds undertook a mix of day (<12h, with nights spent at the colony), and overnight foraging trips (>12h), although the latter was more common in incubating birds (overnight chick-rearing: 55%, incubation 77%).

There were significant seasonal trends in foraging patterns, with individuals taking more distant, longer, and less sinuous foraging trips and using larger core foraging areas during the dry season (December-June) and closer, shorter, and more sinuous trips in the wet season (July-November, Figure 3, Table 3, 6). This pattern is reiterated in the consistent seasonal expansion and contraction of population home ranges (Figure 4, split by breeding stage and colony in Appendix S3).

We found seasonal differences in the spatial overlap between foraging areas, but only between subsequent trips from the same individual, while the overlap between individuals did not vary significantly (Figure 3, Table 3, 6). In subsequent trips from the same individuals, there were higher levels of individual overlap in the dry season, particularly from Jan-March, and lower overlap in the wet season, with lowest overlap from June-September, although there were fewer trips at this time. The amount of overlap was also higher when trips were undertaken during the same time of year (with a smaller absolute difference between Julian dates). This was true for both subsequent trips from the same individual and for trips from different individuals (although the overlap was higher for the prior). Finally, this effect was also stronger when both trips took place within the same year.

Tropicbirds spent the highest proportion of time foraging during twilight, followed by day and finally night. The proportion of time foraging during each of these periods changed seasonally. The highest proportion of time foraging during the night and at twilight occurred in May in contrast to lower values in September and August, respectively (Figure 5, Table 3,6). This decrease in the proportion of time spent foraging in the wet season is particularly steep during twilight, going from ~0.73 to 0.57 between the month of May and September. During the day, tropicbirds spent the lowest proportion of time foraging in wet season, when the duration of both daylight and twilight are longest.

Diet

From the 73 spontaneous regurgitate samples, we obtained 134 individual prey items. We found only one prey item belonging to the crustacean taxon and thus it was excluded from analysis. In 70 of these samples, we were able to identify at least one prey item to at least the family or ecological prey group level, with a total of 132 prey items identified. The identifiable prey within regurgitates were mainly planktivorous fish of the family exocoetidae (61%), followed by various families of small carnivorous fish (9% carangidae, 5% tetraodontidae, 5% belonidae, <1% sparidae) and squid (3% ommastrephidae, and 16% unidentified squid). Of the 132 prey items identified, we were able to extract muscle for isotope analysis from 110 items (74 from planktivorous fish, 25 from carnivorous fish and 11 from cephalopods). We found significant differences in the $\delta15N$ and $\delta13C$ stable isotopes of the 3 ecological groups ($F=25.81$, $p<0.01$ and $F=4.93$, $p<0.01$, respectively). A Tukey's

HSD Test for multiple comparisons found that δ15N values were significantly higher for cephalopods (vs planktivorous fish 2.40, p<0.01, vs carnivorous fish 1.79, p<0.01), followed by carnivorous fish (vs planktivorous fish 0.60, p=0.03). On the other hand, δ13C values only differed significantly for carnivorous fish, which had lower values compared to cephalopods (-0.54, p=0.03) and planktivorous fish (-0.38, p=0.01) while values were similar between cephalopods and planktivorous fish (p=0.69).

When modelling seasonal trends in ecological group frequency in the regurgitates, we found that planktivorous fish were caught with a significantly higher frequency in the wet season, while cephalopods showed a peak at the end of the dry season (although only near-significantly; Figure 6, Table 3, 6).

Moreover, we found that tropicbirds had similar seasonal trends in their blood isotope values: with higher δ15N and lower δ13C values in their blood during the months of May-July (Figure 7, Table 3).

Table 3. Description of the structure of the models of seasonal patterns in tropicbird foraging behavior and their main results. Effective degree of freedom (edf) of non-linear relationships and parametric coefficients of linear parameters. P-values in parentheses. Significant values are in bold. Abbreviations: DA=day, TW=twilight, NI=night, SY=Same Year, SI=Same individual, Δ days=absolute difference in days

Seasonal effects	**Link function**	**Response**	**Non-Linear**		**Parametric Coefficients**					**Random effects**				**Deviance Explained (%)**
			Julian date	**Δ days**	**intercept**	**SI**	**SY**	**Δ days**	**time of day (DA)**	**ring**	**Breeding Phase**	**island**	**year**	
Trip Metrics	gamma(log)	maximum distance	**2.64 (<0.01)**	-	**4.22 (<0.01)**	-	-	-	-	**65.07 (<0.01)**	**0.98 (<0.01)**	**1.81 (<0.01)**	0.10 (0.42)	32.4
	gamma(log)	distance travelled	**2.63 (<0.01)**	-	**5.58 (<0.01)**	-	-	-	-	22.33 (0.37)	**0.98 (<0.01)**	**1.76 (0.00)**	1.21 (0.13)	19.7
	gamma(log)	trip duration	**2.12 (0.01)**	-	**3.55 (<0.01)**	-	-	-	-	0.01 (0.89)	**0.98 (<0.01)**	**1.67 (<0.01)**	**2.07 (0.02)**	12.9
	gamma(log)	95% KDE area	**3.00 (<0.01)**	-	**8.57 (<0.01)**	-	-	-	-	**116.85 (<0.01)**	**0.98 (<0.01)**	**1.84 (<0.01)**	0.11 (0.41)	50.3
	gaussian (identity)	sinuosity	**2.71 (<0.01)**	-	**7.48 (<0.01)**	-	-	-	-	**54.75 (<0.01)**	**0.89 (<0.01)**	0.00 (0.61)	**2.45 (<0.01)**	24.4
	binomial (logit)	Day trip (0/1)	0.00 (0.44)	-	0.77 (0.15)	-	-	-	-	**26.32 (0.05)**	**0.97 (<0.01)**	0.00 (0.90)	1.17 (0.15)	9.24
Area used	gamma(log)	kernel overlap	diff ind 0.00 (0.12), **same ind 2.39 (<0.01)**	-	**-1.89 (<0.01)**	**same 0.57 (<0.01)**	**same 0.20 (<0.01)**	**-0.00 (0.02)**	-	**Ring 1 210.31 (<0.01), Ring 2 159.41 (<0.01)**	**0.94 (<0.0.1)**	**1.98 (<0.01)**	-	23.3
	gamma(log)	kernel overlap	-	**5.26 (<0.01)**	**-1.86 (<0.01)**	**0.52 (<0.01)**	**same 0.04 (<0.01)**	-	-	**Ring 1 300.48 (<0.01), Ring 2 292.01 (<0.01)**	0.99 (0.23)	**1.99 (<0.01)**	-	14.4
Prop. Foraging	binomial (logit)	foraging / rest (1/0)	**DA 4.85 (<0.01), NI 2.41 (0.01), TW 6.98 (<0.01)**	-	**0.50 (<0.01)**	-	-	-	**TW 0.19 (<0.01), NI -0.22 (<0.01)**	**292.74 (<0.01)**	**0.00 (0.44)**	**1.48 (0.01)**	**3.94 (<0.01)**	57.2
Diet	binomial (logit)	Frequency carnivorous	0.00 (0.80)	-	**-1.24 (<0.01)**	-	-	-	-	-	0.97 (0.19)	0.12 (0.29)	0.00 (0.41)	3.8
	binomial (logit)	Frequency planktivorous	**2.55 (<0.01)**	-	0.41 (0.71)	-	-	-	-	-	0.26 (0.30)	0.00 (0.43)	**0.82 (0.01)**	15.8
	binomial (logit)	Frequency cephalopods	2.09 (0.13)	-	**-2.43 (0.02)**	-	-	-	-	-	0.00 (0.74)	**0.77 (0.04)**	0.00 (0.67)	28.5
	gaussian (identity)	$\delta^{15}N$	**3.75 (<0.01)**	-	**12.34 (<0.01)**	-	-	-	-	-	0.04 (0.29)	0.61 (0.11)	**1.93 (<0.01)**	68.0
	gaussian (identity)	$\delta^{13}C$	**3.27 (<0.01)**	-	**-17.81 (<0.01)**	-	-	-	-	-	0.33 (0.21)	0.00 (0.80)	**1.89 (<0.01)**	56.9

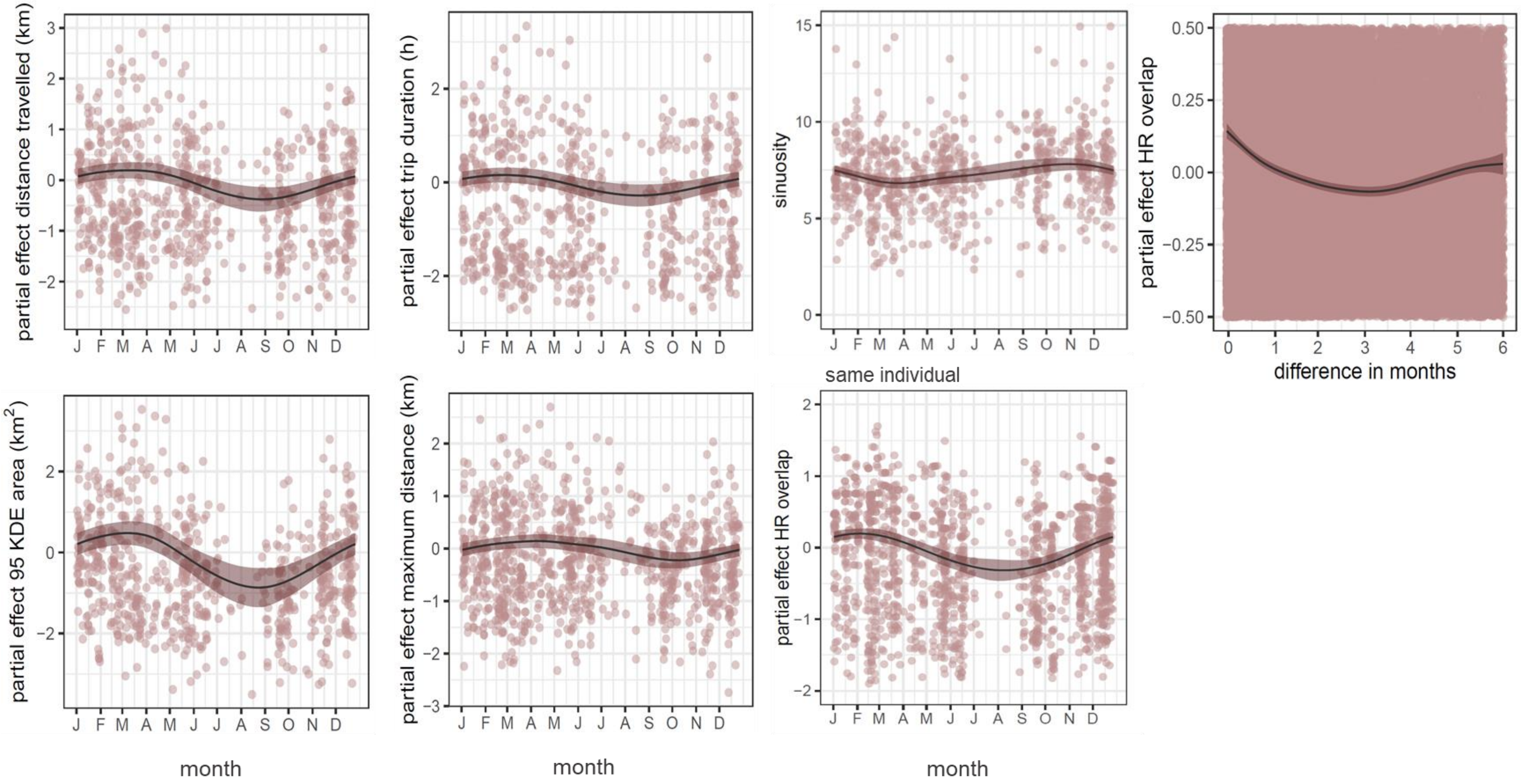


Figure 3. Significant seasonal patterns in tropicbird foraging trip metrics and their spatial overlap. Mean estimated smoothing function (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (shaded area) from generalized additive mixed models of the metrics and spatial overlap in relation to Julian date while taking into the account the effects of individual year, island, and breeding phase as random effects (See table 3). We also present the raw data points in the case of sinuosity and the residuals in other metrics.

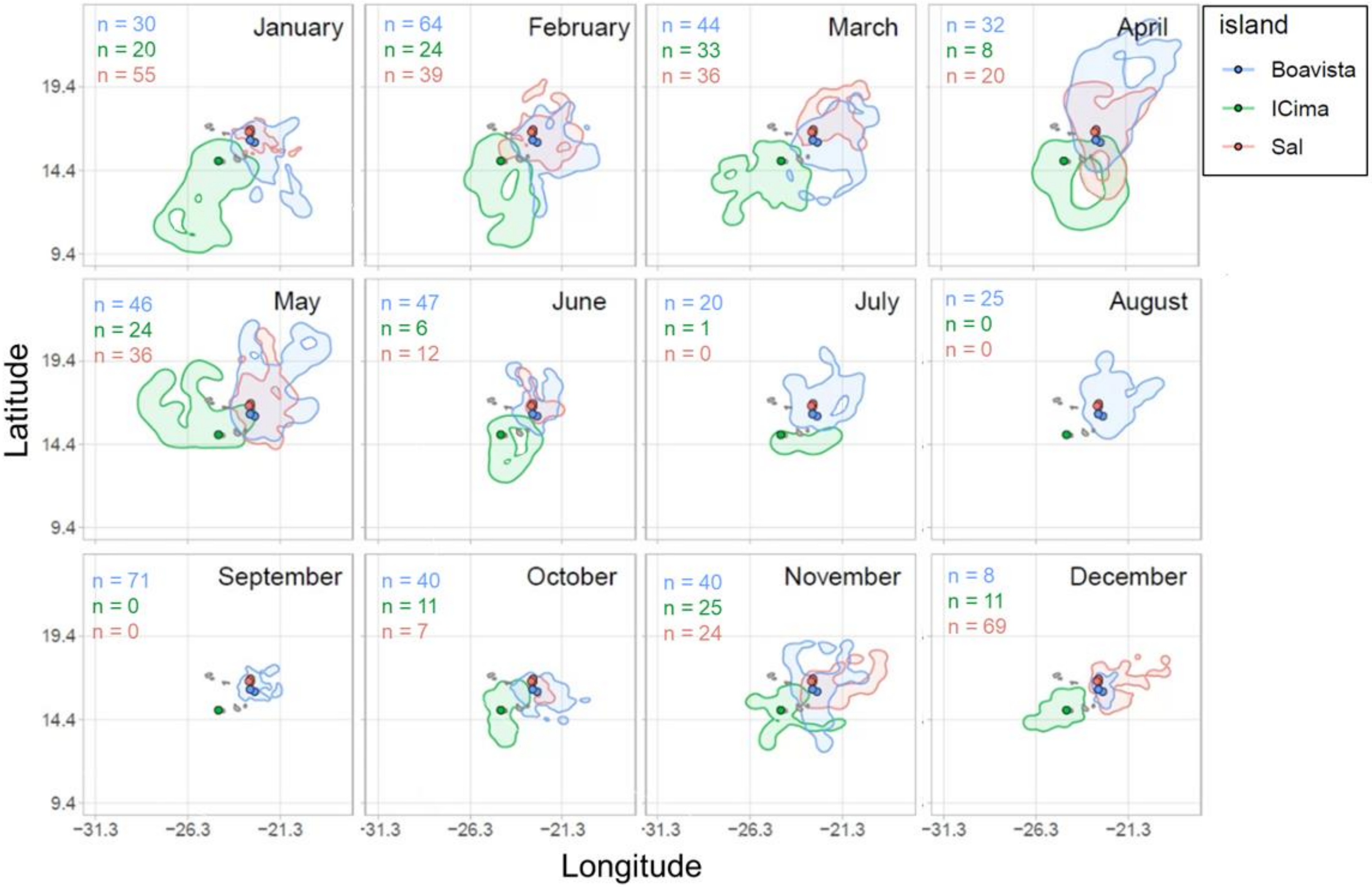


Figure 4. Monthly home range kernels (95% KDE) of breeding Red-billed Tropicbirds from Boavista, Cima islet and Sal. Sample sizes represent the number of trips used to produce each kernel.

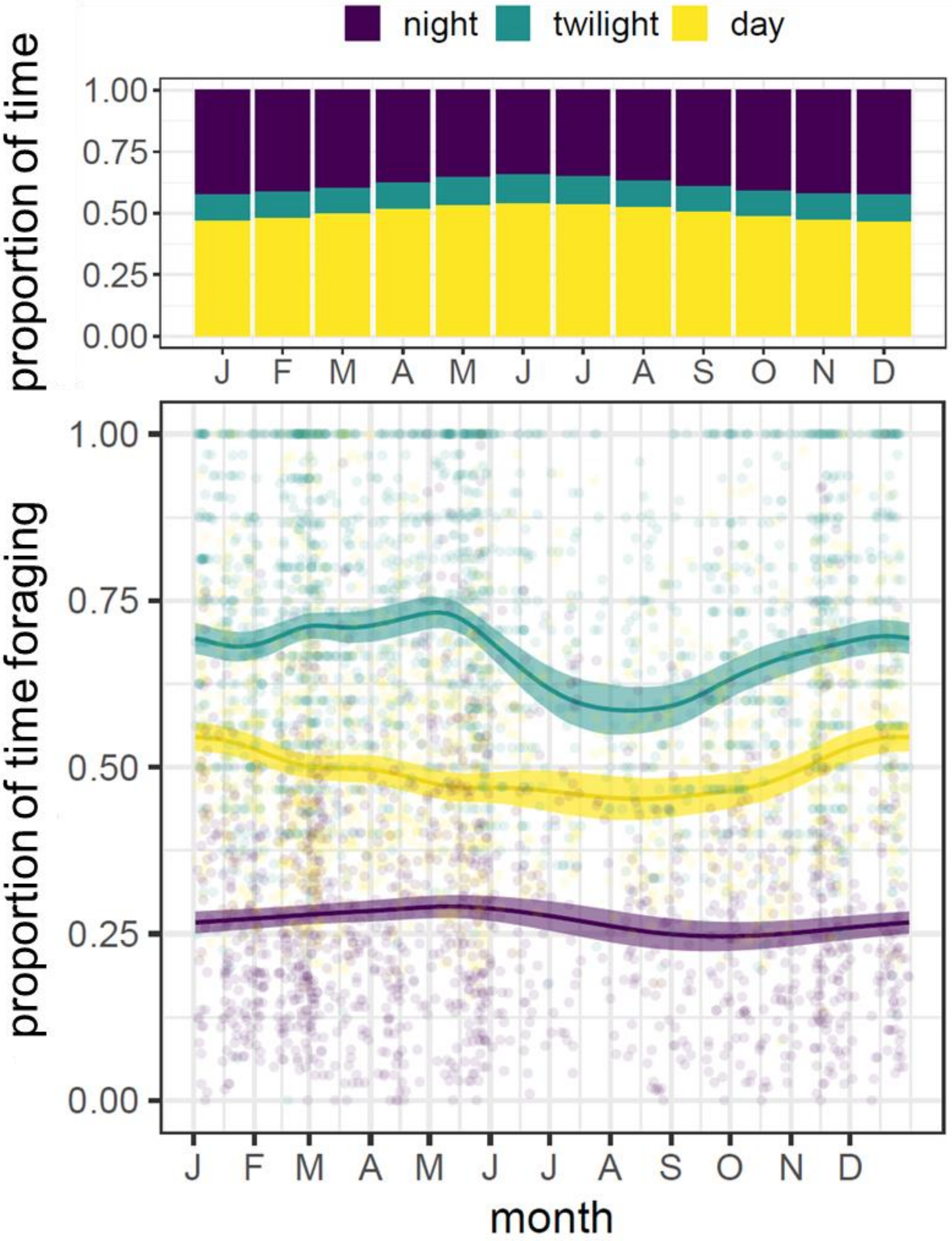


Figure 5. Seasonality of the duration of the day, twilight, and night in Cabo Verde (top) and the proportion of time foraging (bottom) extracted from a generalized additive mixed model of the proportion of time foraging during day, twilight, and night in relation to Julian date while taking into the account the effects of individual, year, island, and breeding phase as random effects (See table 3). The mean estimated smoothing function is shown in solid line with upper and lower confidence intervals at two standard errors above and below the mean (shaded area). We also present the raw data points of the proportion of time foraging per day coloured by day, twilight, and night.

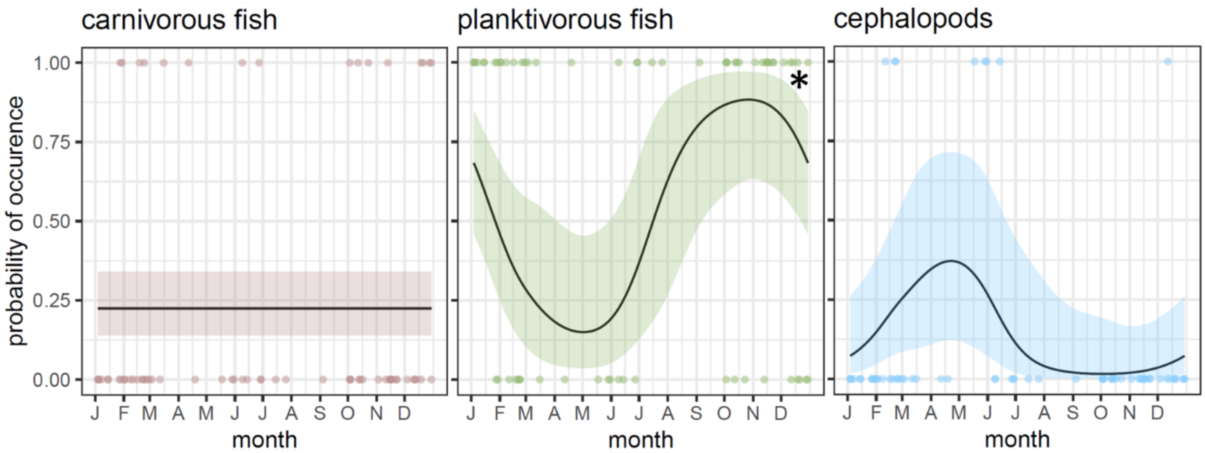


Figure 6. Seasonality in the occurrence (1-presence, 0-absence) of cephalopods, planktivorous fish and carnivorous fish in Red-billed Tropicbird regurgitates. The mean estimated smoothing functions are shown in solid line with upper and lower confidence intervals at two standard errors above and below the mean (shaded area) extracted from generalized additive mixed models in Table 3. Points represent the presence or absence of each ecogroup in the regurgitate samples. Stars indicate significant relationships.

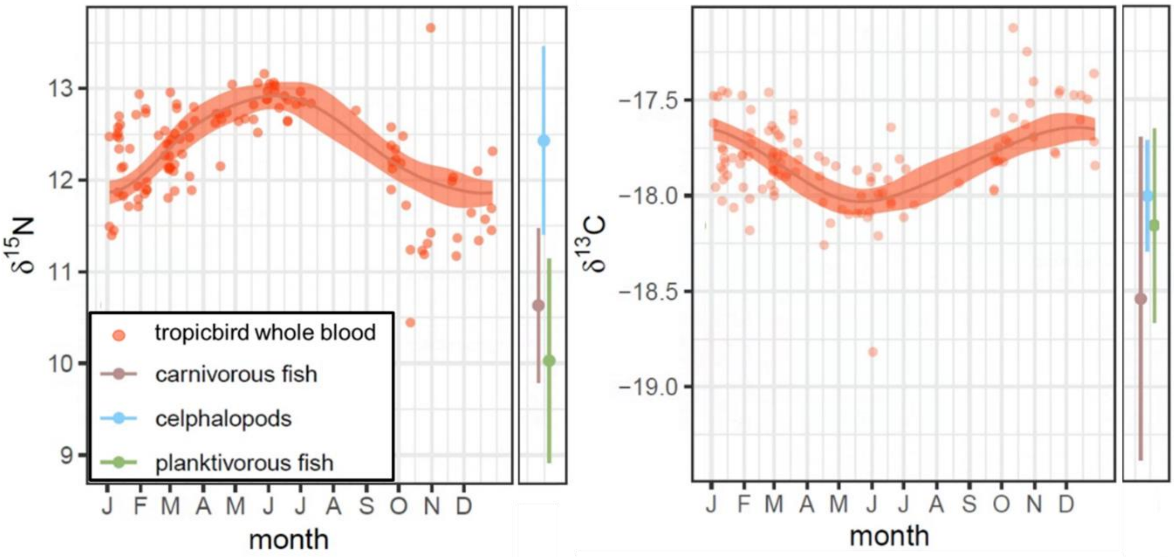


Figure 7. Seasonal variation in the nitrogen and carbon stable isotope values of Red-billed Tropicbird whole blood and mean and standard deviation of stable isotope values extracted from prey muscle tissue separated by ecological prey group (carnivorous fish n=25, cephalopods n=11, and planktivorous fish n=74). Dates represent when blood sampled were collected and therefore stable isotope values represent the values accumulated over the previous month. The mean estimated smoothing functions are shown in solid line with upper and lower confidence intervals at two standard errors above and below the mean (shaded area) extracted from generalized additive mixed models (Table 3). We also present the raw isotope values of tropicbird whole blood as points.

Seasonal patterns in efficiency and fitness

Foraging efficiency

We found no significant seasonal pattern in the relative proportion of weight gained per foraging trip, per km travelled or per hour at sea (Table 4, 6).

Adult condition

We found significant seasonal trends in adult body condition, with a peak in body condition in July (Figure 8, Table 4, 6).

Chick growth and body condition

We found no seasonal trends in tropicbird chick relative weight gain over a 5-day period for chicks between 15 and 30 days old (Table 4). However, we found seasonal trends in the chick body condition index (BCI), suggesting chicks had poorer body condition during the wet season, with the lowest BCI in October and highest in April (Figure 8, Table 4, 6).

Breeding Success

Seasonality in breeding success was only considered for Cima islet because predation of chicks by invasive predators Boavista and Sal caused particularly low fledgling survival (Sal 61%, n=284; Boavista 60%, n=202,4; compared to ICima 74%, n=184) and breeding success (Sal 38%, n=460; Boavista 42%, n=291; ICima 52%, n=261), obscuring any possible seasonal trends. In Cima islet, we found seasonal trends in fledging and overall breeding success of tropicbirds, with a drop in both for nests that hatched in September and October and a peak for nests that hatched or were projected to hatch in April-May (Figure 9, Table 4, 6).

Table 4. Models of seasonal patterns in measures of tropicbird fitness and performance Effective degree of freedom (edf) of non-linear relationships and parametric coefficients of linear parameters. P-values in parentheses. Significant values are in bold.

Seasonal effects	**Link function**	**Response**	**Linear**				**Non-Linear**	**Random effects**							**Deviance Explained (%)**
			Intercept	**after GPS trip (1/0)**	**GPS/no GPS**	**age**	**Julian date**	**individual**	**partners**	**island**	**year**	**breeding phase**	**sex**	**sampler**	
Foraging efficiency	gaussian (identity)	relative weight gain	**0.10 (<0.01)**	-	-	-	0.00 (0.60)	-	-	**1.60 (0.03)**	0.00 (0.70)	-	0.00 (0.47)	-	10.8
	gaussian (identity)	relative gain per hour at sea	**0.00 (<0.01)**	-	-	-	0.00 (0.99)	-	-	0.47 (0.25)	0.00 (0.83)	-	0.38 (0.24)	-	3.22
	gaussian (identity)	relative gain per km	**0.00 (<0.01)**	-	-	-	0.00 (0.96)	-	-	1.46 (0.12)	1.27 (0.20)	-	0.45 (0.17)	-	12.3
Adult condition	gaussian (identity)	BCI	-8.18 (0.50)	after -11.31 (0.10)	-	-	**1.18 (0.03)**	-	-	**0.90 (<0.01)**	1.79 (0.23)	0.00 (0.58)	0.62 (0.11)	0.01 (0.46)	7.49
Chick condition	gaussian (identity)	relative weight gain	**0.50 (<0.01)**	-	-	**-0.01 (<0.01)**	0.00 (0.73)	0.00 (0.68)	-	1.78 (0.27)	0.00 (0.66)	-	-	0.00 (0.56)	11.5
	gaussian (identity)	BCI	0.07 (0.99)	-	-	-	**6.66 (<0.01)**	**86.62 (<0.01)**	-	0.28 (0.22)	0.01 (0.47)	-	-	2.63 (0.17)	44.6
Breeding success	binomial (logit)	hatching success	**1.27 (<0.01)**	-	0.39 (0.19)	-	1.62 (0.10)	-	**37.97 (0.02)**	-	0.00 (0.89)	-	-	-	22.0
	binomial (logit)	fledging success	**1.18 (<0.01)**	-	0.45 (0.19)	-	**1.71 (0.05)**	-	6.99 (0.30)	-	0.00 (0.72)	-	-	-	9.4
	binomial (logit)	breeding success	0.28 (0.23)	-	**0.57 (0.04)**	-	**2.19 (<0.01)**	-	**31.69 (0.04)**	-	0.51 (0.30)	-	-	-	**21.0**

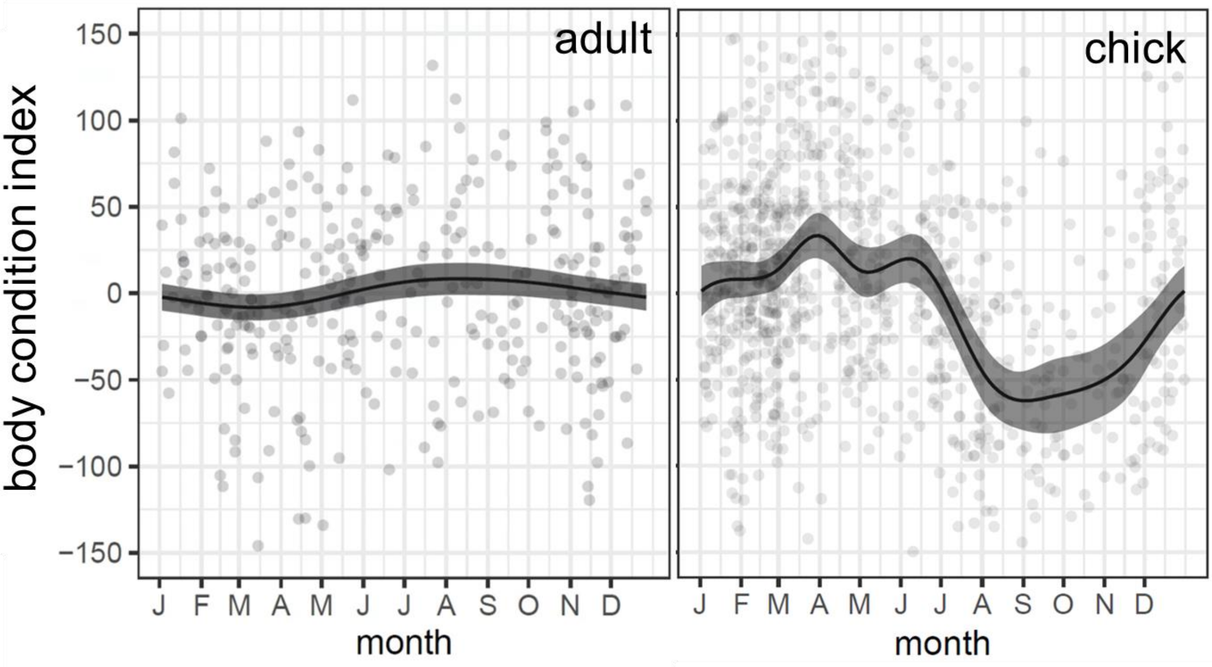


Figure 8. Seasonal trends in tropicbird adult and chick body condition. Mean estimated smoothing function is shown in solid line with upper and lower confidence intervals at two standard errors above and below the mean (shaded area) extracted from a general additive mixed models described in Table 4. We also present the raw data points of the adult and chick body condition index by Julian date. The relationships were significant ($p<0.05$).

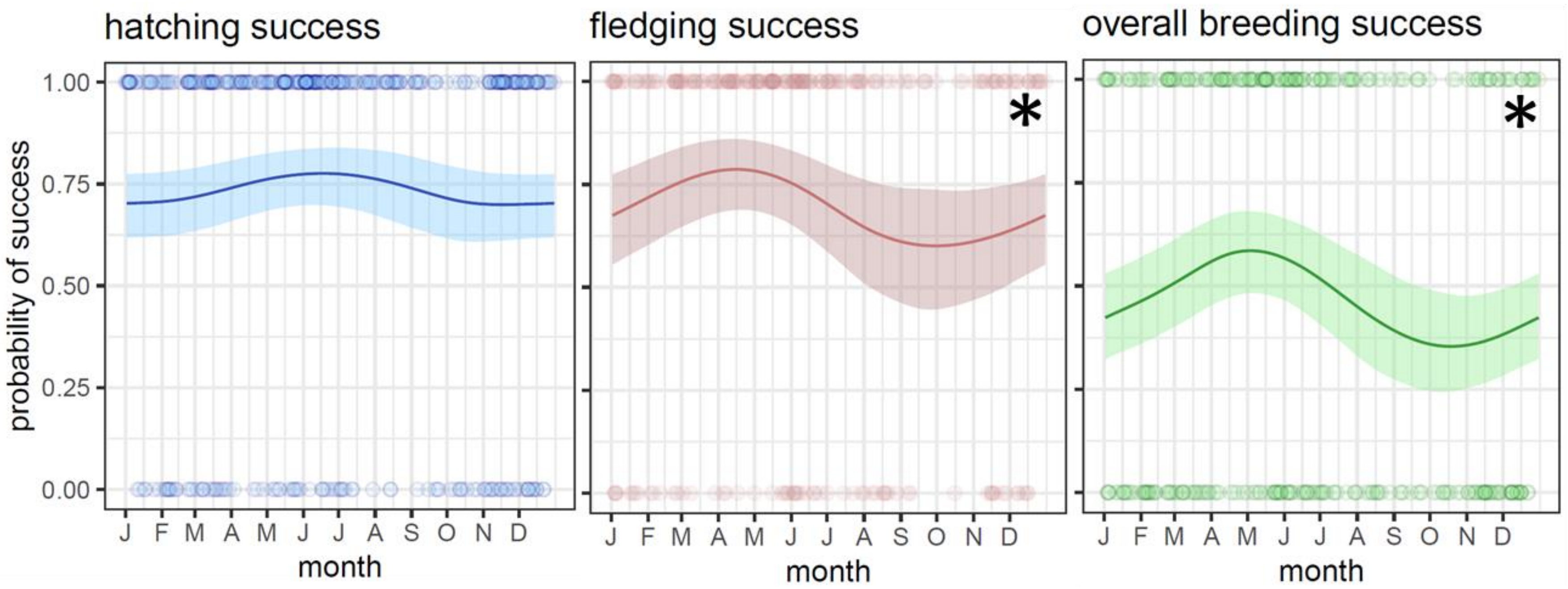


Figure 9. Seasonal differences in hatching, fledging, and breeding success of Red-billed Tropicbirds breeding on Cima islet. For consistency, Julian dates represent the hatching or expected hatching date of the nests in all plots. Mean estimated smoothing function is shown in solid line with upper and lower confidence intervals at two standard errors above and below the mean (shaded) extracted from a general additive mixed models described in Table 4. Points represent the raw data used in these models. Stars indicate significant trends ($p<0.05$).

Seasonal patterns in environmental conditions

Within the minimum foraging ranges of tropicbirds, wind speed, air density and wave height are highest during the dry season and reach their lowest values between August and October, while secchi disk depth is greater in the wet season, peaking in September-October (Figure 10, Table 5, 6). Cloud cover is more variable throughout the year, with a peak in both the dry and wet season, in January and August, respectively (Figure 10, Table 5, 6). At the colony sites, both precipitation and temperature peak during the wet season, between September and October (Figure 10, Table 5, 6).

Although tropicbirds from other localities are affected by inter-annual El Niño events (Castillo-Guerrero et al., 2011), within the time frame of our study, only one of such events occurred (in 2018) and it was considerably weak. As such, an initial analysis found that although there was some variability in environmental conditions between years and colonies, there were similar trends in the seasonal variability of environmental conditions, with peaks and dips at the similar times of year (A5).

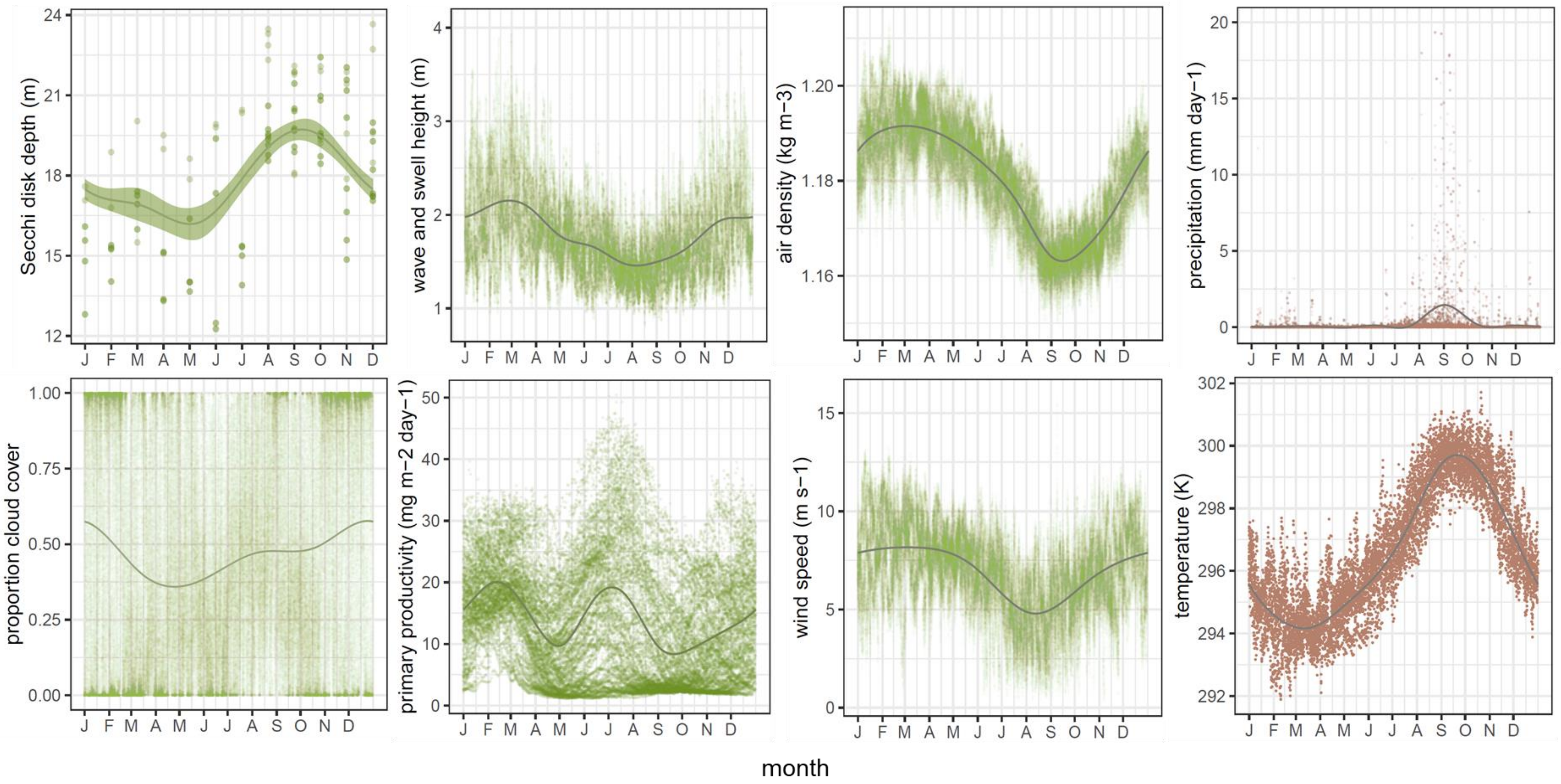


Figure 10. Seasonal variability in environmental variables in the minimum tropicbird foraging range (green) and at the breeding colonies (pink) during the study period. Lines and intervals represent the smoothed relationship and standard error extracted from Generalized additive mixed models (GAMMs) with a Gaussian distribution between the environmental variable and Julian date. Models include random effects for year, island and, in the case of the environmental variables, whether they were extracted from within the chick-rearing or incubation foraging range (Table 5).

Table 5. Models of seasonal patterns of environmental conditions. P-values of non-linear relationships (smoothed terms) and of parametric coefficients in parentheses. All models have a Gaussian distribution.

Driver	Type	Response	Parametric coefficients	Non-linear	Random Effects			Deviance Explained (%)
			Intercept	Julian date	breeding phase	island	year	
Environmental conditions	visibility	Secchi disk depth	**18.96 (<0.01)**	**4.62 (<0.01)**	0.00 (0.84)	**1.96 (<0.01)**	**0.99 (<0.01)**	**71.5**
		Cloud cover	**0.46 (<0.01)**	**4.00 (<0.01)**	**0.91 (<0.01)**	**1.99 (<0.01)**	**4.96 (<0.01)**	**4.3**
		Wave height	**1.80 (<0.01)**	**8.00 (<0.01)**	**1.00 (<0.01)**	**2.00 (<0.01)**	**5.00 (<0.01)**	**36.0**
	flight costs	Wind seed	**6.89 (<0.01)**	**7.99 (<0.01)**	**1.00 (<0.01)**	**2.00 (<0.01)**	**4.99 (<0.01)**	**32.9**
		Air density	**1.18 (<0.01)**	**8.00 (<0.01)**	**1.00 (<0.01)**	**2.00 (<0.01)**	**5.00 (<0.01)**	**85.4**
	resource availability	Primary productivity	**14.03 (<0.01)**	**7.98 (<0.01)**	**1.00 (<0.01)**	**2.00 (<0.01)**	**18.98 (<0.01)**	**50.1**
	brood survival	Mean temperature	**296.53 (<0.01)**	**9.00 (<0.01)**	-	**2.00 (<0.01)**	**5.00 (<0.01)**	**89.4**
		Mean precipitation	**0.25 (<0.01)**	**7.99 (<0.01)**	-	**1.97 (<0.01)**	**4.97 (<0.01)**	**4.9**

Table 6. Summary of seasonal patterns in tropicbird nest occupancy, foraging efficiency, diet, fitness, and environmental conditions.

Variables		Dry Season (Dec-Jun)	Wet Season (Jul-Nov)
Nest occupancy			
Occupancy	Nest occupancy	high	low
Foraging patterns			
Trip characteristics	Maximum distance	high	low
	Distance travelled	high	low
	Trip duration	high	low
	Home range area (95%KDE)	high	low
	Sinuosity	low	high
	Day/overnight trip	-	-
Foraging area	Overlap same individual	high	low
	Overlap different individual	-	-
Activity patterns	Prop foraging day	mid	mid
	Prop foraging twilight	high	low
	Prop foraging night	high	low
Diet			
Regurgitates	Frequency carnivorous fish	-	-
	Frequency planktivorous fish	low	high
	Frequency cephalopods	high	low
Whole blood	$\delta^{15}N$	high	low
	$\delta^{13}C$	low	high
Fitness			
Adult body condition	Adult BCI	low	high
Foraging efficiency	relative weight gain	-	-
	relative weight gain per hour at sea	-	-
	relative weight gain per km	-	-
Chick body condition	relative weight gain	-	-
	chick BCI	high	low

Breeding success	hatching success	-	-
	fledging success	high	low
	breeding success	high	low
Environment			
Visibility	Visibility (Secchi disk depth)	low	high
	Cloud cover	mid	mid
	Wave height	high	low
Flight costs	Wind speed	high	low
	Air density	high	low
Resource availability	Primary productivity	high	low
Brood Survival	Mean temperature at colony	low	high
	Sum precipitation at colony	low	high

Top-down and bottom-up drivers of tropicbird foraging and fitness

Foraging patterns:

We found no critical window of primary productivity within half a year of the foraging trips that predicted any metric better than a randomized model (p>0.05). Therefore, we concluded that primary productivity did not influence tropicbird foraging metrics and it was not included in this series of models.

Principal Component Analysis (PCA) of environmental variables that may affect trip metrics, revealed the importance of the first two PCs (eigenvalue PC1: 1.71, PC2: 1.12), which jointly explained 70% of dataset variability (49 and 21%, respectively). PC1 positively related with air density (0.53), wind speed (0.47), and wave height (0.45), and negatively with temperature (-0.53), indicating harsh conditions. PC2 was positively associated with cloud cover (0.71) and rain (0.69), representing cloudy and rainy conditions.

The best GAMM for predicting distance travelled explained 30.4% of the deviance and included a significant non-linear relationship with PC2 (rainfall; effective degrees of freedom (edf): 5.97, p<0.01) and with the proportion of nests occupied (edf: 4.66, p=0.01). Distance traveled generally increased with cloudy and rainy conditions and initially with nest occupancy, stabilizing once 7.5% of total nests per year and island were occupied during a specific month. (Fig. 11, model selection A6).

The best GAMM for predicting trip sinuosity explained 21.7% of the deviance and only included a non-significant effect with PC2 (rainfall; edf: 1.00, p=0.11), suggesting that the seasonal patterns observed in sinuosity cannot be explained by the environmental and biological factors measured (A6).

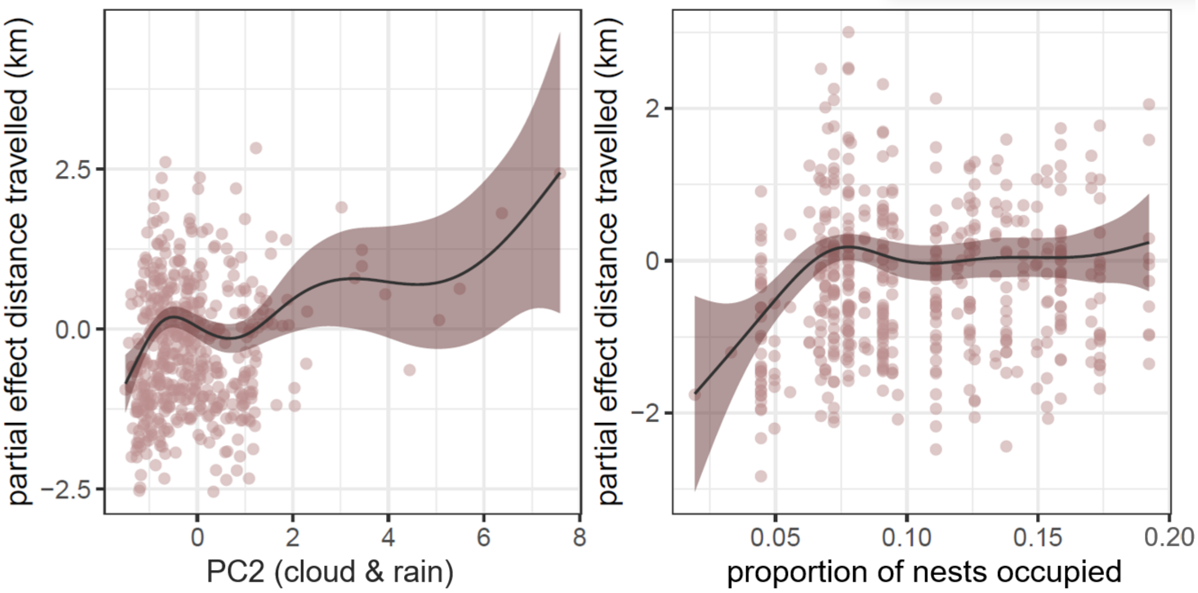


Figure 11. Significant non-linear relationships from the best supported Generalized Additive Mixed models with Gamma distributions of the top-down (nest occupancy) and bottom-up (environmental conditions grouped using Principal Components Analyses) drivers of the distance travelled by a tropicbird during a foraging trip. The distance travelled was related with PC2, representing cloudy and rainy conditions, and the proportion of nests occupied. Shown are the mean estimated smoothing functions (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (shaded). Points represent model residuals. Models include random effects for individual ID, breeding stage, year, and island.

When determining the top-down and bottom-up drivers of the proportion of time spent foraging, we found that critical windows of primary productivity significantly predicted the proportion of time spent foraging during twilight better than randomized models (window: 1-11 weeks, $p<0.01$, n=1626), near-significantly during the day (window: 11-4 weeks prior, p=0.08, n=1294), and non-significantly during the night (window: 22-4 weeks, p=0.14, n=1144). In all cases, the maximum statistic and linear function best explained the relationships. Therefore, for twilight and day, we extracted the values of maximum primary productivity during the critical windows to be analysed alongside the other top-down and bottom-up drivers expected to affect the proportion of time foraging in-situ.

The PCA of the environmental variables related to the proportion of time foraging during twilight and day, revealed the importance of the first three PC's (eigenvalue PC1: 1.70, PC2: 1.11, PC3: 1.01), collectively explaining 73% of the dataset variability (41, 18 and 15%, respectively). PC1 related positively with air density (0.54), wind speed (0.47), and wave height (0.45), and negatively with temperature (-0.53), representing harsh conditions. PC2 related positively with the critical window of productivity (0.63) and negatively with cloud cover (-0.69), representing high productivity and sunny conditions. PC3 related positively with precipitation (0.88) and cloud cover (0.43), representing rainfall.

The best GAMM for predicting the proportion of time spent foraging during twilight explained 17.6% of the deviance and included a significant relationship with PC1 (harsh conditions; edf: 2.64, p=0.05), PC2 (productive and sunny; edf: 1.00, p=0.04), and a non-significant relationship with PC3 (rainy; 1.00, p=0.12). The proportion of time spent foraging during twilight was lowest in mild and extremely harsh conditions, generally increased when productive and sunny during the critical window of 1-11 weeks prior and decreased with rainfall (Figure 12). The best GAMM for predicting the proportion of time spent foraging during day explained 14.4% of the deviance and included a significant relationship with PC2 (productive and sunny; edf: 2.65, p=0.05), with individuals spending more time foraging during in either low or very high productivity and sunniness during the critical window of 4-22 weeks prior (Figure 12, A6).

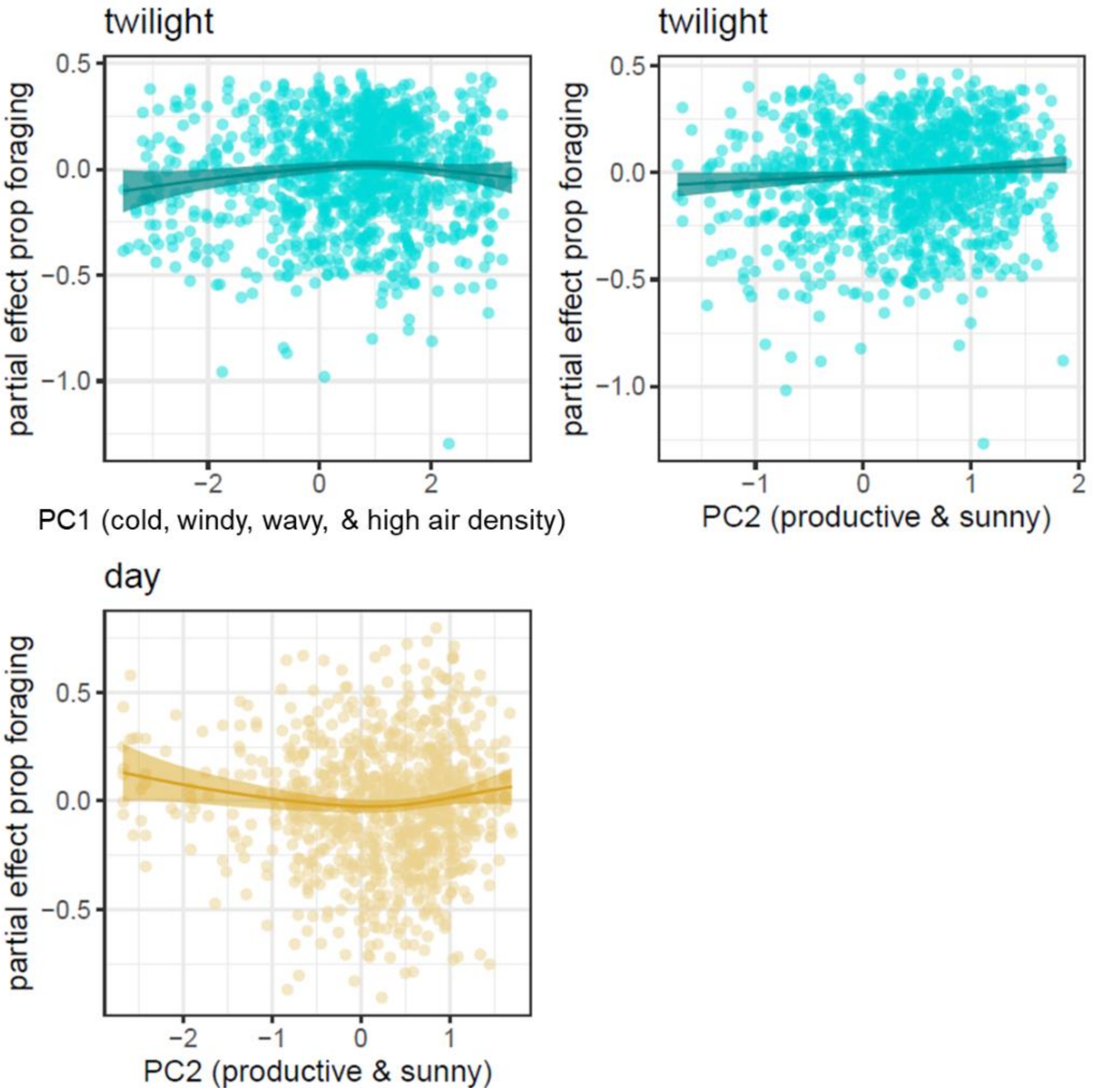


Figure 12. Significant non-linear relationships from the best supported Generalized Additive Mixed models with Gamma distributions of the top-down (nest occupancy) and bottom-up (environmental conditions grouped using Principal Components Analyses) drivers of the proportion of time foraging during twilight (cyan) and day (yellow). The proportion of time spent foraging during twilight was related with PC1, representing harsh conditions, and PC2 representing productive and sunny conditions, while proportion of time spent foraging during the day was only related with PC2. Shown are the mean estimated smoothing functions (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (shaded). Points represent residuals. Models include random effects for individual ID, breeding stage, year, and island.

Diet

When determining the top-down and bottom-up drivers of stable isotope levels in tropicbird blood, our analysis was restricted to 80 blood samples from distinct individuals, for which environmental data was available within one month prior to the blood sampling (isotopes integration rate; Hobson & Clark 1993). The PCA of the environmental variables during these months, revealed the importance of the first two PC's (eigenvalue PC1: 2.12, PC2:1.21), collectively explaining 85% of the variability in the dataset (64 and 21%, respectively). PC1 related positively with wind speed (0.45), wave height (0.45), and air density (0.43), and negatively with temperature (-0.42), representing harsh conditions. PC2 related positively with primary productivity (0.63), and negatively with cloud cover (-0.59), representing productive and sunny conditions.

The best GAMM for predicting $\delta^{15}N$ explained 71.8 % of the deviance and included a significant relationship with PC1 (edf=1.00, $p<0.01$), and PC2 (edf=3.19, $p<0.01$), but not with the proportion of nests occupied. We found that δ15N levels generally decreased in harsh conditions and increased in more productive and sunny conditions (Figure 13)

The best GAMM for predicting $\delta^{13}C$ explained 31.6 % of the deviance and included a significant relationship with PC1 (edf=1.00, $p<0.01$) and PC2 (edf=1.00, $p<0.01$), but not with the proportion of nests occupied. We found that δ13C levels increased in harsh conditions and decreased in more productive and sunny conditions (Figure 13).

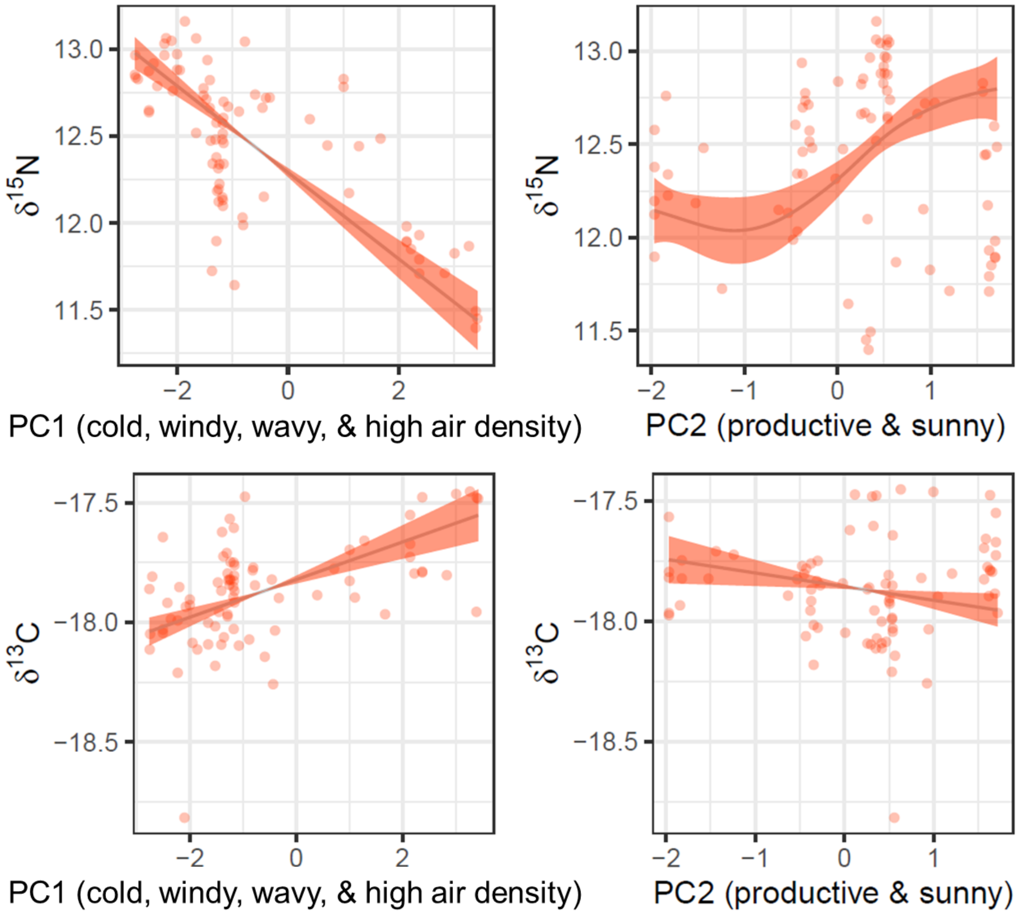


Figure 13. Significant non-linear relationships in the best General Additive Mixed models of the top-down (nest occupancy) and bottom-up (environmental conditions grouped using a Principal Components Analysis) predictors of incubating tropicbird blood isotope ratios of Nitrogen (top) and Carbon (bottom). In both cases, these relationships were with PC1, representing harsh conditions, and PC2 representing productive and sunny conditions. Shown are the mean estimated smoothing functions (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (shaded). We also present the raw data points. Models include random effects for year and island.

Adult body condition

When determining the top-down and bottom-up drivers of adult body condition, we found that all environmental variables had critical windows that predicted body condition significantly better than randomized models (Table 8). These windows were 18-8 weeks (cloud cover), 23-14 week (wave and swell height), 26-13 weeks (wind speed), 19-9 weeks (air density) 18-13 weeks (primary productivity), 20-14 weeks (temperature), and 22-0 weeks (precipitation) prior to the measurement of adult biometry (Table 7).

The PCA of the environmental variables related to adult body condition, revealed the importance of the first and second PCs (eigenvalues PC1: 1.83, PC2:1.25), collectively explaining explained 70% of the variability in the dataset (48 and 22%, respectively). PC1 related positively with to air density (0.48), wind speed (0.45), wave height (0.45), and primary productivity (0.41) and negatively related to temperature (-0.40), representing harsh conditions. PC2 related positively with cloud cover (0.68) and negatively with temperature (-0.41), representing cloudy & cool weather.

The best GAMM for predicting adult body condition included a significant relationship with PC1 (harsh conditions; edf 1.00, p<0.01), PC2 (cool and cloudy; edf 3.61, p<0.01), and with the proportion of nests occupied (edf 4.48, p=0.03; Table 9). We found that adult body condition generally increased in harsh conditions, and decreased in cool and cloudy weather and nest occupancy (Figure 14)

Chick body condition

When determining the top-down and bottom-up drivers of chick body condition, we found that all environmental variables had critical windows that predicted chick body condition significantly better than randomized models (Table 8). These windows were 73-23 days (cloud cover), 58-38 days (wave and swell height), 85-2 days (wind speed), 20-6 days (air density), 23-2 weeks (primary productivity), 34-4 days (temperature), and 21-0 days (precipitation) prior to the measurement of chick biometry (Table 7).

The PCA of the environmental variables related to chick body condition, revealed the importance of the first and second PCs (eigenvalues PC1: 2.03, PC2:1.02), collectively explaining 74% of the variability in the dataset (59 and 15%, respectively). PC1 related positively with wind speed (0.47), and air density (0.45), and negatively with temperature (-0.46), and primary productivity (0.45), representing harsh conditions with low productivity. PC2 was positively related to rain (0.96) during its critical window, representing rainfall.

The best GAMM for predicting chick body condition explained 44.4% of the deviance and included a significant relationship with PC1 (harsh conditions with low productivity; edf=2.46, p<0.01) and PC2 (rain; edf=4.41, p<0.01), but not with the proportion of nests occupied A6). We found that chick body condition generally increased in harsh conditions and decreased with rainfall (Figure 14).

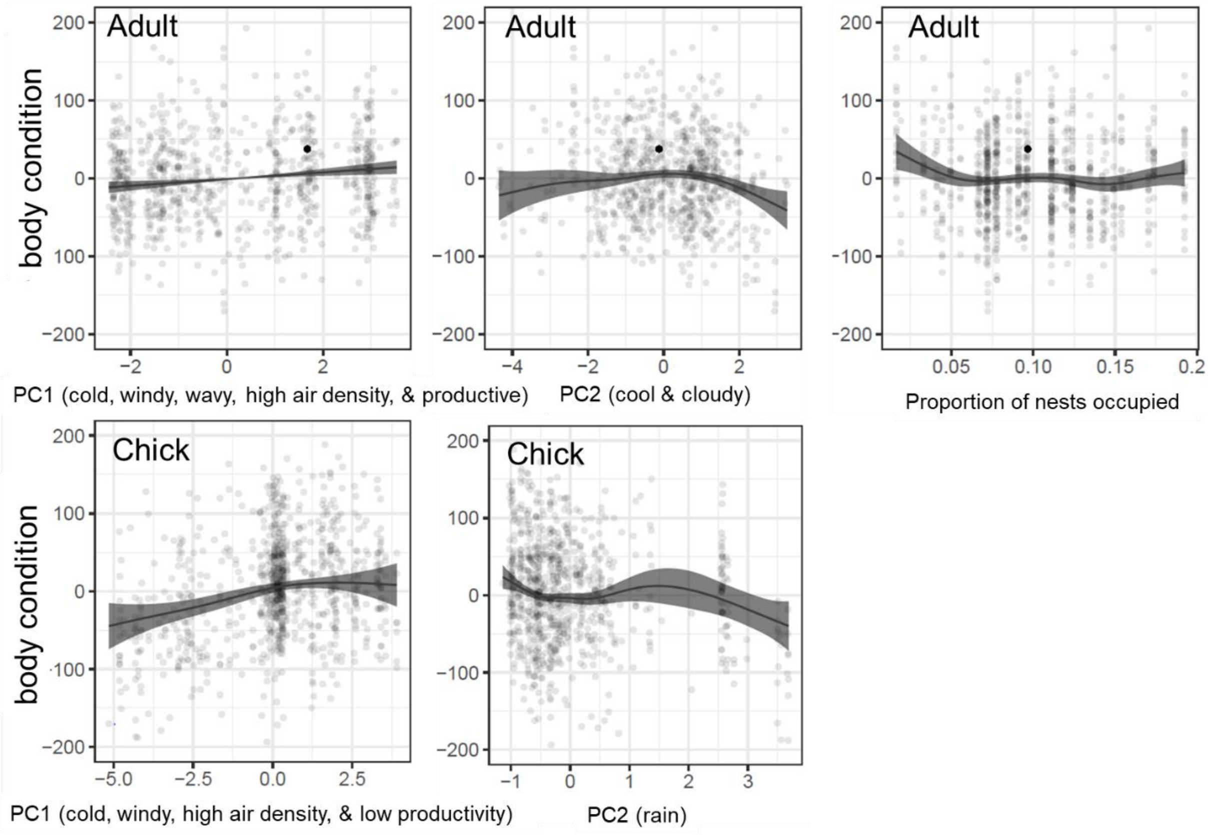


Figure 14. Significant non-linear relationships from the best General Additive Mixed models of the top-down (density dependence) and bottom-up (environmental conditions grouped as Principal Components) drivers of adult (top) and chick (bottom) body conditions. For adult body condition, these relationships were with PC1, representing harsh conditions, PC2 representing cool and cloudy conditions and the proportion of nests occupied. For chick body condition, these relationships were with PC1, representing harsh conditions, and PC2, representing rainfall. Shown are the mean estimated smoothing functions (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (shaded). Points represent residuals. Models include random effects for individual ID, sampler, year, island, and breeding stage (adult only), and a categorical variable for whether the bird carried a GPS or not (adult only).

Table 7. ClimWin analysis of the effects of environmental conditions, showing the best temporal windows, statistics, and functions, for four biological outcomes: tropicbird adult body condition, chick body condition, hatching success, and fledging success. Sample sizes varied based on the temporal availability of the environmental datasets. Significant values marked in bold and highlighted in grey.

Env. Variable	**Biological Outcome**																			
	Adult body condition					**Chick body condition**					**Hatching success**					**Fledging success**				
	window	**p-value**	**stat**	**func**	n	**window**	**p-value**	**stat**	**func**	n	**window**	**p-value**	**stat**	**func**	**n**	**window**	**p-value**	**stat**	**func**	n
Cloud cover	18-8 weeks	**<0.01**	mean	cub	1317	73-23 days	**<0.01**	min	cub	936	40-10 days	0.11	min	quad	243	17-0 days	**0.02**	mean	quad	181
Wave height	23-14 weeks	**<0.01**	min	cub	1317	58-38 days	**<0.01**	min	cub	936	18-4 days	0.15	min	cub	247	68-5 days	0.77	min	cub	181
Wind speed	26-13 weeks	**0.03**	mean	cub	1317	85-2 days	**<0.01**	mean	cub	936	36-5 days	0.32	min	cub	247	76-62 days	0.08	max	cub	181
Air density	19-9 weeks	**<0.01**	min	quad	1317	20-6 days	**0.05**	max	quad	936	41-27 days	**0.04**	max	cub	243	84-70 days	**0.05**	max	quad	181
Primary productivity	18-3 weeks	**<0.01**	min	lin	973	23-2 weeks	**<0.01**	max	lin	917	22-9 weeks	**<0.01**	min	quad	79	24- 5 weeks	0.21	max	cub	50
Temperature	20-14 weeks	**<0.01**	min	quad	1315	31-0 days	**<0.01**	max	cub	936	39-18 days	**0.01**	min	cub	247	84-70 days	**<0.01**	min	quad	181
Precipitation	22-0 weeks	**<0.01**	mean	cub	1119	21-0 days	**<0.01**	mean	cub	926	34-4 days	**<0.01**	max	lin	143	65-51 days	**<0.01**	mean	cub	91

Breeding success

When determining the top-down and bottom-up drivers of hatching and fledging success, we found that air density, precipitation, temperature, primary productivity (hatch only) and cloud cover (fledging only), had critical windows that predicted success better than randomized models (Table 7). For hatching success, these windows were 41-27 days (air density), 22-9 weeks (primary productivity), 39-18 days (temperature) and 34-4 days (precipitation) prior to either hatching or egg failure. For fledging success, these windows were 84-70 days (air density), 17-0 days (cloud cover), 84-70 days (temperature) and 65-51 days (precipitation) prior to either fledging or chick failure.

Unfortunately, since primary productivity data was only available until 2020, while consistent monitoring data in Cima Islet only started in late 2019, we were unable to model nest occupancy and the environmental PC simultaneously as drivers for hatching and fledging success. Therefore, we modelled each variable separately. Moreover, due to a small sample size, modelling the partner ID as a random effect resulted in singularity in the model, therefore, we randomly selected one breeding event per tropicbird pair, resulting in a sample size of 69 nests for hatching success vs environmental variables, 122 for hatching success vs nest occupancy, 59 for fledging success vs environmental variables, and 119 for fledging vs occupancy. We modelled these along with a random effect for year.

The PCA of the environmental variables related to hatching success revealed that only the first PC was of importance (eigenvalue: 1.76). This PC explained 78% of the variance and was positively related to temperature (0.55), precipitation (0.49), and negatively related with air density (-0.54), and primary productivity (-0.41), therefore we considered PC to represent rainy warm conditions with low productivity.

We found that while there was no significant relationship with nest occupancy (edf=2.83, p=0.14), there was a significant relationship between hatching success and the PC representing rainy warm conditions with low productivity (edf: 1.00, p<0.01, Figure 15). Moreover, this model had a higher deviance explained (32.6%) than the nest occupancy model (6.5%).

For fledging success, only the first PC had an eigenvalue over 1 (1.70). This PC explained 72% in the variance and was negatively related with rain (loading -0.42), temperature (-0.56), and cloud cover (-0.43) and positively related with air density (0.57), therefore we considered to PC to represent cold aridity (dry, cold, sunny days with high air density).

We found that the probability of fledging success was lowest when the proportion of nests occupied was at in the mid-range (between 0.10 and 0.15; edf=4.06, p<0.01, n=119, Figure 15). However, there was no significant relationship between the probability of fledging and the PC representing dry, cold sunny days with high air density (edf=3.50, p=0.16). The nest occupancy model with had a higher deviance explained (19.9%), then the environmental PC model (18.5%).

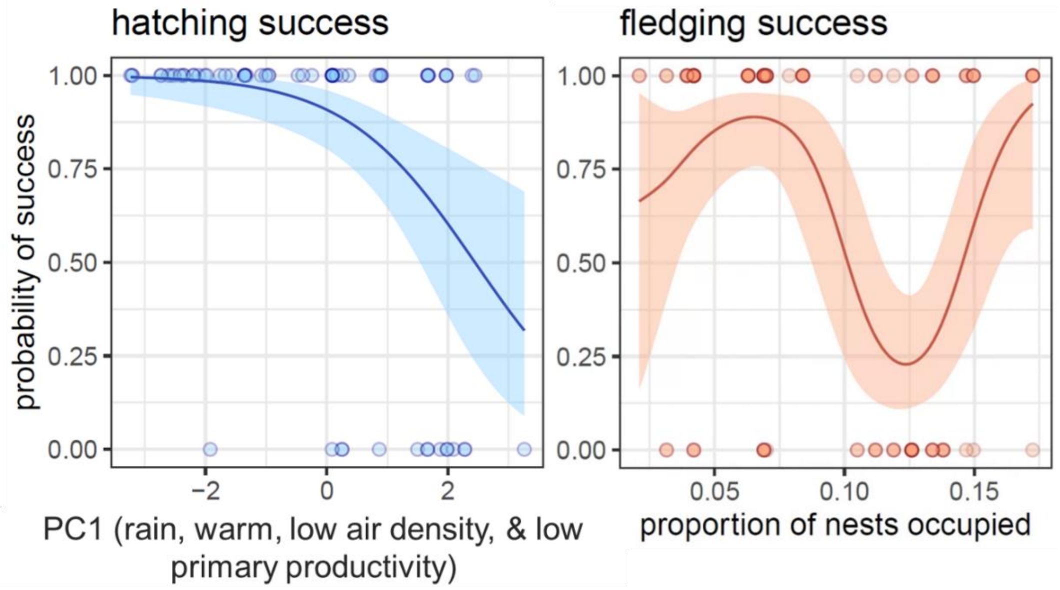


Figure 15. Likelihood of tropicbird chicks successfully hatching (blue) and fledging (orange) in relation to PC1 (rainy, warm, low air density and low primary productivity) and the proportion of nests occupied with a hatching chick during the same month, respectively. Shown is the significant mean estimated smoothing function (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (shaded) extracted from a generalized additive mixed models with the binomial response variables hatching and fledging success (0=failed, 1=success) and a smoothed relationship with the PC1 and the proportion of nests occupied, respectively. Both models include random effects for year and points represent model residuals.

DISCUSSION

Although tropicbirds in Cabo Verde breed year-round, we found consistent seasonal patterns in nest occupancy, foraging patterns, diet, fitness components and local environmental conditions, which together represent changes in both intrinsic and extrinsic pressures that individuals face throughout the year. Peaks in nest occupancy coincided with trends in environmental conditions that resulted in two distinct periods: a dry season (December to June) characterised by low rainfall, and high windspeeds, air density, cloud cover and wave heights, and a wet season (July to November) characterised by high rainfall and good visibility (i.e. increased secchi depth). As in other studies on tropicbirds, tropicbirds breed mainly in the colder dry season (Diop et al., 2018; Hernández-Vázquez et al., 2018). Moreover, as in other studies, there was an association between tropicbird breeding phenology and high primary productivity (Hernández-Vázquez et al., 2018), although, in this case, with a lag of 1-5 months which may represent the turnover period from primary productivity to tropicbird prey. Seasonal patterns in foraging, diet, adult and chick body condition, and breeding success also varied according to these two seasons and primary productivity. During the dry season, individuals foraged across a larger area, spent a larger proportion of time foraging during twilight and night and after a lagged peak in productivity, consumed more squid compared to patterns observed during the wet season. Breeding success was high during the dry season. During the wet season, fewer individuals breed, and those that did took more sinuous trips and foraged closer to the colonies, consuming more planktivorous fish. Although adult body condition was slightly better during the wet season, chick body condition was much higher during the dry season. High nest occupancy coupled with increased breeding success suggests that general conditions in the dry season are preferential, although seasonal differences do not appear to be enough to eliminate breeding in the wet season, during which some disadvantages (e.g. reduced breeding success and lower chick body condition) may be offset by advantages such as a reduction in intra and interspecific nest and foraging competition. We suggest that a combination of seasonal variability in environmental conditions and resource availability are the drivers of the observed patterns in tropicbird foraging behavior, diet, body condition, and breeding success. Specifically, we suggest that our observations are likely related to a combination of three processes relating to changes in prey availability, nest site suitability and weather conditions, and competition for nest sites. Tropicbird's ability to adjust their behavior in response to these changes has implications for how these animals might respond to climate change.

Changes in prey availability as a driver of seasonal changes

In our study, both stable isotope analysis and tropicbird regurgitates indicated an increase in the consumption of cephalopods near the end of the dry season (April-May). This dietary shift to cephalopods also aligns with alterations in foraging behavior, with tropicbirds travelling further and increasing their foraging activity during twilight and night, implying that there are foraging on deeper water prey with diel vertical migrations such as squid (Arkhipkin et al., 2015). This shift can either be attributed to plasticity in tropicbird foraging behavior, enabling them to take advantage of a seasonally abundant of a food resources, or to the decline in availability of a preferred food types near the colony.

Tropicbirds may forage on more cephalopods during this period because of a peak in the abundance of squid. Squid spawning is highly seasonal and related to peaks in primary productivity and increasing sea surface temperatures (Roberts, 2005), resulting seasonal population spikes (Arkhipkin et al., 2015). Although there is little research available on seasonal variation in the abundance of squid in Cabo Verde, one common species, Todarodes sagittatus, spawns in early April in the Canary Current (Piatkowski et al., 1998) and is commonly consumed by seabirds in Cabo Verde, especially those foraging further from the coast, in more pelagic waters (N. Almeida et al., 2021). If spawning is spatiotemporally consistent between years, tropicbirds may travel further to exploit this predictable resource, in an otherwise unpredictable environment. This is also supported by our finding that tropicbirds have a higher foraging site fidelity during this period, which is often associated with foraging success and predictability of food resources (Carroll et al., 2018; Pettex et al., 2010). Moreover, as deep-water species, squid generally store large energy reserves so they can fast for extended periods and maintain near neutral buoyancy over a wide range of depths and pressures (Visser & Jónasdóttir, 1999), which may make them a high-quality food source for seabirds, potentially outweighing the costs of the longer foraging trips needed to take advantage of this seasonally available prey. This increase in the abundance of a high-quality resource is also consistent with the peak in both breeding success and chick body condition at the end of the dry season.

Alternatively, tropicbirds may have modified their foraging behavior and diet during this period because of local resource depletion caused by fluctuations in natural prey cycles (Thiaw et al., 2017) or competition (Ashmole, 1971). The larger travel distances and broadening of the tropicbird diet to include other prey like squid may indicate a local depletion of planktivorous fish around the colony sites. This aligns with the theory predicting that diets of generalist predators become more diverse in response to a decrease in the availability of preferred food types (Perry & Pianka, 1997). For instance, during the 2007 El

Niño event, tropicbirds breeding on the Pacific coast of Mexico responded to the decreased productivity by increasing their consumption of secondary prey (Castillo-Guerrero et al., 2011). However, in this study, the consumption of both squid and flying fish consumption decreased during the El Niño event, indicating that both may be preferred. Moreover, the effect of El Niño events on squid populations is variable (Alabia et al., 2016; Chen et al., 2007; Pecl & Jackson, 2008), and this change in diet may be related to a decrease in the relative abundance of squid and flying fish during this event. Moreover, whether tropicbirds prefer planktivorous fish over squid, remains unknown. In the South Atlantic, Red-billed Tropicbirds mainly feed on squid, whereas in the North, their diet is mainly composed of planktivorous fish (Diop et al., 2018; Madden et al., 2022). Unfortunately, the restricted time frame of previous studies makes it impossible to determine whether these are seasonal changes in diet at these locations as well.

Fluctuations in food availability may also stem from intensified intra and interspecific foraging competition near the colonies, forcing individuals to travel further for resources (Ashmole, 1971). Although this period doesn't coincide with peak nest occupancy, tropicbird chicks take nearly three months to fledge, so a high number of nests may still be occupied by energy-demanding chicks in the spring (Beard et al., 2023), potentially leading to heightened competition for foraging resources. However, in comparison to other colonies in which density-dependent resource depletion was observed (i.e. Oppel et al., 2015; Weber et al., 2021), the population of Red-billed Tropicbirds in Cabo Verde is relatively small (between 2,198 and 5,504 individuals; BirdLife International 2023 Species factsheet). This makes it unlikely that intraspecific competition alone can be the cause of a local depletion of prey (Gaston et al., 2007). Moreover, although the distance travelled initially increased with the proportion of nests occupied, it stabilized rapidly, suggesting that intra-specific competition release would only occur at very low density, which is unlikely. Prey may also be reduced by inter-specific competition. Recent metabarcoding diet analyses of Cabo Verde seabirds, found that the local populations of Brown Booby *Sula leucogaster* and Cape Verde Shearwater *Calonectris edwardsii* are also based on flying fish, suggesting that they may compete for prey with tropicbirds (Carreiro et al., 2023). However, these three species differ greatly in their main foraging areas; Brown Boobies are restricted to day trips relatively close to their colonies (N. M. Almeida et al., 2021), while incubating Cape Verde Shearwaters forage near the continental shelf (Navarro-Herrero et al., 2024; Paiva et al., 2015) and therefore direct competition for resources is unlikely (Gaston et al., 2007). Therefore, we suggest that the dietary shift to squid is more likely driven by a peak in squid abundance than the local depletion of planktivorous fish.

Weather driven changes in nest site suitability

Patterns in foraging behavior, body condition and breeding success may also be driven by weather driven changes in nest site suitability. A decrease in chick body condition, and in fledging and overall breeding success in the wet season, suggests that there is a reproductive cost in breeding during this time of the year. This period is also when both temperatures and precipitation reach their highest in Cabo Verde, which may be impacting nest survival directly through the thermoregulatory needs of the offspring or the collapse/flood of nesting cavities. Red-billed Tropicbirds breeding in the Caribbean were found to have higher breeding success when minimum nest temperatures were lowest (Danielson-Owczynsky, 2022). Moreover, in other tropical species, such as Brown Pelicans (*Pelecanus occidentalis*), an increase in the maximum daily temperature of 1°C resulted in a 40-fold decrease in daily survival rate (Streker et al., 2021). Moreover, during our study period, heavy rain events in September 2018 and 2020 in Cima Islet caused the collapse of at least 2 tropicbird burrows. Therefore, tropicbirds may be taking shorter foraging trips during this period to brood chicks, as the probability of survival increased with nest attendance in other localities (Danielson-Owczynsky, 2022). Interestingly, this relationship is inversed in the adult body condition, which showed better overall condition from June to September. This may indicate that the reasons for the poor body condition of the chicks is not related solely to the foraging efficiency of the adults, but rather the environmental conditions at the nest site, which reduce growth and survival. Otherwise, there may be an extra cost for adults to forage at a greater distance for squid at the end of the dry season. Moreover, environmental conditions in the spring may facilitate foraging close to the colony in the wet season. During this period there was greater visibility related to clearer waters (reduced turbulence, wave, and swell height), and low wind speeds and air density may increase flight costs at this time.

Competition for nest sites

Although our study measured seasonal ecological pressures by using nest-occupancy as a measure of intra-specific competition, we were unable to quantify breeding failure caused directly by competition nor the impact of other ecological pressures, such as predation and inter-species competition, that may be influencing tropicbird phenology and foraging behavior.

In the breeding colonies, however, both intra-and inter-specific competition for nesting cavities has been recorded. Tropicbirds are highly philopatric to their nest site and, intra-specific competition for nest sites can result in nest failure, through the expulsion of the chick from the nesting cavity (directly observed on 4 occasions during our study), and/or adult injury (observed on 2 occasions). Therefore, both intraspecific competition for nests sites may influence seasonal patterns of nests occupancy, favouring reproduction during the wet season, despite the apparent costs to breeding success and chick body condition.

Moreover, in colonies where both Cape Verde Shearwaters and Red-billed Tropicbirds breed, fierce competition for nests sites at the onset of shearwater arrival was recorded, with 41 of 80 pairs breeding on the islet of Raso being expelled from their nest cavities within the first two weeks of Cape Verde Shearwaters arrival (Semedo, 2020). Populations of Cape Verde Shearwaters have been greatly reduced by invasive predators, poaching and bycatch, and although they were previously widespread throughout the archipelago, their breeding range has now mainly been limited to uninhabited islets. Within the current study, Cape Verde Shearwaters were present in one small colony in Sal with 10 Red-billed Tropicbird nests. Even with this small overlap, however, two cases of tropicbird chicks being expelled from their nest upon arrival of the shearwaters in October were recorded. Therefore, although inter-specific nest competition with shearwaters is an unlikely driver of the observed seasonal pattens in tropicbird breeding success in our study area, this does not eliminate the possibility of it being a historical driver of tropicbird breeding phenology within the archipelago.

Climate Change

While our dataset's timeframe wasn't sufficient to explore climate change-induced shifts in tropicbird foraging behavior, phenology, and fitness (Orgeret et al., 2022), understanding how this species adapts to seasonal variations in bottom-up and top-down pressures offers insights into its potential response to climate change. Despite significant plasticity in their foraging behavior and diet, changes in environmental conditions and prey availability across seasons influenced tropicbird body condition and breeding success. This suggests that environmental and ecological changes resulting from climate change may have notable effects on their populations.

Climate change-induced alterations in environmental conditions and prey availability may be expected to impact tropicbirds. In the eastern tropical Atlantic, Climate change is leading to warmer sea surface temperatures, an increase in wind speed and more frequent hurricanes and extreme rainfall events (Cropper et al., 2014; Mann & Emanuel, 2006; Servain et al., 2014). Given the lower reproductive success and chick body conditions during the wet season, these increases in temperatures and rain may eventually restrict the breeding phenology of tropicbirds to the dry season. Climate change-induced phenological shifts caused by microevolution and/or plasticity have already been observed in White-tailed Tropicbirds (*Phaethon lepturus*; Campioni et al., 2023) as well as other tropical species (e.g. Oro et al. 200). Moreover, increases in the frequency of extreme rainfall events may also strongly affect tropicbird reproduction. Previous extreme rainfall events temporarily halved the yearly reproductive output in other tropicbird species (Hennicke & Flachsbarth, 2009).

Furthermore, alterations in environmental conditions lead to species-specific changes in survival, phenology, and distribution. These changes can result in predator-prey mismatches, eventually altering ecosystems (Stenseth & Mysterud, 2002). In the Eastern Atlantic, climate change is expected to have variable impacts on small epipelagic fish and squid populations. For epipelagic fish, climate change in the Canary Current is expected to result in species, specific changes in distribution and abundance (Sambe et al., 2016). In the case of squid, rising water temperatures associated with climate change are expected to benefit squid populations by increasing growth rates and accelerating population turnover (Pecl & Jackson, 2008). However, these elevated temperatures may also result in smaller size and shorter lifespans potentially impacting population structure (Pecl & Jackson, 2008), and habitat squid suitability for commercial squids on the western coast of Africa is expected to decrease with climate change (Guerreiro et al., 2023). Overall, tropicbird prey are expected to exhibit life-history plasticity and rapid responses to environmental shifts driven by climate change, and therefore, the ability for tropicbirds to forage opportunistically and track these changes, may be key to their survival in the face of climate change.

CONCLUSIONS

Our results provide some of the first in-depth knowledge on seasonal variation in foraging behavior of a tropical seabird species, suggesting seasonality in tropical systems may be a stronger driver of the movements of top predators than previously thought. We found that even small changes in environmental conditions and resource availability can have important repercussions on tropicbird foraging ecology, and although this species displayed some plasticity in foraging behavior, these effects translated into differences in fitness metrics throughout the year. This flexibility may give us insight into the adaptability to climate change and the importance of understanding the seasonal variability in behavior.

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DATA AVAILABILITY

GPS Tracking data is available in the Seabird Tracking Database of Birdlife International.

ETHICS APPROVAL

All procedures involving animal manipulations were in accordance with required European legislation. All research and monitoring was conducted under permission from the Direção Nacional do Ambiente from Cabo Verde “Autorização N.º91/2018; Autorização N.º107/2019; Autorização N.º016/DNA/2020”.

SUPPLEMENTARY MATERIAL

S1. Diet analysis

Conventional analysis (prey identification):

To determine whether there were seasonal patterns in tropicbird diet, 73 regurgitates from 69 individuals breeding in Sal and Boavista were collected opportunistically from adults breeding in these islands during nest monitoring. Each sample was originally stored in plastic bags with ethanol, and later frozen. In the lab, we first defrosted and cleaned the samples with distilled water over a 3mm sieve. Then the identifiable prey items and otoliths in each sample were counted, measured, and classified to the lowest possible taxonomic level using morphological identification (Goyena & Fallis, 1988; Schneider, 1990). Due to the level of the digestion of the prey, the identification at species, family, or order level was not always possible. Therefore, we classified the prey into three ecological group levels cephalopods, zooplanktivorous fish, and carnivorous fish for the analysis. We found only one prey item belonging to the crustacean taxon and thus it was excluded from analysis.

Stable isotope analysis

Processing of prey muscle

In addition, stable isotope analyses were undertaken on muscle tissue samples from 110 prey items. For this, we extracted 0.5-2gr of muscle tissue from undigested prey. The muscle tissue was sampled from the epaxial muscle (fish), mantle (cephalopods), or abdomen/thorax (crustaceans). The tissue samples were first oven-dried at 60ºC during 48h, then ground down and twice agitated in a 1:2 chloroform:methanol solution for 24 h (Hobson & Welch 1992). Tissue samples were then oven-dried again at 60°C for 48 h to remove remaining solvent and divided into approximately 1 μg subsamples for stable isotope analysis. To understand the isotopic variation of tropicbirds in relation to the isotopic values of their prey, we segregated the prey by ecologic group, as in the conventional analysis (carnivorous fish, zooplanktivorous fish, and cephalopods).

Processing of blood

We collected 64 blood samples from adult tropicbirds to identify seasonal patterns in nitrogen and carbon stable isotope values. These samples were stored in 100% ethanol while in the field and, and later frozen at -20ºC. One in the lab, we lyophilized blood samples for 24 hours at -50ºC and 0.3 millibars and weighed subsamples (0.19–0.29 mg) in tin capsules.

Stable isotope analysis (SIA) of prey muscle and tropicbird blood samples

The blood and muscle samples were analysed through Elemental Analysis with the Isotopic Ratio Mass Spectrometer Flash EA1112, conducted at the Centres Científics i Tecnològics of the Universitat de Barcelona. We expressed the isotope ratios as δ values in part per mil (‰), according to the following equation:

$\delta X=[(Rsample/Rstandard) - 1]$,

Where X is 13C or 15N and R is the 13C/12C or 15N/14N ratio for the sample and the standard respectively. International standards are Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric air (AIR) for nitrogen (Weiser & Powell, 2011). International laboratory (IAEA N1, IAEA N2, IAEA CH7, IAEA 600, USGS 40) and internal laboratory standards (Acetanilide, Fructose, UCGEMA P and Urea) were analysed every 12 blood samples to compensate for any drift over time and obtain the correct values of δX with an overall precision of 0.2‰.

S2. Description of biometric measurements taken from Red-billed Tropicbird chicks and adults.

Metric	Description
Weight	Mass measured using a Pesola spring balance to the nearest gram.
Wing length	flattened wing length from the carpal joint to the tip of the longest primary. Measured using a ruler to the nearest 1 mm
Tarsus length	tarsus length from the distal point of the inter-tarsal joint to the foot. Measured using a calliper to the nearest 1 mm.
Bill depth	Perpendicular length from the top to the bottom of the bill starting at the junction with the skull. Measured using a calliper to the nearest 1 mm.
Culmen	length from the base of the skull to the tip the bill. Measured using a calliper to the nearest 1 mm
Head-bill length	bill trip to the posterior ridge formed by the parietal-supraoccipital junction. Measured using a calliper to the nearest 1 mm.

S3. Monthly home range kernels

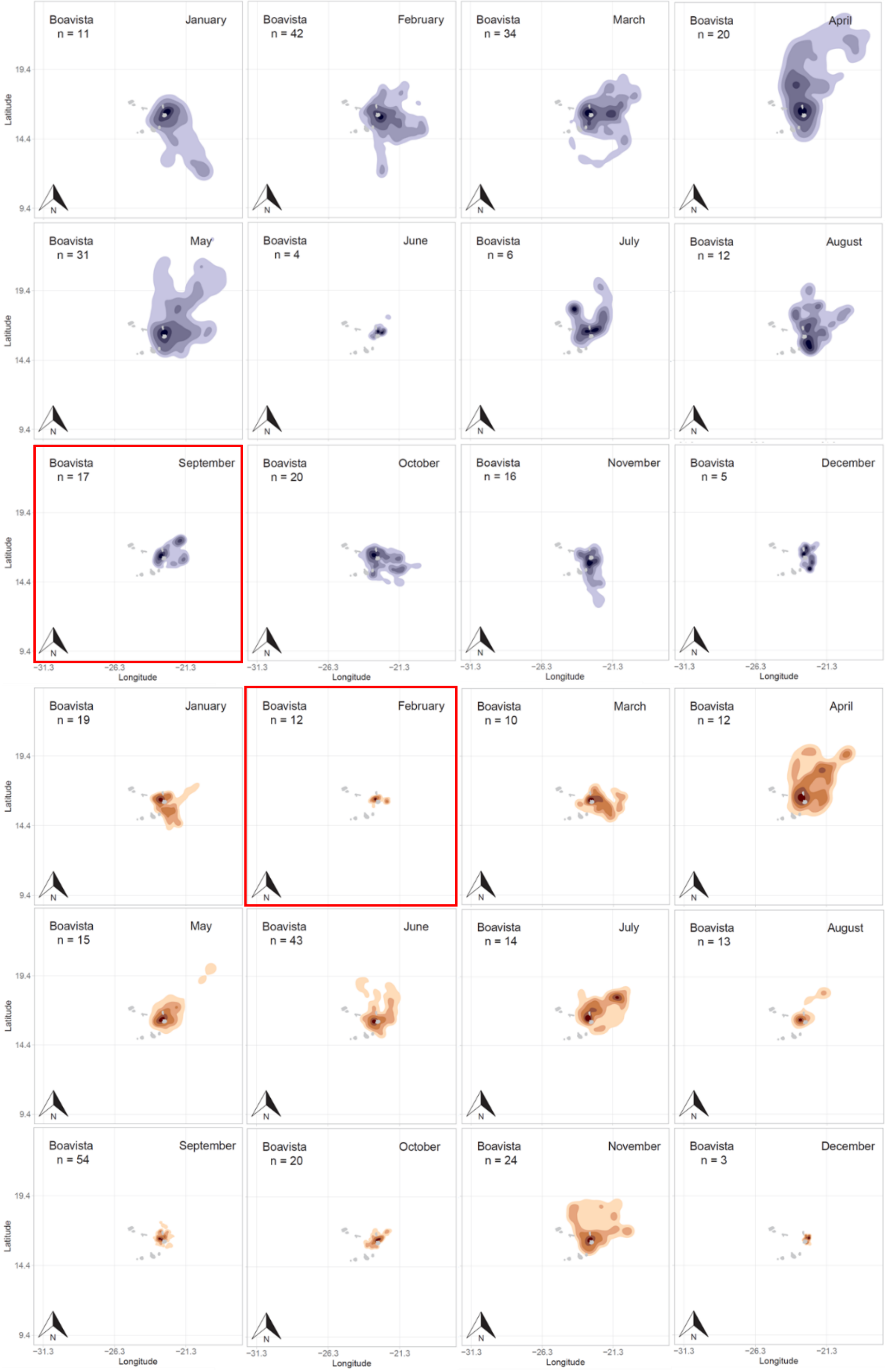

Figure 1. Monthly home range kernels (95, 75, 50, 20, 5 KDE) of incubating (blue) and chick-rearing (Orange) Red-billed tropicbirds breeding in Boavista. Months indicated in red represent the smallest monthly kernel built on over 10 trips, which were used to extract environmental data for this island and breeding stage.

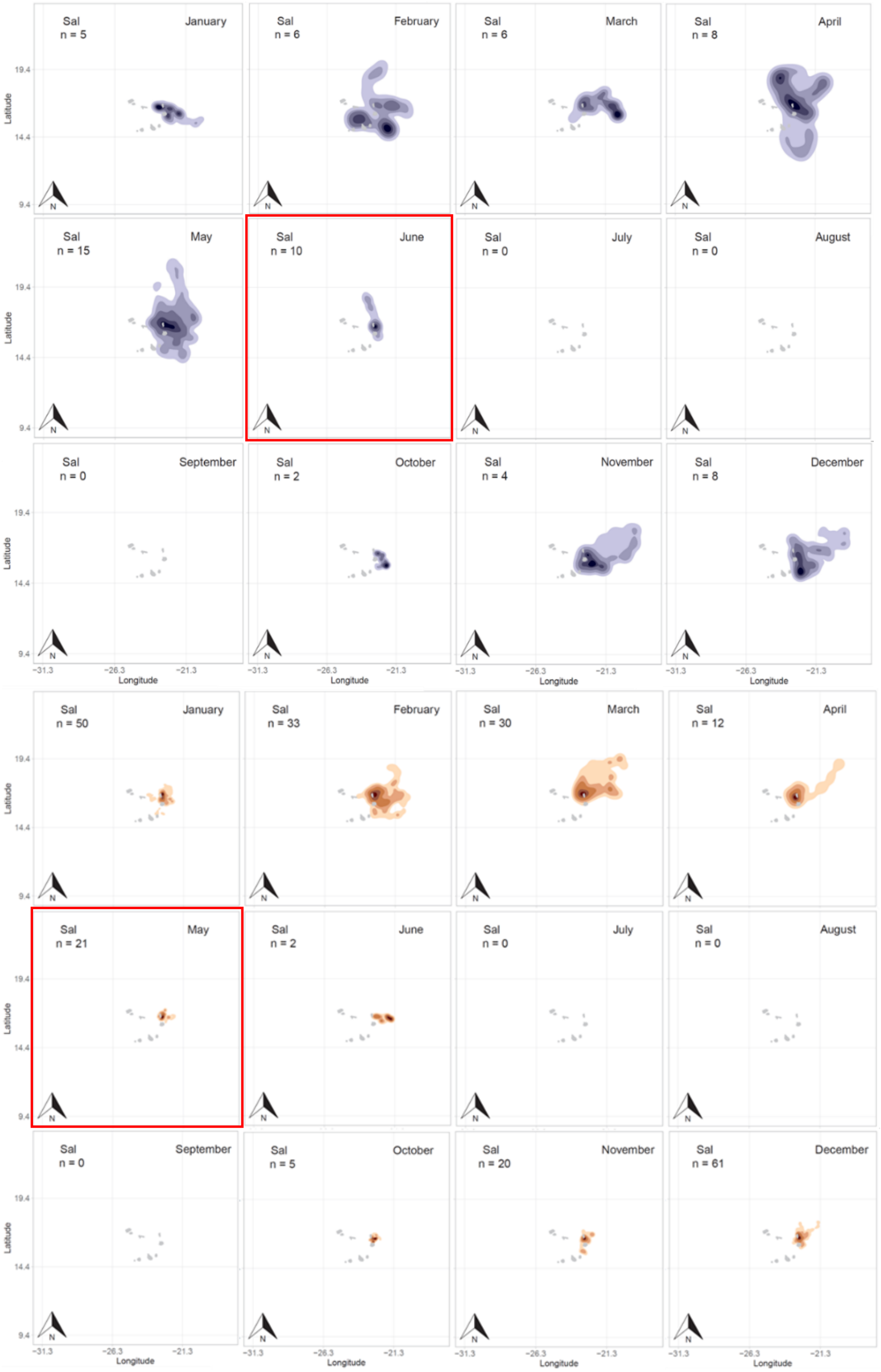

Figure 2. Monthly home range kernels (95, 75, 50, 20, 5 KDE) of incubating (blue) and chick-rearing (Orange) Red-billed tropicbirds in breeding in Sal. Months indicated in red represent the smallest monthly kernel built on over 10 trips, which were used to extract environmental data for this island and breeding stage.

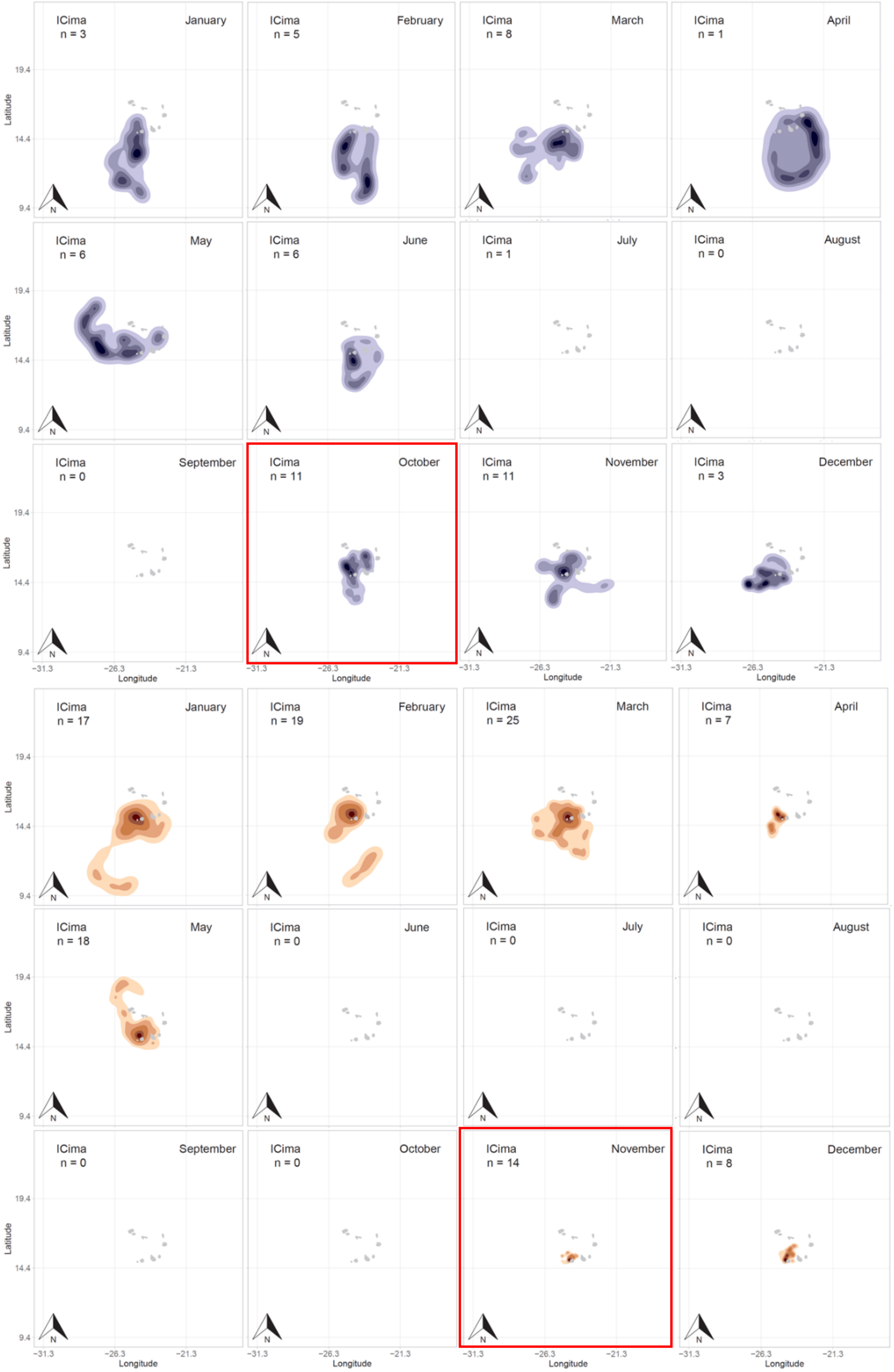

Figure 3. Monthly home range kernels (95, 75, 50, 20, 5 KDE) of incubating (blue) and chick-rearing (Orange) Red-billed tropicbirds in breeding in Cima islet. Months indicated in red represent the smallest monthly kernel built on over 10 trips, which were used to extract environmental data for this island and breeding stage.

S4. ClimWin Analysis

Using the “slidingwin” function, we created a series of models using four descriptive metrics of environmental variables (mean, max, min, and sum) extracted from time periods of all window sizes within half a year before each biological outcome (e.g. end of foraging trip, predicted hatch/fledging etc) for primary productivity and within the mean duration of incubation (41 days) and chick-rearing (84 days) for all other environmental variables related to eggs (hatching success) and chicks (fledging success and chick body condition), respectively. For primary productivity, we chose to look for windows up to half a year prior to the biological outcomes since the timeframe for the conversion of primary productivity to tropicbird prey is unknown. For the environmental variables related to hatching and fledging success, we searched for windows within the incubation and chick-rearing period respectively, as we assumed these could have cumulative effects on 1) the progenitor’s foraging ability and nest attendance during these periods, or 2) the thermoregulation and survival of the egg sand chicks. Since we did not have prior knowledge of the aspect of the relationships, we modelled each relationship with three functions (linear, quadratic, and cubic). When appropriate, we also included random intercepts for breeding stage, island, individual, and progenitors to control for their effects. Then, for each biological outcome, we selected the best window, descriptive metric (mean, max, min or sum) of the environmental variable and the best function (linear, quadratic, or cubic) for the relationship based on the model with the lowest AICc. Next, to avoid over-fitting the models, we determined whether the relationship between the environmental variables of the selected window and the biological outcomes was greater than expected by chance. To do this, we used the “randwin” function of the same package to compare the distribution of AICc values of the best-supported models with 100 randomized data sets of the environmental variables and considered the relationship to be reliable only when the probability of obtaining the AICc of the best-supported models through randomization was less than 0.05 (van de Pol et al. 2016).

S5. Consistency in seasonal patterns

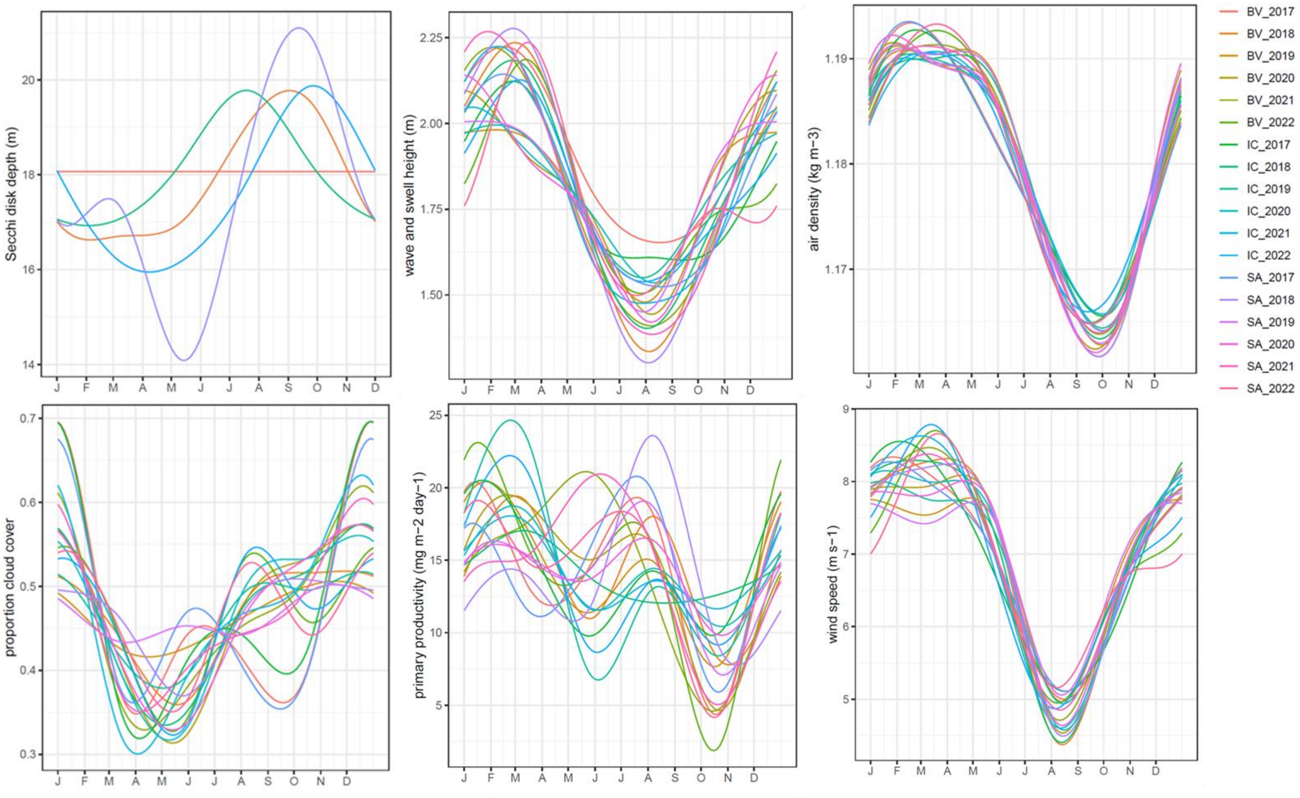

Figure A5.1: Consistency of seasonal patterns of environmental variables in Red-billed Tropicbird minimum foraging range between years and islands. Each line represents the smoothed relationship extracted from a GAM model with a Gaussian distribution between the environmental variable and Julian date extracted within the minimum foraging range for birds breeding on each island and year. Abbreviations: SA=Sal, IC=Cima Islet, BV=Boavista.

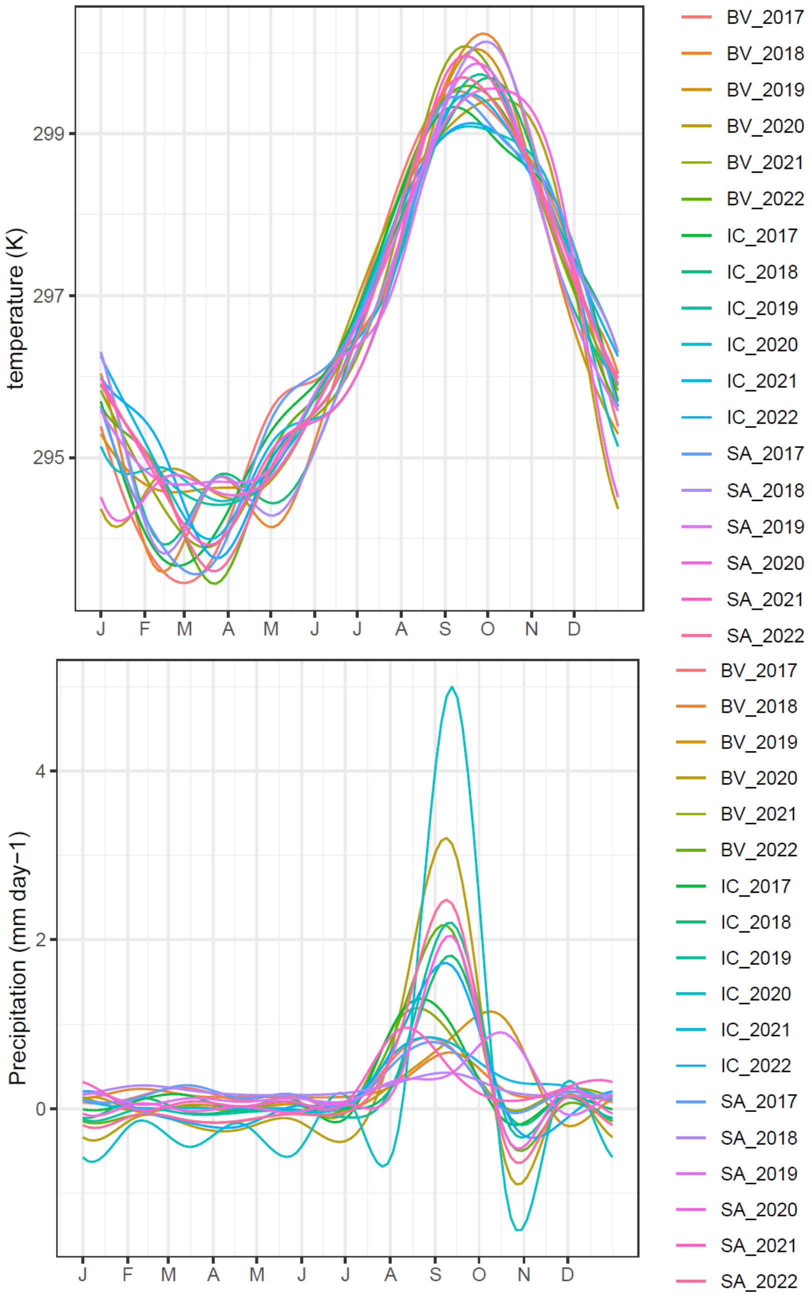

Figure A5.2. Consistency of seasonal patterns of environmental variables recorded at Red-billed Tropicbird colony sites between years and islands. Each line represents the smoothed relationship extracted from a GAM model with a Gaussian distribution between the environmental variable and Julian date extracted at the colony site for birds breeding on each island and year. Abbreviations: SA=Sal, IC=Cima Islet, BV=Boavista.

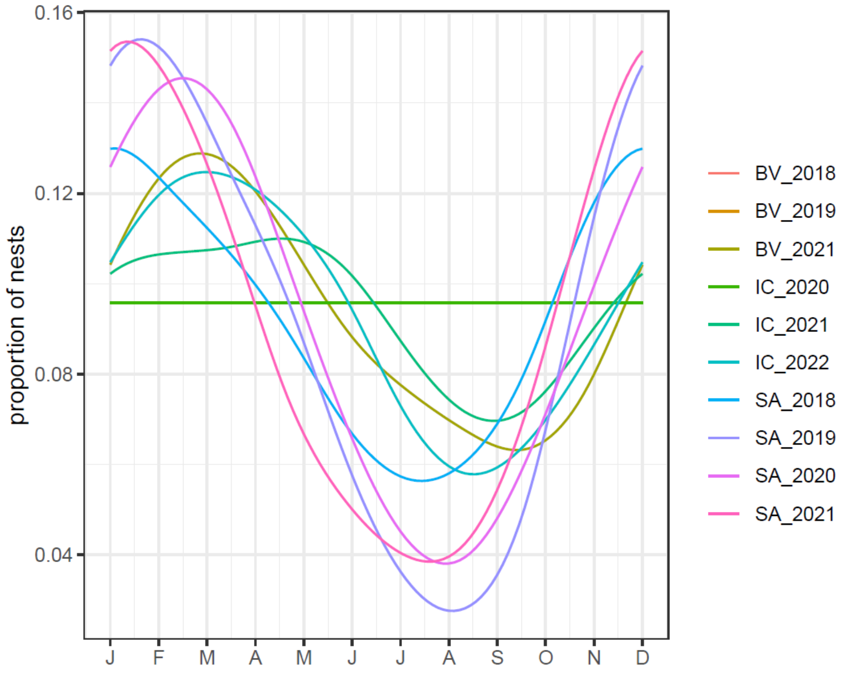

Figure A5.3. Consistency of seasonal patterns nest occupancy between years and islands. Each line represents the smoothed relationship extracted from a GAM model with a Gaussian distribution between the proportion of nests occupied in each island and year and Julian date. Shown are only the year-island combinations for which there were at least 8 months with over 5 days of fieldwork. Abbreviations: SA=Sal, IC=Cima Islet, BV=Boavista.

S6. Model Selection bottom-up and top-down drivers of Metrics

Table S6.1 Model selection of bottom-up and top-down drivers of metrics. Shown are the minimum number of models to sum a weight of 0.95. Models marked with *included random intercepts for individual ID, breeding stage (incubation or chick-rearing), year, island, ** included random intercepts for breeding stage, year, and island, *** included random intercepts for individual ID, breeding stage, year, island, and sampler, **** included random intercepts for individual ID, year, island, and sampler, and ***** included random intercepts for year, only.

Model	**df**	**LogLik**	**AIC**	**Δ AIC**	**weight**
Distance travelled *					
PC2 (rain & cloud) + Prop. nests occupied	**45**	**-3064.73**	**6221.4**	**0.00**	**0.84**
PC1 (cold, windy, wavy, low visibility & high air density) + PC2 (rain & cloud) + Prop. nests occupied	**45**	**-3062.79**	**6224.8**	**3.35**	**0.16**
Sinuosity *					
PC2 (rain & cloud)	**50**	**-940.03**	**1981.2**	**0.00**	**0.36**
NULL	**50**	**-940.76**	**1981.7**	**0.57**	**0.27**
PC1 (cold, windy, wavy, low visibility & high air density) + Prop. nests occupied	**51**	**-940.25**	**1984.0**	**2.86**	**0.09**
PC1 (cold, windy, wavy, low visibility & high air density) + PC2 (rain & cloud) + Prop. nests occupied	**52**	**-939.46**	**1984.1**	**2.93**	**0.08**
PC1 (cold, windy, wavy, low visibility & high air density)	**54**	**-938.04**	**1984.8**	**3.62**	**0.06**
PC1 (cold, windy, wavy, low visibility & high air density) + PC2 (rain & cloud)	**54**	**-937.71**	**1985.1**	**3.90**	**0.05**
Prop. nests occupied	**50**	**-941.91**	**1985.4**	**4.19**	**0.05**
Proportion of time foraging during the day *					
PC2 (productive & sunny)	**47**	**431.92**	**-769.4**	**0.00**	**0.28**
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny)	**47**	**432.04**	**-768.1**	**1.61**	**0.12**
PC2 (productive & sunny) + PC3 (rain & cloud)	**48**	**432.24**	**-767.9**	**1.79**	**0.11**
PC2 (productive & sunny) + Prop. nests occupied	**48**	**432.35**	**-766.7**	**2.04**	**0.10**
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny) + Prop. nests occupied	**49**	**432.91**	**-766.6**	**2.96**	**0.06**
Null	**42**	**425.48**	**-766.3**	**3.13**	**0.06**
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny) + PC3 (rain & cloud)	**49**	**432.36**	**-766.3**	**3.40**	**0.05**
PC2 (productive & sunny) + PC3 (rain & cloud) + Prop. nests occupied	**49**	**432.65**	**-765.8**	**3.40**	**0.05**
PC3 (rain & cloud) + Prop. nests occupied + Prop. nests occupied	**42**	**425.68**	**-765.1**	**3.86**	**0.04**
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny) + PC3 (rain & cloud) + Prop. nests occupied	**50**	**433.19**	**-764.9**	**4.60**	**0.03**

PC1 (cold, windy, wavy, & high air density) + Prop. nests occupied	**43**	**425.50**	**-764.8**	**4.79**	**0.03**
PC3 (rain & cloud)	**43**	**425.58**	**-764.9**	**4.87**	**0.02**
Proportion of time foraging during twilight *					
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny) + PC3 (rain & cloud)	**75**	**361.99**	**-572.5**	**0.00**	**0.47**
PC1 (cold, windy, wavy, & high air density) + PC3 (rain & cloud)	**73**	**358.17**	**-569.7**	**2.79**	**0.12**
PC2 (productive & sunny) + PC3 (rain & cloud) + Prop. nests occupied	**78**	**363.43**	**-568.9**	**3.55**	**0.08**
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny) + Prop. nests occupied	**79**	**368.87**	**-568.5**	**3.99**	**0.07**
PC3 (rain & cloud) + Prop. nests occupied	**76**	**362.63**	**-568.4**	**4.06**	**0.06**
PC2 (productive & sunny) + PC3 (rain & cloud)	**78**	**356.90**	**-568.1**	**4.36**	**0.05**
PC1 (cold, windy, wavy, & high air density)	**73**	**364.12**	**-567.4**	**5.02**	**0.04**
PC2 (productive & sunny)	**80**	**364.12**	**-566.9**	**5.58**	**0.03**
PC3 (rain & cloud) + Prop. nests occupied	**76**	**359.46**	**-566.8**	**5.70**	**0.03**
δ15N in whole blood **					
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny)	**8**	**2.77**	**11.00**	**0.00**	**0.52**
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny) + Prop nests occupied	**7**	**1.47**	**12.2**	**1.22**	**0.28**
PC1 (cold, windy, wavy, & high air density) + Prop nests occupied	**14**	**7.77**	**13.6**	**2.59**	**0.14**
PC1 (cold, windy, wavy, & high air density)	**11**	**4.16**	**15.4**	**4.46**	**0.06**
δ13C in whole blood **					
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny)	**4**	**22.30**	**-41.5**	**0.00**	**0.55**
PC1 (cold, windy, wavy, & high air density) + PC2 (productive & sunny) + Prop nests occupied	**5**	**26.18**	**-40.6**	**0.92**	**0.35**
PC1 (cold, windy, wavy, & high air density)	**4**	**22.21**	**-37.1**	**4.44**	**0.06**
Adult body condition***					
PC1 (cold, windy, wavy, high air density & high productivity) + PC2 (cool & cloudy) + Prop nests occupied + after GPS (yes/no)	**158**	**-4308.12**	**8933.1**	**0.00**	**0.64**
PC1 (cold, windy, wavy, high air density & high productivity) + PC2 (cool & cloudy) + after GPS (yes/no)	**158**	**-4308.53**	**8934.7**	**1.63**	**0.29**
PC1 (cold, windy, wavy, high air density & high productivity) + PC2 (cool & cloudy) + Prop nests occupied	**159**	**-4309.82**	**8938.6**	**2.57**	**0.04**
Chick body condition ****					
PC1 (cold, windy, high air density, & low productivity) + PC2 (rain)	**104**	**-4817.69**	**9843.5**	**0.00**	**0.61**

PC1 (cold, windy, high air density, & low productivity) + PC2 (rain)+ Prop nests occupied	**104**	**-4817.42**	**9844.8**	**1.31**	**0.32**
PC2 (rain)	**102**	**-4821.55**	**9848.6**	**5.14**	**0.05**
Hatching Success vs environment *****					
PC1 (rainy, warm, low productivity, low air density)	**3**	**-24.34**	**56.5**	**0.00**	**1.00**
Hatching Success vs nest occupancy *****					
Null	**1**	**-70.30**	**142.6**	**0.00**	**0.69**
Prop. Nests occupied	**3**	**-68.45**	**144.4**	**1.63**	**0.31**
Fledging Success vs environment *****					
PC1 (cold aridity)	**4**	**-35.70**	**79.9**	**0.00**	**0.69**
Null	**1**	**-39.75**	**81.5**	**1.63**	**0.31**
Fledging Success vs occupancy *****					
Prop. Nests occupied	**8**	**-56.26**	**128.7**	**0.00**	**1.00**

Picture by Marcos Hernández-Montero

Chapter 3. Seasonality in a tropical asynchronous migrant

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In preparation for submission

ABSTRACT

In polar and temperate regions, strong seasonality in environmental conditions drives animal phenology, resulting in synchronous breeding and migration timings. The association between phenology and seasonality is less pronounced in tropical systems, where environmental conditions remain relatively constant throughout the year. As a result, many species exhibit asynchronous or year-round breeding patterns. In these cases, the drivers of migration and migratory strategies are more ambiguous since the environmental conditions surrounding the breeding areas are presumably adequate for the species year-round. Here, we investigated whether seasonal changes in migratory patterns and non-breeding areas relate to changes in oceanographic conditions in the Red-billed Tropicbird (*Phaethon aethereus*), a poorly studied pantropical species that breeds year-round in Cabo Verde. Specifically, we first investigate whether there are seasonal patterns in tropicbird non-breeding areas and evaluate whether these patterns are consistent at the individual level. We then investigated whether there are seasonal differences in activity patterns and whether these differences differ between migratory stages. Finally, we determine whether seasonal patterns are related to season-specific environmental niche tracking between the breeding and non-breeding period or through population-wide habitat preferences. From 2017 to 2022, we monitored tropicbird nests at three islands (Boavista, Sal and the Cima Islet) and GLS tracked 111 individuals, extracting 149 migratory trips. Almost all birds were migratory, but dry season breeders migrated to the central Atlantic north of Cabo Verde, while wet season breeders migrated west of Cabo Verde. We found a higher overlap between repeated migrations from the same individual and those breeding around the same time of year, indicating individual and seasonal repeatability of non-breeding areas. Although we did not find evidence of season-specific niche-tracking, tropicbirds shifted their non-breeding areas to avoid seasonal extremes in Sea Surface Temperatures (SST) and air density, effectively remaining within a similar range to what they experience year-round in

Cabo Verde waters. We suggest that this range of SST and air density represent population-wide habitat preferences. Our results provide some of the first in-depth knowledge on the seasonal variation in the non-breeding areas of a tropical seabird and suggest that even a weak seasonality in tropical systems may be a strong driver of the migratory movements of top predators than previously thought.

Keywords: Seasonality; tropical ocean; seabird; phenology; non-breeding area; migration

INTRODUCTION

Seasonality and the predictable intra-annual changes in climate and resources that it entails are major drivers of animal phenology (Dufour et al., 2020; Forrest & Miller-Rushing, 2010). To cope with seasonal changes, many species synchronize reproduction with favorable conditions and avoid unfavorable ones or negative ecological interactions such as predation or competition through migration, a seasonal round-trip movement between breeding and non-breeding regions (Alerstam et al., 2003; Dufour et al., 2020; Winger et al., 2019). As an evolutionary adaptive trait, migration can improve fitness by increasing both reproductive success and survival (Shaw & Couzin, 2013; Winger et al., 2019) and is observed in a wide array of taxa in both marine and terrestrial environments (Chapman et al., 2014; Hobson & Norris, 2008). Through migration, species can either track preferred climatic conditions year-round (niche tracking, e.g. Gómez et al., 2016; Péron & Grémillet, 2013; Ramos et al., 2015; Shaffer et al., 2006) or occupy different climatic niches at different periods of their annual cycle (niche switching, e.g. Lambert & Fort, 2022; Martínez-Meyer et al., 2004; Nakazawa et al., 2004; Quillfeldt et al., 2020).

In the last decades, the study of migration and migratory strategies has rapidly progressed due to breakthroughs in remote tracking technologies. Particularly, light-level geolocators have facilitated the study of migratory ecology at the individual level and through multiple annual cycles, shedding light on the within and between individual variability in migratory strategies. Within populations, individual migrations can differ in direction, routes, distance, and location of non-breeding areas and can include various stopovers and stages along the way (e.g., Alves et al., 2012; Finch et al., 2017; Vardanis et al., 2016). In the most extreme cases of variability, some species are partial migrants, with some individuals undertaking migratory journeys to distant locations, while others remain close to the breeding grounds year-round (Newton, 2012). Within a species, these strategies can differ between populations (Ramos et al., 2016), ages, classes (Péron & Grémillet, 2013), sexes (Deakin et al., 2019; C. Pérez et al., 2014), or individuals (Pérez, 2019).

This population-wide variability in migratory strategies results in individuals from the same breeding population experiencing disparate ecological environments and pressures throughout their life cycles (Boyle, 2008; Chapman et al., 2011; Grayson & McLeod, 2009), which can result in among-individual variation in key fitness components (i.e. survival and/or reproductive performance (Alves et al., 2013; Grist et al., 2017; Gunnarsson et al., 2005; Lago et al., 2019; Méndez et al., 2018). Moreover, differences in migratory strategies and phenologies can result in assortative mating based on the timing of arrival at the breeding sites (Morrison et al., 2019), which can influence not only breeding success but also the population's genetic structure (Gilsenan et al., 2017; Grist et al., 2017). Individual variation in migratory behavior can therefore have population-scale implications.

By studying individual migration over multiple annual cycles, it is possible to determine whether individuals consistently use the same migratory strategy (individual repeatability) or whether they can switch strategies between years (adaptability). Both have their specific advantages. By repeatably migrating to the same areas, individuals benefit from prior knowledge of the availability of key resources and predator or competitive avoidance, facilitating individuals to optimize their migratory phenology and non-breeding habitat use (Gill et al., 2014; Gunnarsson et al., 2004; Winger et al., 2019). However, in a changing environment, the ability to modify individual migratory phenology and non-breeding areas to track ideal conditions may be more advantageous (Gilroy et al., 2016).

In polar and temperate regions, strong seasonal changes in environmental conditions often result in population-wide phenological synchrony since the costs of a temporal mismatch between key phenological stages and environmental conditions are high or even fatal. In these environments, organisms generally synchronize their phenology and movements to coincide with periods with high resource availability (e.g., insect emergence (Youngflesh et al., 2023) or spring green up (Nemes et al., 2024) and/or to avoid the fitness or survival cost of local competition or seasonal resource-depletion (Alerstam et al., 2003; Cresswell et al., 2013). Conversely, in tropical regions where climatic conditions are generally more homogeneous (Longhurst, 1995), the association between phenology and seasonality weakens, leading to asynchronous or year-round breeding (Lundberg, 1988). In these cases, the drivers of migration are more ambiguous since the environmental conditions surrounding the breeding areas are presumably adequate for the species year-round (Lambert & Fort, 2022). However, although weakened, many tropical environments do exhibit at least some climatic seasonality (such as changes in precipitation; Vázquez & Stevens, 2004, this thesis chapter 2), which can result in seasonal differences in foraging ecology and fitness (Esparza et al., 2022, this thesis chapter 2). However, very few studies have tracked individual foraging movements in tropical species, leaving many questions about how variable their migratory strategies are and what drives them (Franklin et al., 2022a; Franklin et al., 2022b; Jaeger et al., 2017; Pinet et al., 2011).

Seabirds, as highly mobile marine top predators, exhibit various migratory strategies. While all seabirds are central place foragers during the breeding season, during the non-breeding season, some species may range widely throughout marine habitats (Weimerskirch & Wilson, 2000) while others remain resident year-round. As such, and due to the low availability of breeding sites (Coulson, 2002), many seabird species breed colonially (Causey & Kharnitonov, 1990) and may experience resource depletion near colony sites (Ashmole, 1971). However, during the non-breeding period, individuals may travel unhindered by constraints of central place foraging and occupy a wide array of marine environments.

In the face of climate change, investigating species' adaptability to environmental change and its cascading effects on ecological interactions is important for evaluating threats and developing management strategies. In a meta-analysis of the phenology of worldwide seabird populations between 1952 and 2015, seabirds had not adjusted their breeding seasons over time or in response to sea surface temperature, suggesting a particular vulnerability to climate change impacts (Keogan et al., 2018). This same meta-analysis underlines significant knowledge gaps about the adaptability of tropical species to environmental change. Understanding the drivers of seasonal changes in tropical oceans can shed light on the evolutionary constraints acting upon species in these poorly studied systems.

We aim to identify how asynchronously breeding topical species adapt their migratory strategies to seasonality year-round. To achieve this, we focused on Red-billed Tropicbirds (*Phaethon aethereus*), a poorly studied pantropical species that breed year-round in Cabo Verde. Recent studies have found seasonal differences in this species' foraging ecology during the breeding season (this thesis chapter 2) and that breeding and migratory phenology for this species are highly repeatable at the individual level and heritable (this thesis chapter 4). This begs the question of whether this species adapts to seasonal changes via its migratory strategies and whether these differences are also repeatable at the individual level. Specifically, we GLS tracked 111 individuals for one to 3 years to determine whether 1) there are seasonal patterns in tropicbird non-breeding areas and whether these patterns are consistent at the individual level, 2) there are seasonal differences in activity patterns and whether these differences differ between migratory stages, and 3) seasonal patterns are related to season-specific environmental niche tracking between the breeding and non-breeding period or through population-wide habitat preferences. By enhancing our understanding of how Red-billed Tropicbirds adapt their migratory strategies to seasonal changes, we shed light on broader patterns of sensibility of tropicbirds to environmental change.

METHODS

Field site

Field work took place in Cabo Verde, located approximately 600 to 850 km west of Senegal, Africa, on the southern boundary of the Canary Current Large Marine Ecosystem (Valdés & Déniz-González, 2015), at the eastern edge of the North Atlantic subtropical gyre (Fernandes et al., 2005). In particular, data collection took place across three colonies situated on Boavista and Sal islands, and a single colony on the islets of Raso and Cima in Cabo Verde in 2008-2009 and from 2017 to 2022.

Nest monitoring & Geolocator deployment & recovery

To monitor breeding success and to deploy and recover GLS, nests were generally visited every 1-3 days, but some isolated nests (<5%) were only visited monthly. At each nest visit, the contents of the nest were recorded (empty, chick/egg, and whether there was an adult or not) to determine breeding success and to deploy and recover light-level geolocators (GLS). We deployed 133 Migrate Technology Ltd C330 and Biotrack BAS_MK19 GLS on 111 different individuals on Red-billed Tropicbirds breeding on Raso in 2008-2009 and at the remaining study sites in 2009 and between 2017-2021. Breeding individuals were captured whilst on the nest using noose-poles and GLS were attached with cable-ties to their metal identification ring. Devices were opportunistically recovered in subsequent breeding seasons. Since monitoring was inconsistent at certain times of the year and at more isolated nests, data breeding success (hatching success and fledging success) were only used in analysis when the window of uncertainty for these data was less than 30 days. Whenever possible, 1ml of blood was also drawn from the tarsus of individuals, for molecular sexing (Griffiths et al., 1998) and morphometrics (wing length, culmen, head and bill length, tarsus and bill height) were measured to calculate and index of skeletal size using a principal component analysis (S1).

The total tag weight of the GLS used was approximately 3.3g (0.5% of tropicbird mean tropicbird weight 630g±55, n=1297 individuals). During both deployment and recovery of GLS, birds were handled for the shortest time possible and immediately released back on to their nest after handling. Migrate Technology GLS recorded light intensities every minute, maximum light intensities every five minutes and conductivity (salt-water immersion data) every six seconds, while Biotrack GLS recorded both light intensity and wetness every 10 minutes. All GLS underwent at least one pre-deployment calibration near colony sites at an unshaded known location for a minimum of 3 days (Lisovski et al., 2020). Upon recovery, a single post-deployment calibration at a known site was performed on GLS. Data from all available pre- and post-deployment calibrations were used to estimate the corresponding average zenith angle for each deployment, using the designated software IntiProc© from *Migrate Technology Ltd*. In cases for which post-recovery calibration was not possible, due to battery failure or technical issues with GLS, pre-deployment calibrations alone were used to calculate zenith angles (n=15). For devices which were deployed on birds for multiple years, each seasonal migration was analysed separately.

GLS data processing

We used the raw light-level data downloaded from recovered GLS to estimate the latitude and longitude of individuals each day, throughout the duration of the GLS deployment. This was done based on sunrise and sunset transitions identified with the function “preprocesslight”, using a light intensity threshold of 2, in the R package GeoLight (Lisovski et al., 2020; Lisovski & Hahn, 2012). This package was also used to visualise and manually repair sunrise and sunset transitions with evident interferences. Maps of resulting tracks for each seasonal migration were created and inspected in R Studio, using the package Shiny (Chang et al., 2015). A speed filter was applied to estimate at-sea positions to remove points assumed to be erroneous due to speeds larger than the 95% percentile (Austin et al., 2003). For seasonal migrations, this corresponded to a speed of 17.19 km/h.

GPS data processing

To determine whether differences in the non-breeding areas is related to individual habitat tracking of conditions experienced during the breeding period, we compared the habitat use of breeding and non-breeding tropicbirds. Since the GLS were recovered from birds upon first discovery at the colony, we were unable to use these tags to study habitat selection during the breeding period. Instead, we used a GPS tracking dataset to determine foraging areas during this period.

For this, Red-billed Tropicbirds were captured on their nests during incubation or early chick-rearing and equipped with CatLog Gen2 GPS. The GPS loggers weighed 18g (2.9% of mean tropicbird weight; 630g±55, n=1,297 individuals) and were programmed to record GPS positions every 5 minutes. The GPS tracks were cleaned of erroneous positions using a speed filter (30m/s) and split into discrete foraging trips with periods in the nest between trips omitted. As in Saldanha et al., 2023, a sub-sample of tropicbirds were also equipped with Axy-Trek loggers (which record GPS, tri-axial accelerometer, and time-depth information; 33 foraging trips from 14 individuals), Migrate Technology C330 geolocators (GLS) with a wet-dry sensor (salt water immersion logger; 74 foraging trips from 19 individuals) or both (16 trips from 6 individuals) to semi-supervise Hidden Markov Models for the classification of GPS positions into behavior states. Axy-Trek loggers weighed 17g (2.7 % of tropicbird weight) and recorded GPS, acceleration, and pressure data at 5-minute, 25 Hz and 1s intervals, respectively. As in the non-breeding GLS, the Migrate Technology GLS with a wet-dry sensor weighed 3.3g

(0.5% of tropicbird weight) and registered if the bird was wet or dry every 6 seconds. GPS and Axy-Trek were attached to the 6 central tail feathers with Tesa tape while GLS were attached to the tarsus, on the bird's metal ring with the help of a zip tie. All tracking data was processed as in Saldanha et al., 2023, however, we followed the authors' suggestion to classify GPS positions into two instead of three discrete behavioral states. Small step lengths and low turning angles were inferred as inactive (i.e. resting on water), and large steps with a large variety of turning angles were inferred as active (foraging/flight) states. Since tropicbirds mainly forage on the go (Saldanha et al., 2023), we hereafter refer to the GPS-derived active state as foraging.

To estimate tropicbird habitat use during the breeding season, for each GLS track, we randomly selected 30 GPS foraging trips (10 incubation and 20 chick-rearing trips) and trips that took place during the estimated breeding periods of GLS-tracked birds (125 days prior to the initiation of migration or 125 days after returning to the colony from birds breeding on the same island. Using this selection of GPS trips, the core foraging areas was estimated as the 50% of the Kernel Density Estimate (KDE; Calenge C., 2006) of all GPS positions classified as foraging using WGS84 projection.

Seasonal shifts in non-breeding areas

To identify seasonal shifts in main non-breeding areas, the core area of each non-breeding distribution was estimated as the 50% of the KDE (Calenge C., 2006) of all GLS positions after the outgoing and before the ingoing migrations, using WGS84 projection. We then extracted the centroid of each of these kernels and modelled the latitude, longitude and distance of the centroids in relation to the day of the year (DOY) using a GAMM, with a random intercept for individual ID and an identity link function using the R package 'mgcv'(Wood, 2001). Since DOY is circular, it was modelled as non-linear variable using a cubic regression spline. In these models, we also included year and island as categorical parametric coefficients. Since sex, body size and previous breeding success (failed/successful) have been found to influence the migratory strategies and non-breeding areas used in other species, we originally also included these variables in the GAMMs as parametric coefficients. However, as for the models of activity patterns this greatly reduced the sample size (from 149 to 33) Therefore, for all three response variables (latitude, longitude and distance), we first ran preliminary models using only the 33 trips with all potential coefficients (non-linear effect of DOY, year, island, sex, body size and previous breeding success) and then only included the coefficients for sex, body size and previous breeding success in the main GAMMs if they had a significant effect in the preliminary model (S2).

To determine whether there are seasonal patterns in the overlap of the non-breeding areas, we calculated the spatial overlap (Bhattacharyya's Affinity, BA) between all core areas kernels. Then, using the calculated overlap, we assessed: 1) seasonal patterns in overlap, and 2) relationships between overlap and the difference in days between the beginning of the non-breeding periods. In the first model, we assessed seasonal changes in overlap by comparing the overlap between pairs of non-breeding periods that started in the same month using a GAM with separate cyclic cubic regression splines of Julian date for trips of the same vs different individuals. This model was used to determine whether at certain times of year, the non-breeding areas used by different individuals are more diverse than at other times. In the second overlap model, we assessed whether the core non-breeding areas of individuals which migrated during the same time of year, overlapped more than those breeding at different times. To do this, we modelled the overlap of the core non-breeding areas against a non-linear relationship with the absolute difference in days between the beginning of each overlapped non-breeding area again using a GAM with a cyclic cubic regression spline for DOY. In addition, both models included parametric coefficients for whether the core non-breeding areas were from the same individual, year, island and sex or not, whether the individuals were partners or not, and the absolute difference in days between the start of the two non-breeding periods compared.

Seasonality in activity patterns

To determine whether there were seasonal patterns in tropicbird activity patterns during migration and non-breeding periods, we calculated the proportion of time dry (active) per day, night and twilight based on the salt-water immersion data from the GLS. We then modelled the seasonality of the proportion of time active using a binomial GAMM with a cyclic cubic regression spline for DOY and a random intercept for individual ID. Since activity patterns at night (and not day or twilight) are often associated to moon illumination in seabirds (e.g. Ravache et al., 2020; Regular et al., 2011), we create a separate model for the proportion of time active during each of these periods. Moreover, since stage (inward migration, outward migration, and non-breeding) may have a strong effect on activity patterns we also created separate models for each, resulting in a total of nine models (three phenological stages by three time periods). To account for the progression of time in each of the stages, we also included a non-linear relationship with the proportion of the inward migration, non-breeding period and outward migration completed for each given date. Moreover, since sex and previous breeding success, year, and island could affect activity patterns, we also originally included these variables in the GAMs as parametric coefficients. However, as in the models of the seasonal shifts in non-breeding areas, sex and prior breeding success greatly reduced the sample size (from 149 to 33). Therefore, for each activity pattern model, we first ran preliminary models using only the trips when sex and previous breeding success were available to determine if they had a significant effect. If no effect was detected in the preliminary model, these variables were excluded from the model, so that the final model could be run on the full dataset (S2).

Population-level habitat tracking

To determine whether tropicbirds changed their non-breeding areas seasonally to align with specific environmental conditions, we extracted the mean primary productivity, sea surface temperature, air density, and Secchi disk depth from each individual core non-breeding area (Table 1). Then, to compare these values to what was available during each individual's non-breeding period, we extracted the mean environmental values form all other individual core non-breeding areas during the same period. In doing so, for each track, we had the mean environmental variables from 148 "simulated" tracks during the same period. We then compared all real and simulated environmental means using GAMs with the mean environmental variable as the response and a unique cyclic cubic regression spline for Julian date for real and simulated data. We then determine whether the smoothed relationship for the seasonal changes in environmental conditions in real and simulated core areas differed (indicating population-wide habitat tracking) or was the same (indicating that differences in the environmental conditions experienced during the non-breeding season, were the result of seasonal changes only) based on the overlap of the 95% confidence intervals around the curves.

Table 1. Source, resolution (spatial & temporal), aggregating metric and time window of environmental variables.

Variable	**Units**	**Metric**	**Temporal Res.**	**Spatial Res.**	**Years available**	**Source**
Primary productivity	mg m-2 day-1	mean	daily	0.08	2017-2020	Copernicus-Global Ocean low and mid trophic levels biomass content hindcast
Sea Surface Temperature	Kelvin	mean	hourly	0.25	2017-2022	Copernicus-ERA5 Reanalysis
Air density	kg m-3	mean	hourly	0.50	2017-2022	Copernicus-ERA5 Reanalysis
Secchi disk depth	m	mean	monthly	0.25	2017-2018	Pitarch et al., 2021

Individual-level habitat tracking based on breeding period

To determine whether differences in the non-breeding areas is related to individual habitat tracking of conditions experienced during the breeding period, we compared the habitat use of tropicbirds during breeding and non-breeding periods. To do this, we extracted the mean primary productivity, sea surface temperature, air density, and Secchi disk depth from each individual core breeding area and non-breeding areas and compared paired values using GAMs with an identity link function. In these GAMs the mean oceanographic conditions during the non-breeding period as the response and the mean oceanographic conditions during the breeding as an explanatory viable with a non-linear relationship.

RESULTS

From the 133 GLS deployed, we identified 149 complete non-breeding periods from 111 individual. Of these 149 non-breeding periods, 146 tracks showed clear migration while three tracks from two individuals remained resident year-round.

Seasonality in tropicbird migratory patterns

We found seasonal patterns in the non-breeding areas used by GLS tracked Red-billed Tropicbirds, with individuals which started migration in the spring travelling to the central north Atlantic, while those that started migration in the dry season using the area to the west of Cabo Verde (Figure 1). These seasonal patterns were reflected in the models predicting the latitude and longitude of the bird’s core non-breeding areas, but not the distance of the centroids. In preliminary analysis, we found no significant effect of sex, breeding success and body size on the centroid latitude, longitude, or distance (S2). Therefore, these were not included in the models. The models for predicting the latitude and longitude of non-breeding centroids included a significant non-linear relationship with DOY (Figure 1, Table 2). Tropicbirds which started migration after the dry season (peak May-July) used higher latitudes and longitudes then those which migrate after the wet season (low from October-January; Figure 1, Table 2). In the longitude and distance models, we also found a significant effect of year (Table 2). However, this mainly appears to be driven by higher longitudes and lower distances in the two centroids from 2008 (S3).

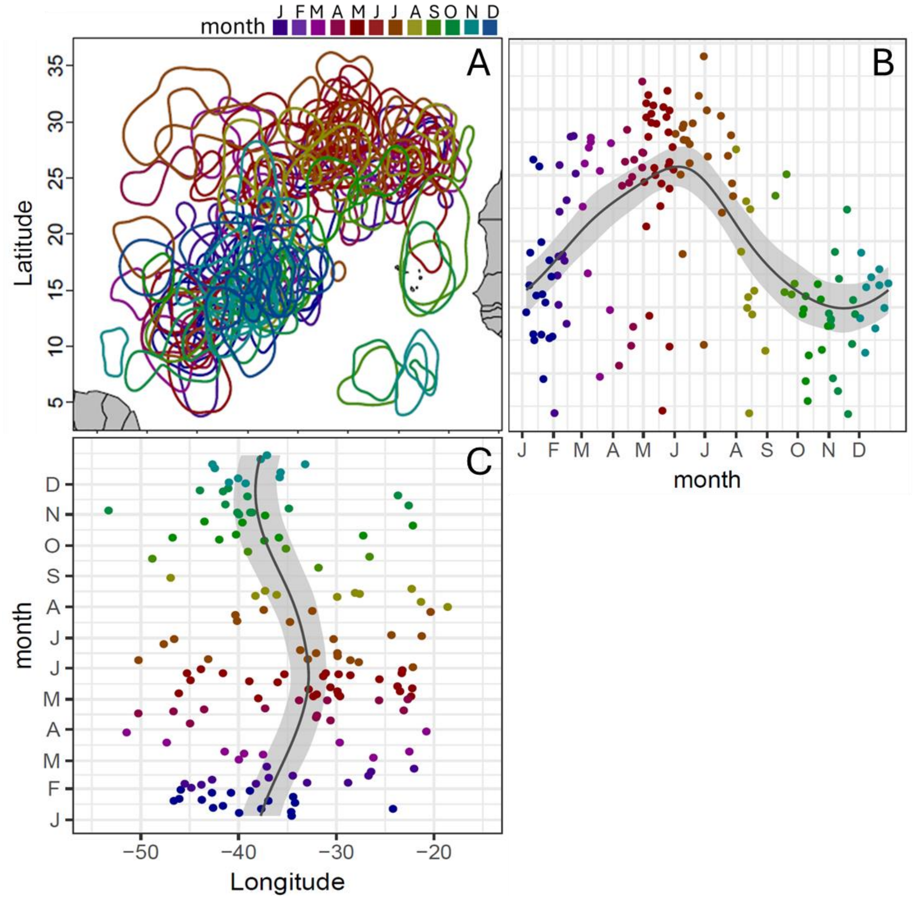

Figure 1. Seasonal patterns in tropicbird non-breeding areas. Showing individual tropicbird 50% Kernel Density Estimates coloured by the month of initiation of migration (A), as well as seasonal patterns in centroid latitude (B) and longitude (C) extracted from GAMMs (Table 2). The mean estimated smoothing functions are shown in solid lines with upper and lower confidence intervals at two standard errors above and below the mean (shaded area). We also present the raw data points of centroid latitude and longitude in relation to day of the year, coloured by the month of initiation of migration.

The best model for predicting the overlap between core non-breeding areas, included a significant r smoothed relationship with the absolute difference in days of the year and whether the kernels were from the same individual or not. We found that the amount of overlap generally was higher when from consecutive migrations from the same individual and when the migrations started at the same time of year (Table2).

While determining the effect of seasonality on kernel overlap in non-breeding areas, we found no significant effect of sex and breeding success in preliminary analyses (S2), therefore, these variables were not included in the models. We found higher overlap between core non-breeding areas of from the same individual. Moreover, we also found higher overlap between migrations that took place during the same time of year (with a smaller absolute difference between the DOY of the start of migration; Figure 2, Table 3). We also found seasonal differences in the amount of overlap between trips which took place during the same month. We found that the overlap between core non-breeding areas were higher from September-December, and lower from March-May. Again, in this model we also found that the overlap was greater when both kernels were from the same individual.

Table 2: Model outputs of seasonal patterns in non-breeding areas. Model output of GAMMs P-values in parenthesis. DOY=day of year

Response	Parametric coefficients			Non-linear	Random Intercept	Deviance explained	N
	Intercept	Year (2008)	Island (Boavista)	DOY	ring		
Latitude	**23.36 (<0.001)**	2017: -0.69 (0.89) 2018: -6.67 (0.43) 2019: -3.63 (0.44) 2020: -2.78 (0.56) 2021: -3.25 (0.51)	ICima: 2.00 (0.22) Raso: -4.50 (0.15) Sal:0.85 (0.53)	**3.89 (<0.001)**	**64.33 (<0.001)**	88.7	149
Longitude	**-21.13 (0.003)**	2017: -11.63 (0.08) **2018: -13.49 (0.05)** **2019: -13.92 (0.04)** 2020: -12.72 (0.07) 2021: -12.83 (0.09)	ICima: 0.82 (0.73) Raso: -7.24 (0.11) Sal: -1.51 (0.44)	**2.11 (0.004)**	**68.02 (<0.001)**	83.4	149
Distance	540.43 (0.28)	**2017: 960.44 (0.05)** **2018: 1061.86 (0.03)** **2019: 1144.82 (0.02)** **2020: 1043.41 (0.04)** 2021: 913.17 (0.09)	ICima: 55.48 (0.74) Raso: 322.53 (0.29) Sal: 138.15 (0.27)	0.00 (0.54)	**64.49 (<0.001)**	79.2	149

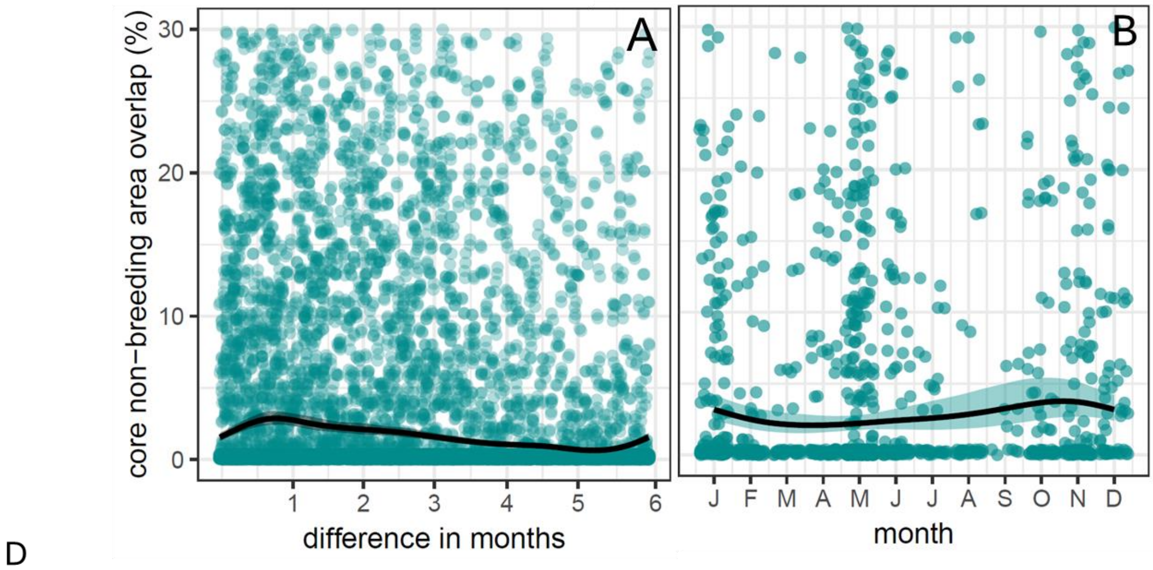

Figure 3. Difference in the kernel overlap of non-breeding core areas based on the differences in days between the start of migration (A) and, seasonally, for migrations which took place during the same month, seasons (B). Relationships extracted from GAMs (Table 2). The mean estimated smoothing functions are shown in solid lines with upper and lower confidence intervals at two standard errors above and below the mean (shaded area). We also present the raw data points of the kernel overlap.

Table 3: Model outputs of seasonal patterns in non-breeding area overlaps. Model output of negative binomial GAMs. P-values in parenthesis. DOY=day of year

Response	Parametric coefficients					Non-linear		Deviance explained	N
	Intercept	Same year	Same island	Same individual	partners	Diff DOY	Month		
Overlap	**0.54 (<0.001)**	-0.07 (0.23)	0.05 (0.47)	**1.41 (0.004)**	-0.04 (0.89)	**2.66 (<0.001)**	**-**	2.99	22052
Overlap	**1.06 (<0.001)**	-0.05 (0.76)	-0.03 (0.85)	**1.65 (0.04)**	-0.45 (0.43)	**-**	**4.43 (<0.001)**	2.80	2034

Seasonality in activity patterns

Tropicbirds spent the highest proportion of time active during twilight, followed by day and finally night (Figure 3, Table 4). Moreover, they generally spent more time active during migration than during the non-breeding area. Tropicbirds spend a higher proportion of time active during twilight from December to February, than from June to October during both migration and the non-breeding period. Moreover, the proportion of time active during the day drops in June in the non-breeding period but is generally stable during outward and inward migrations. The proportion of time active during the night was also highest from December to Ferbruary during the outward migration and the non-breeding period. During the outward migration and non-breeding period, the proportion of time active in day, night and twilight decreased as the proportion of the phenological stage advanced. On the contrary, during the inward migration, the proportion of time active increased in day, night and, twilight increased. In all phenological stages, the proportion of time active during the night increase with the moon fraction.

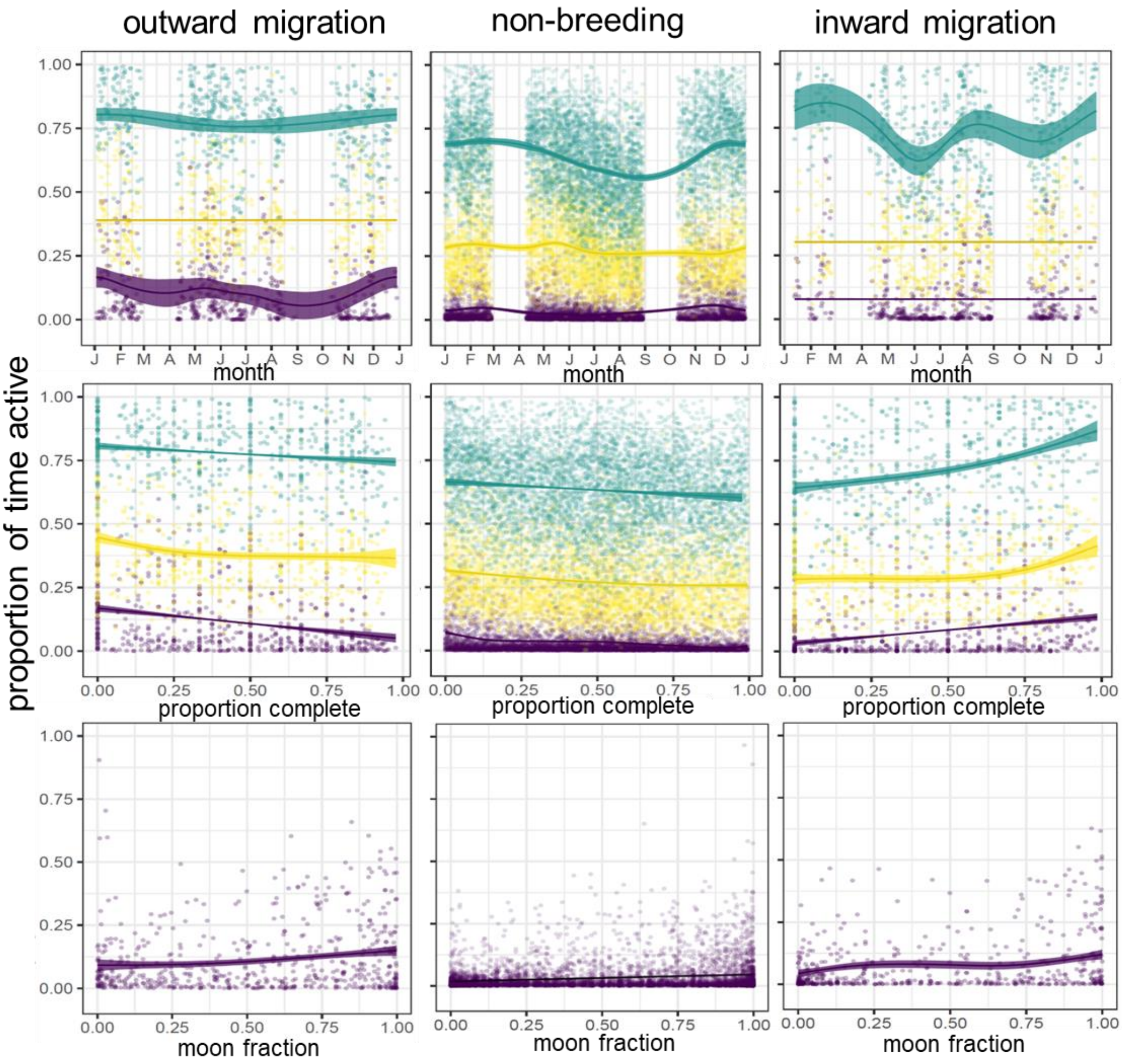

Figure 3. Proportion of time active (dry) during outward migration, the non-breeding period and inward migration per day, night, and twilight period by (row 1) day of year, (row 2) proportion of phenological period complete, and (row 3) moon fraction. Relationships extracted from binomial GAMMs with random intercepts for individual ID and the linear co-variates year, island and in the case of the non-breeding period, breeding stage (Table 4). The mean estimated smoothing functions are shown in solid lines with upper and lower confidence intervals at two standard errors above and below the mean (shaded area). We also present the raw data points of the proportion of time active in each period. The gaps in the data in the top row are caused by unreliable GLS positions during the equinox.

Table 4. Output of models of seasonality in tropicbird activity patterns during the outward migration, the non-breeding period and the inward migration during day, twilight, and night. P-values of non-linear relationships (effective degree of freedom, edf) and of parametric coefficients in parentheses. Significant values are in bold.

Model	Timing	Parametric coefficients				Non-linear			Random	Deviance explained	N
		Intercept	Breeding success (s)	Year (2017/2018*)	Island (Boavista)	DOY	Prop complete	Moon frac	ring		
Prop. Active Outward Migration	Day	**0.59 (<0.001)**		**2018: -0.21 (0.005)** **2019: -0.21 (0.003)** **2020: -0.30 (<0.001)** **2021: -0.41 (0.02)**	ICima: 0.15 (0.20) Raso: 0.14 (0.22) Sal: 0.04 (0.22)	0.00 (0.47)	**2.67 (<0.001)**		**47.52 (<0.001)**	47.1	574
	Twilight	**0.70 (<0.001)**		2018: 0.09 (0.14) 2019: 0.11 (0.06) 2020: 0.10 (0.10) 2021: 0.31 (0.82)	ICima: -0.04 (0.66) Raso: 0.00 (0.95) Sal: -0.00 (0.91)	**1.58 (0.03)**	**1.08 (<0.001)**		**45.47 (<0.001)**	50.4	574
	Night	0.11 (0.07)		2018: 0.01 (0.86) 2019: 0.04 (0.51) 2020: 0.00 (0.94) 2021: -0.07 (0.61)	ICima: -0.02 (0.88) Raso: -0.03 (0.74): Sal: -0.00 (0.91)	3.97 (0.06)	**1.00 (<0.001)**	**1.94 (0.002)**	**44.46 (<0.001)**	48.7	574
Prop. Active Non-Breeding	Day	**0.25 (<0.001)**	**0.08 (<0.001)**	2019: -0.01 (0.19) **2020: -0.06 (<0.001)** **2021: -0.09 (<0.001)**	ICima: 0.01 (0.99) Raso: 0.01 (0.96) Sal: 0.01 (0.77)	**6.67 (<0.001)**	**2.90 (<0.001)**		**35.50 (<0.001)**	36.2	5684
	Twilight	**0.64 (<0.001)**	0.04 (<0.001)	2019: -0.01 (0.35) **2020: -0.04 (<0.001)** **2021: -0.12 (<0.00**1)	ICima: -0.02 (0.76) Raso: -0.07 (0.48) Sal: -0.01 (0.67)	**6.68 (<0.001)**	**6.62 (<0.001)**		**35.34 (<0.001)**	41.0	5684
	Night	0.02 (0.06)	**0.02 (<0.001)**	**2019: 0.01 (0.006)** 2020: 0.00 (0.98) 2021: -0.01 (0.20)	ICima: -0.01 (0.77) Raso: 0.01 (0.66) Sal: 0.00 (0.87)	**7.20 (<0.001)**	**6.66 (0.001)**	**1.01 (<0.001)**	**34.72 (<0.001)**	26.8	5684
Prop. Active Inward Migration	Day	**0.35 (<0.001)**		2019: 0.00 (0.97) 2020: -0.04 (0.18) 2021: 0.07 (0.35)	ICima: -0.09 (0.11) Raso: 0.05 (0.65) Sal: -0.02 (0.51)	0.00 (0.99)	**3.36 (<0.001)**		**37.67 (<0.001)**	40.8	540
	Twilight	**0.76 (<0.001)**		2019: -0.03 (0.32) 2020: -0.05 (0.10) 2021: -0.12 (0.21)	ICima: -0.02 (0.80) Raso: 0.13 (0.41) Sal: 0.02 (0.63)	**3.61 (<0.001)**	**2.58 (<0.001)**		**40.69 (<0.001)**	57.0	540
	Night	**0.13 (<0.001)**		2019: -0.03 (0.18) 2020: -0.10 (<0.001) 2021: -0.04 (0.60)	ICima: 0.01 (0.86) Raso: -0.02 (0.84) Sal: 0.01 (0.82)	0.00 (0.46)	**1.00 (<0.001)**	**3.42 (<0.001)**	**43.32 (<0.001)**	58.1	540

Population-level habitat tracking

We found that the primary productivity, sea surface temperate, air density and Secchi disk depth of tropicbird non-breeding areas changed seasonally (Figure 4, Table 5). Moreover, tropicbirds which initiated migration in the spring selected non-breeding areas with particularly cooler temperatures and higher air density, while those that initiated migration in the spring selected areas with higher sea surface temperatures and lower air density, effectively attenuating the impacts of seasonality in these variables. Moreover, the three resident individuals occupied an area with higher primary productivity than the simulations (Figure 4, Table 5).

Table 5. Output of Generalized Additive Models of the effects comparing oceanographic conditions within the real and simulated non-breeding areas. P-values of non-linear relationships (effective degree of freedom, edf) and of parametric coefficients in parentheses. Significant values are in bold.

Response	Parametric coefficients		Non-linear	Deviance explained	n
	Intercept	real/simulation (simulation)	DOY start migration		
Primary productivity	**257.37 (<0.001)**	23.02 (0.10)	**Real: 2.10 (0.003)** **Simulation: 6.28 (<0.001)**	7.54	12348
SST	**298 .23 (<0.001)**	-0.17 (0.38)	**Real: 2.51 (0.002)** **Simulation: 7.01 (<0.001)**	28.90	10245
Air density	**1.18 (<0.001)**	0.00 (0.70)	**Real: 2.40(<0.001)** **Simulation: 6.84 (<0.001)**	21.00	12348
Secchi disk depth	**34.77 (<0.001)**	-0.47 (0.65)	**Real: 1.30 (0.03)** **Simulation:2.65 (<0.001)**	6.71	625

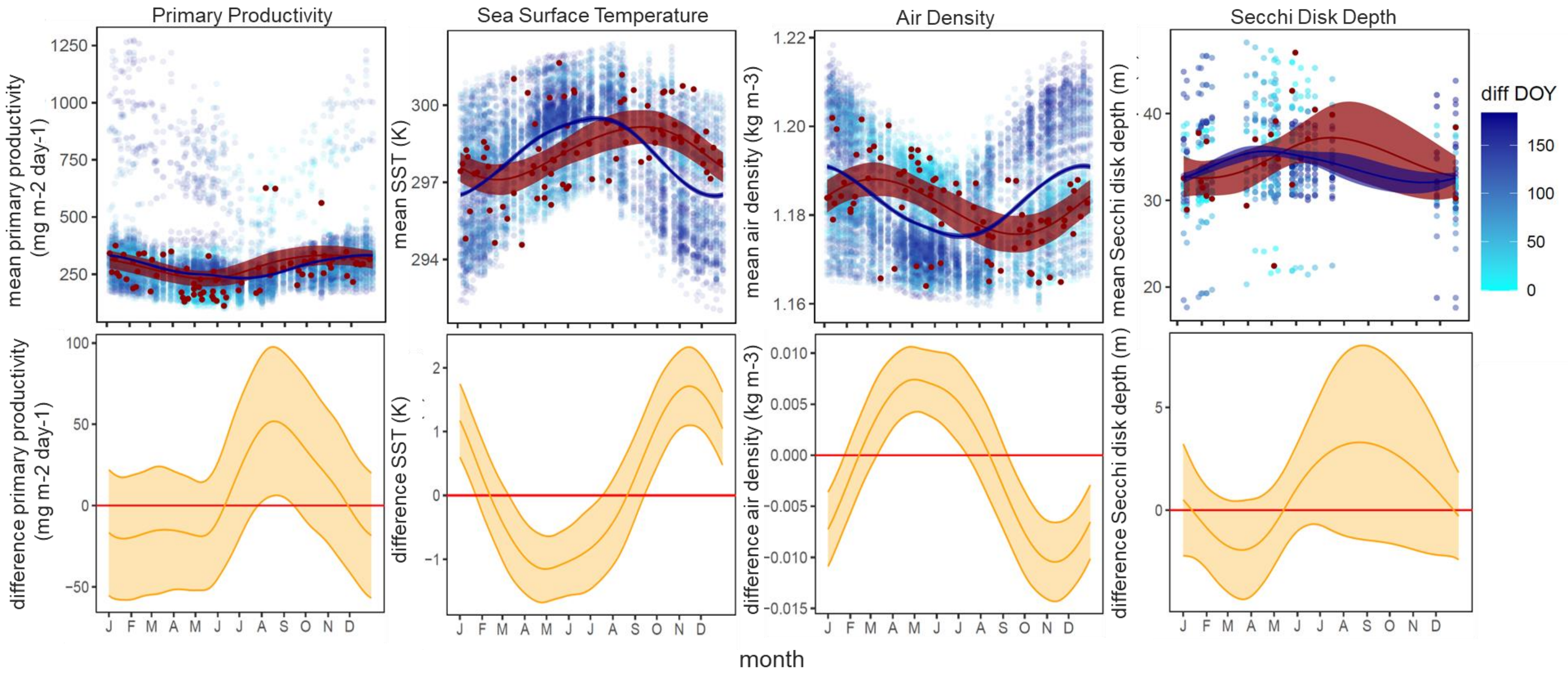

Figure 4.Seasonality of the mean oceanographic conditions (primary productivity, SST, Secchi disk dept and air density) in the core non-breeding areas of Red-billed Tropicbirds during the true non-breeding period (red) and simulated non-breeding periods (blue) and the difference between the two (bottom row in orange with a 95% confidence interval) The relationship of the top row is extracted from a generalized additive model of the mean oceanographic condition in relation to the day of the year (DOY) of the initiation of migration. The mean estimated smoothing functions are shown in solid lines with upper and lower confidence intervals at two standard errors above and below the mean (shaded area). We also present the raw data points of the mean oceanographic conditions in the true (red) and simulated (blue) kernels. Simulated points coloured by the absolute difference in days between the start of the true non-breeding period and the simulated non-breeding period. The difference between the curves (orange) is considered significant for dates when the 95% confidence does not cross zero.

Niche-tracking at the individual level

We found that tropicbirds experienced distinct oceanographic conditions during the breeding and non-breeding periods (Table 6). Although the differences were considered significant, the effect size of for sea surface temperature and air density were nearly negligeable, while those of primary productivity and Secchi disk depth were more important. We found that the primary productivity experienced during the breeding season was much higher than that of the non-breeding season, except in the case of resident individuals. Moreover, we found that the Secchi disk depth was greater in the non-breeding period, indicating clearer waters.

Table 6. Comparison of the mean environmental conditions tropicbirds experienced during the breeding and non-breeding period, showing the results of a t-test comparing the two.

Oceanographic Variable	**Breeding (mean ±SD)**	**Non-breeding (mean ±SD)**	**t-value**	**df**	**p-value**
Primary productivity	719.07±110.49	246.68±77.25	45.28	294	<0.001
SST	297.24±1.39	297.74±1.74	-2.92	319.97	<0.001
Air density	1.18±0.01	1.19±0.01	-3.99	312	<0.001
Secchi disk depth	17.91±1.20	35.09±4.63	-37.83	125	<0.001

When comparing the oceanographic conditions experienced during the breeding and non-breeding periods, we found that, in general, the relationship follows what would be expected in a seasonal environment (Table 7, Figure 5,6). For example, birds that nested in the Cabo Vede wet season and, thus, experienced high sea surface temperatures and low air density in the breeding season, migrated during the dry season and experience lower sea surfaces temperatures and higher air density in the non-breeding seasons. The same pattern continued with primary productivity, although the variability in primary productivity experienced during the non-breeding period was much lower to that of the breeding period. The relationship with Secchi disk depth was somewhat complex, with individuals which experience both low or high secchi disk depth during the breeding period, experiencing higher secchi disk depth during the non-breeding period.

Table 7. Output of Generalized Additive Models of the relation of oceanographic conditions experienced during the breeding season and non-breeding season in Red-billed Tropicbirds. P-values of non-linear relationships (effective degree of freedom, edf) and of parametric coefficients in parentheses (estimates). Significant values are in bold. Sample sizes are also given since these varied based on the variable.

Response	Parametric coefficients (est)	Non-linear (edf)	Deviance explained	n
	Intercept	Oceanographic variable breeding		
Primary productivity non-breeding	**472.48 (<0.001)**	**Primary productivity breeding 2.87 (<0.001)**	42.20	166
SST non-breeding	**297.74 (<0.001)**	**SST breeding: 4.40 (<0.001)**	52.70	169
Air density non-breeding	**3.75 (<0.001)**	**Air density breeding: 3.75 (<0.001)**	36.70	169
Secchi disk depth non-breeding	**35.15(<0.001)**	**Secchi disk depth breeding 4.92 (<0.001)**	70.80	110

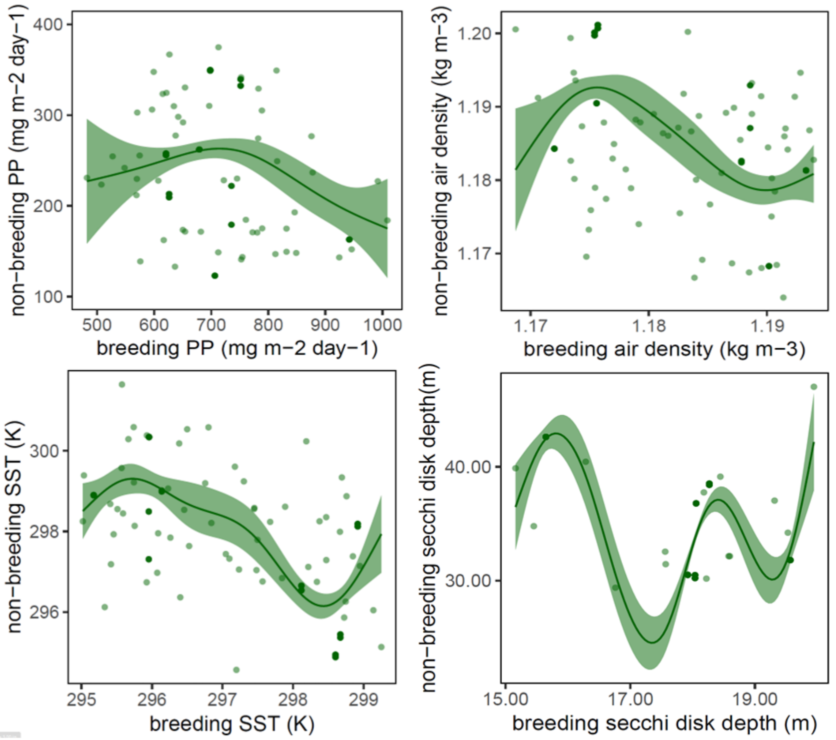

Figure 5. Relationships extracted from General Additive Models between the mean oceanographic conditions from 50%KDE of breeding and non-breeding areas of Red-billed Tropicbirds. The mean estimated smoothing functions are shown in solid lines with upper and lower confidence intervals at two standard errors above and below the mean (shaded area). We also present the raw data points of the oceanographic condition experience by individuals during their breeding and non-breeding periods.

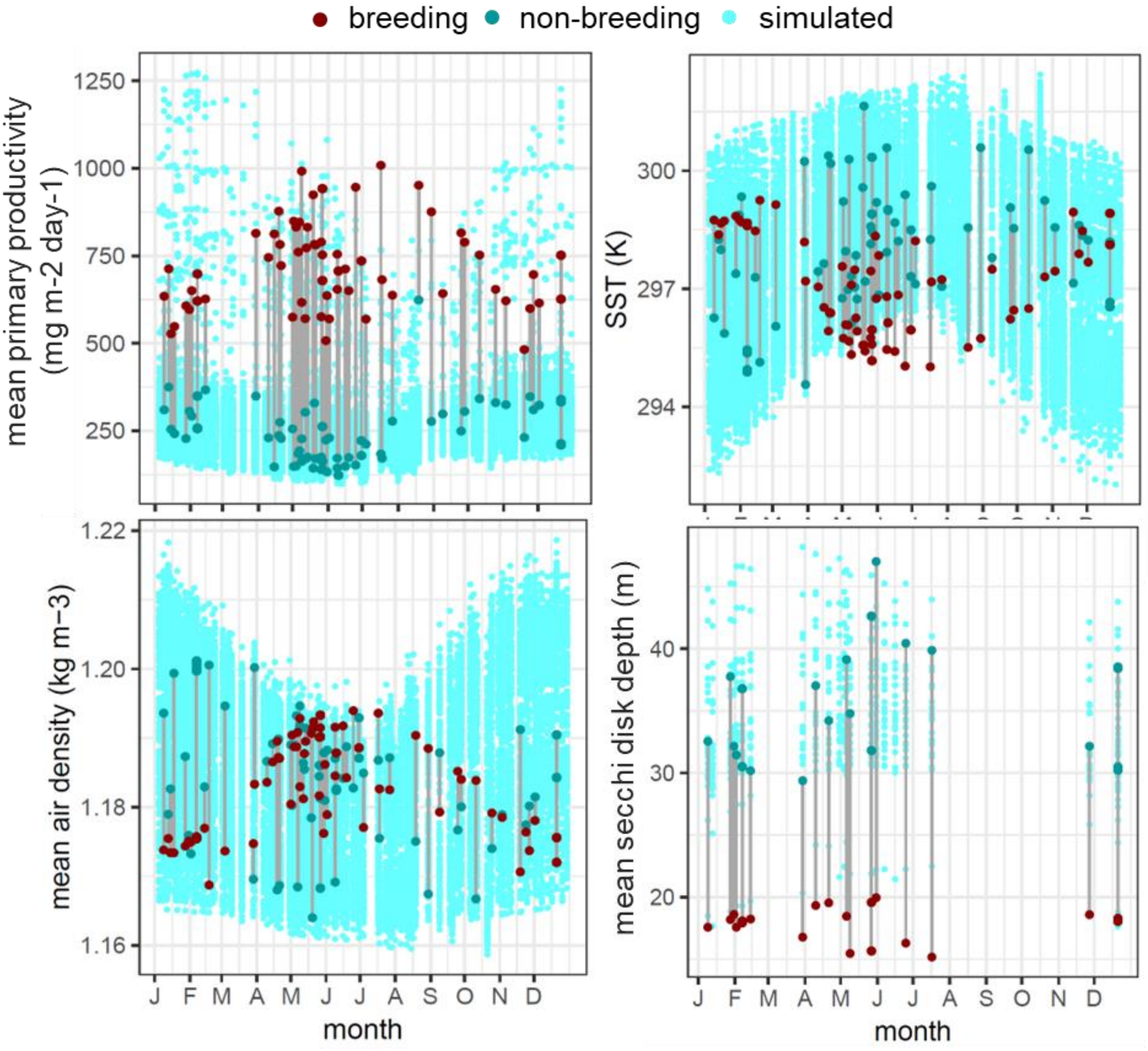

Figure 6. Mean oceanographic conditions from 50% KDE of breeding (red) and non-breeding (dark cyan) areas of Red-billed Tropicbirds in relation to the day of the year of initiation of migration. Values from the same individual during the breeding and non-breeding periods are linked. We also present the mean values of simulated non-breeding areas (cyan).

DISCUSSION

We found that almost all Red-billed Tropicbirds were migratory, with only two individuals remaining resident in Cabo Verde waters year-round. This finding starkly contrasts the previous belief that the species was generally resident (Orta et al., 2020). Of those that migrated, we found seasonal patterns in the non-breeding areas used, with dry season breeders using the central Atlantic to the north of Cabo Verde, while wet season breeders migrated to the west of Cabo Verde. Despite these seasonal differences, the distance to non-breeding areas remained similar year-round, and other potential sources of variability such as sex, island, year, previous breeding success, or bird size did not explain the spatial patterns. Moreover, we found that tropicbirds that initiated migration in the fall spent a higher proportion of time in flight during twilight than those that initiated migration in the spring, potentially alluding to seasonal differences in foraging behavior during the non-breeding season. Given the variability of environmental conditions during the non-breeding and breeding seasons, we suggest that these shifts in the non-breeding area allow tropicbirds to avoid seasonal extremes in SST and air density, indicating consistent population-level habitat preferences year-round.

By modifying their non-breeding areas seasonally, tropicbirds appear to remain within a preferred range of SST (from ~ 21-28 °Celsius) and air density (~1.16- 1.20 kg/m^3) year-round. Both SST and air density are known to influence the distribution and foraging behavior in seabirds (e.g. Shepard et al., 2023; Tremblay et al., 2009), however, they are strongly negatively correlated, making inferences about their unique relationships complicated. Since a larger volume of seabird research has focused on the effects of SST, we will also focus on the range of SST for this discussion, although it is important to keep in mind the relationship between the two variables. For SST, this range is similar to what has been found in the foraging areas of Red-billed Tropicbirds during the breeding season in St-Eustatius (Madden et al., 2022), Senegal (Diop et al. 2018) and St-Helena (Diop et al., 2018) and, in Mexico, breeding stops during summer months, when SST reaches over 30°C (Hernández-Vázquez et al., 2018), suggesting that this may be the thermal range for this species. If this is the case, tropicbirds may modify their non-breeding distributions to remain within this preferred range, suggesting population or even species-level habitat preferences.

However, since this range of SST and air density is available within the breeding area year-round, niche tracking cannot be the primary driver of migration in Red-billed Tropicbirds. This is consistent with the findings of (Lambert & Fort, 2022), who, in a review of seabirds, found that migratory status was not related to the unavailability of favorable conditions at the breeding or non-breeding grounds, concluding that niche availability cannot be the main driver of migration in seabirds.

An alternative driver of migration is competition. In other partial migrants, nest occupancy, sex, and body condition were shown to predict migratory status (e.g., Fayet et al., 2017; C. Pérez et al., 2014; Pettex et al., 2017), suggesting that individuals are driven to migrate through competitive exclusion. Although we found no effect of typical delineators of intraspecies competition (sex, body size, breeding success) on migratory distance, future studies incorporating more resident Red-billed Tropicbirds may help shed light on whether some of the within-season variability of non-breeding areas is driven by competitive exclusion. As solitary foragers and specialists in finding prey in nutrient-poor and unpredictable environments, tropicbirds may be highly sensitive to intra and inter-specific competition (Ashmole, 1971; Spear & Ainley, 2005; Stonehouse, 1962).

Moreover, we found that breeding and non-breeding areas had drastically different values of primary productivity and visibility, suggesting that a certain level of niche switching occurs between phenological periods, as in several other species (e.g., Lambert & Fort, 2022;

Martínez-Meyer et al., 2004; Nakazawa et al., 2004; Quillfeldt et al., 2020). This may also suggest that these are not important indicators of suitable habitat for tropicbirds. In previous studies on this species, chlorophyll a, as a measure of resource availability related to primary productivity, had variable effects on tropicbird foraging behavior. Foraging was related to high chlorophyll a concentration in St-Eustatius (Madden et al., 2022), while it was related to intermediate chlorophyll a concentration in Senegal (Diop et al., 2018). This suggests that productivity may not be an important predictor of tropicbird movements at a species level.

With repeat tracking, we also found that the non-breeding area used by individuals was often similar from year to year, and birds that migrated around the same time of year also used similar areas. These findings are similar to those of a recent study of asynchronously breeding tropical gadfly petrels (Franklin et al., 2022a) and suggest that familiarity with non-breeding areas may be more beneficial than tracking specific conditions in a tropical system where resources are patchy and unpredictable (Ashmole, 1971; McNamara & Dall, 2010; Weimerskirch, 2007). However, since individuals who departed closer together in time used more similar non-breeding distributions, it is possible that oceanographic conditions at departure, such as SST and air density, also influenced individual non-breeding distributions, resulting in more overlap when individuals migrated simultaneously.

The seasonal patterns in the proportion of time active during the day, night, and twilight follow a similar pattern to what was observed during the breeding period (this thesis chapter 2). In both cases, there is a peak in activity during twilight around April. This suggests that the driver of this seasonal change, potentially a peak in squid availability (this thesis chapter 2), acts on individuals in both the breeding and non-breeding seasons.

In addition to seasonal patterns, we also found that the proportion of time active during day, night, and twilight varied between phenological stages and, in the case of night, with moon fraction. The proportion of time spent active generally decreased during the outward migration and non-breeding period and increased again during the inward migration. This pattern is similar to that found in a recent review of the activity patterns of seabirds during migration and the non-breeding period (Bonnet-Lebrun et al., 2021). Seabirds spend more time in flight during migration, prioritizing displacement to non-breeding areas over other activities. Moreover, in the non-breeding period, tropicbirds may spend less time active while molting. Although little is known about tropicbird molt, (Stonehouse, 1962) suggested that Red-billed Tropicbirds undergo prebasic molt in 19 to 29 weeks, finishing before courtship, and that individuals who returned to the colony after a shorter than usual non-breeding period often returned with flight feathers in various stages of growth, suggesting that molt is mainly concentrated in the non-breeding period. Since molt impedes flight efficiency, it is generally avoided during migration (Ramos et al., 2009). Moreover, we also found that in all phenological stages, the proportion of time active during the night increases with the moon fraction, suggesting that tropicbirds may travel or even forage at night if light conditions are sufficient. These findings are consistent with those of (Bonnet-Lebrun et al., 2021), who found that several seabird species also increase the proportion of time in flight during the full moon, suggesting that this may be a common feature across many seabird species.

In a changing environment, the ability of tropicbirds to shift their non-breeding areas to track ideal conditions suggests adaptability in the face of change. However, as central place foragers during the breeding season, a strict SST and air density range may eventually restrict the breeding season of tropicbirds in Cabo Verde as it does in Mexico (Hernández-Vázquez et al., 2018). Moreover, a recent review (Orgeret et al., 2022) found that tropicbirds have a relatively narrow thermal tolerance, making them more sensitive to climate change-induced environmental shifts. A closely related species, the White-tailed Tropicbird *(Phaethon lepturus)*, is already experiencing climate-induced phenology shifts (Campioni et al., 2023), suggesting that tropicbirds may be more sensitive to environmental change than previously thought.

CONCLUSIONS

Our results provide some of the first in-depth knowledge on the seasonal variation in the non-breeding areas of a tropical seabird species, suggesting seasonality in tropical systems may be a more potent driver of the non-breeding movements of top predators than previously thought. The individual consistency in the migratory areas suggests that either familiarity with the non-breeding areas or niche tracking drives these seasonal patterns. These seasonal differences suggest that tropicbirds with different phenologies may be exposed to various environmental conditions and human-associated impacts, with potentially important consequences for breeding success and survival (Fayet et al., 2017).

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SUPPLEMENTARY MATERIAL

S1. Biometric measurements and calculation of the index of tropicbird skeletal body size

To calculate an index of tropicbird skeletal body size, we collected the biometric measurements of GLS tracked birds (wing length, tarsus length, bill depth, culmen and head-bill length; Table 1) opportunistically during nest monitoring. We then normalized the biometric measurements and conducted a principal component analysis (PCA) to generate a composite measure of skeletal size (e.g., Benson, Suryan, & Piatt, 2003). The first principal component explained 38.52 % of the variance and was negatively related to all individual loadings of biometric measurements (wing: -0.25, culmen: -0.61, bill height; -0.28, head-bill: -0.62 and tarsus -0.30). To facilitate interpretation, we inverted the factor of body size by multiplying it by -1, so that higher values represent larger birds.

Table.1 Description of biometric measurements taken from Red-billed Tropicbird chicks and adults.

Metric	Description
wing length	flattened wing length from the carpal joint to the tip of the longest primary. Measured using a ruler to the nearest 1 mm.
tarsus length	tarsus length from the distal point of the inter-tarsal joint to the foot. Measured using a calliper to the nearest 1 mm.
bill depth	Perpendicular length from the top to the bottom of the bill starting at the junction with the skull. Measured using a calliper to the nearest 1 mm.
culmen	length from the base of the skull to the tip the bill. Measured using a calliper to the nearest 1 mm.
head-bill length	bill trip to the posterior ridge formed by the parietal-supraoccipital junction. Measured using a calliper to the nearest 1 mm.

S2. Model outputs of seasonal patterns in non-breeding areas, overlap and activity with sex and breeding success.

Table 1. Model outputs of seasonal patterns in non-breeding areas including categorical variables for sex and previous breeding success. Model output of GAMMs P-values in parenthesis. DOY=day of year

Response	Parametric coefficients						Non-linear	Random Intercept	Deviance explained	N
	Intercept	Sex (Male)	Breeding success (success)	Body Size	Year (2018)	Island (Boavista)	DOY	ring		
Latitude	**17.08 (0.04)**	0.76 (0.81)	-1.59 (0.29)	-0.06 (0.95)	2019: 1.53 (0.37) 2020: 3.54 (0.19) 2021: -3.98 (0.24)	Sal: 1.84 (0.61)	1.69 (0.64)	**21.36 (0.03)**	99.8	33
Longitude	**-44.98 (<0.001)**	4.67 (0.28)	1.99 (0.35)	0.85 (0.52)	2019: 1.74 (0.50) 2020: 0.53 (0.86) 2021: -10.60 (0.08)	Sal: 5.41 (0.23)	0.00 (0.90)	**21.29 (0.005)**	99.3	33
Distance	**2268.83 (<0.001)**	-531.11 (0.11)	-95.65 (0.63)	-105.69 (0.30)	2019: 11.56 (0.96) 2020: 138.95 (0.65) 2021: 882.72 (0.10)	Sal: -248.29 (0.45)	0.00 (0.90)	**19.45 (0.005)**	97.9	33

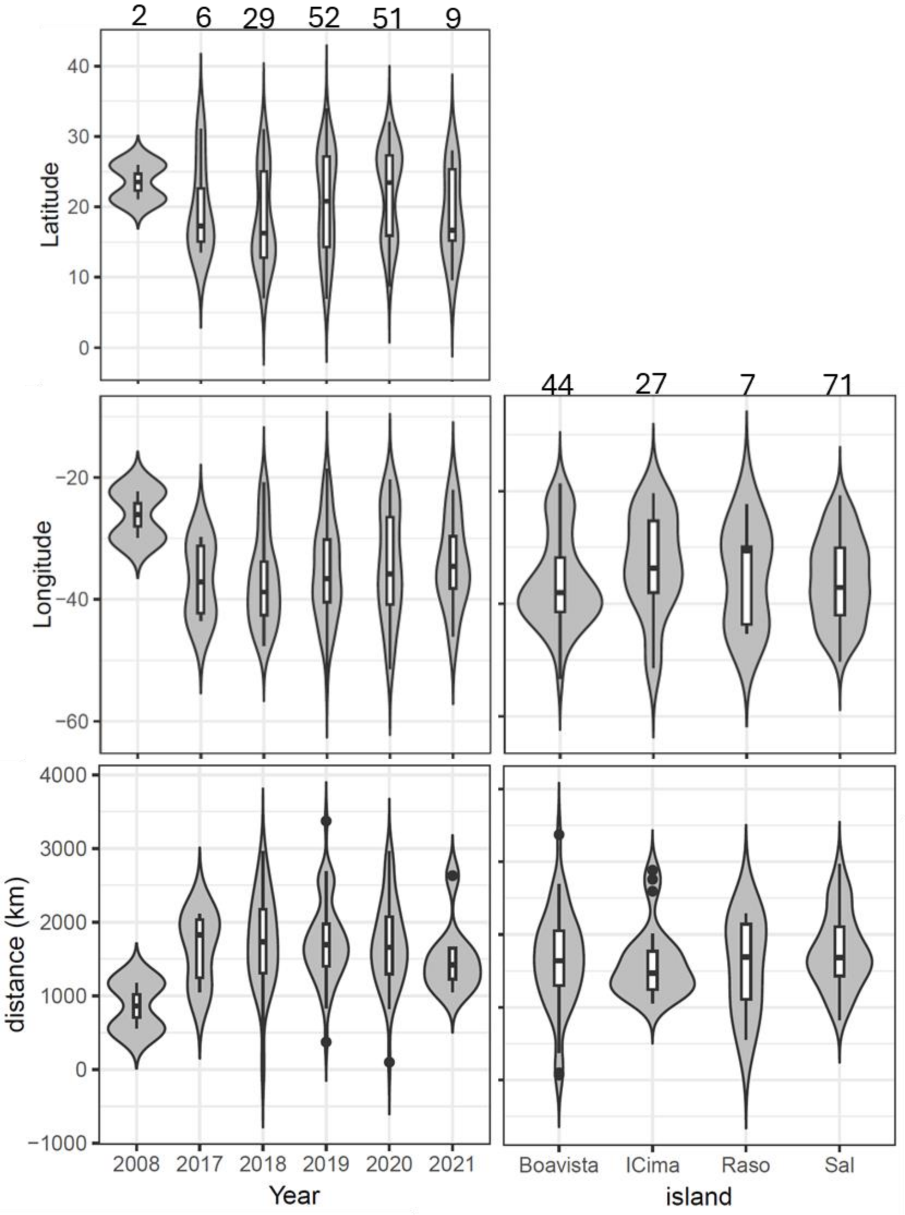
Table 2. Model outputs of seasonal patterns in non-breeding area overlaps including categorical variables for sex and previous breeding success. Model output of GAMMs P-values in parenthesis. DOY=day of year

Response	Parametric coefficients							Non-linear		Deviance explained	N
	Intercept	Sex (Female)	Success (Failure)	Same year	Same island	Same individual	partners	Diff DOY	Month		
Overlap	0.42 (0.10)	Male: -0.24 (0.24) Mix: -0.19 (0.35)	Success: 0.18 (0.40) Mix:0.29 (0.16)	0.10(0.49)	0.02 (0.87	0.99 (0.30)	0.14 (0.85)	**1.08 (<0.001)**	-	2.75	5112
Overlap	-1.26 (0.09)	Male: 1.37 (0.10) Mix: 1.29 (0.07)	Success: 0.47 (0.42) Mix: 0.47 (0.40)	**0.90 (0.02)**	-0.08 (0.83)	2.35 (0.08)	-63.25 (1.00)	-	**1.70 (0.04)**	8.49	402

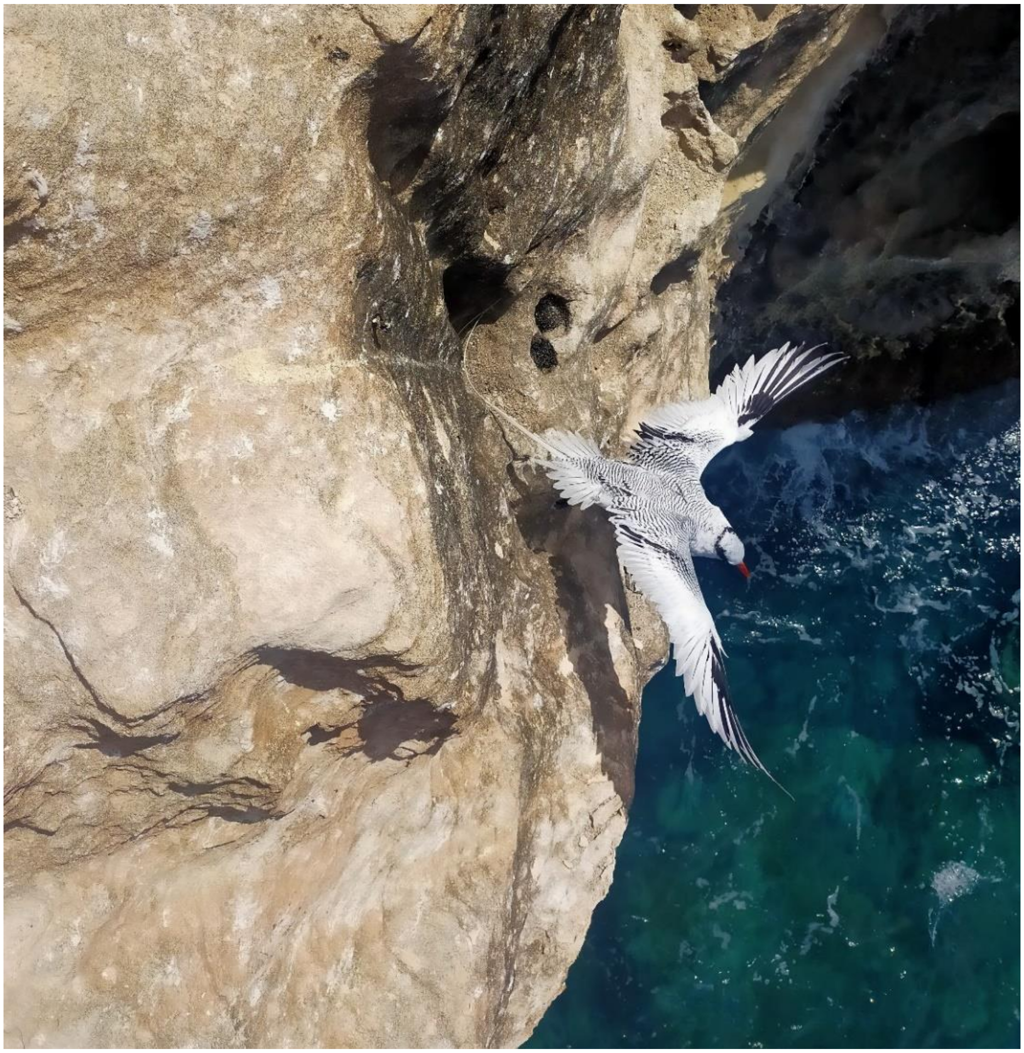
Table 3: Models of the proportion of time activity during day, night and twilight in the different stages of migration with Sex and Breeding success showing no significant effects of these variables.

Model	Timing	Parametric coefficients					Non-linear			Random	Deviance explained	N
		Intercept	Sex (Male)	Breeding success (success)	Year (2018)	Island (Boavista)	DOY	Prop complete	Moon fraction	ring		
Prop. Active Outward Migration	Day	**0.37 (<0.001)**	-0.05 (0.16)	-0.00 (0.95)	2019: 0.01 (0.75) 2020: -0.01 (0.83) 2021: -0.04 (0.65)	ICima: 0.00 (NA) Sal: -0.01 (0.79)	0.00 (0.49)	**2.89 (<0.001)**		**16.60 (<0.001)**	41.9	233
	Twilight	**0.79 (<0.001)**	0.01 (0.78)	0.02 (0.52)	2019: 0.03 (0.46) 2020: 0.08 (0.10) 2021: -0.16 (0.18)	ICima: -0.00 (NA) Sal: -0.09 (0.09)	**5.08 (0.05)**	**1.00 (<0.001)**		**16.92 (<0.001)**	69.1	233
	Night	0.05 (0.21)	-0.01 (0.70)	0.05 (0.08)	2019: 0.05 (0.10) 2020:0.06 (0.16) 2021:0.00 (NA)	ICima: -0.02 (0.81) Sal: -0.00 (0.90)	0.00 (0.54)	**1.25 (<0.001)**	**1.67 (0.02)**	**18.34 (<0.001)**	58.2	233
Prop. Active Non-Breeding	Day	**0.24 (<0.001)**	0.04 (0.28)	**0.05 (<0.001)**	2019: -0.01 (0.08) **2020: -0.05 (<0.001)** **2021: -0.09 (0.01)**	ICima: 0.01 (0.92) Sal: -0.02 (0.62)	**4.88 (<0.001)**	**3.21 (<0.001)**		**30.42 (<0.001)**	354.6	4844
	Twilight	**0.65 (<0.001)**	0.01 (0.85)	0.02 (0.17)	2019: -0.01 (0.30) 2020: -0.04 (0.003) **2021: -0.16 (<0.00**1)	ICima: 0.03 (0.71) Sal: -0.00 (0.95)	**6.70 (<0.001)**	**5.22 (<0.001)**		**30.25 (<0.001)**	39.5	4844
	Night	0.01 (0.56)	0.00 (1.00)	**0.02 (<0.001)**	**2019: 0.01 (<0.001)** 2020:0.00 (0.53) 2021: -0.01 (0.35)	ICima: 0.03 (0.25) Sal: -0.01 (0.38)	**7.34 (<0.001)**	**5.98 (<0.001)**	**1.22 (<0.001)**	**29.93 (<0.001)**	27.5	4844
Prop. Active Inward Migration	Day	**0.29 (0.002)**	0.00 (0.97)	-0.02 (0.65)	2019: 0.04 (0.55) 2020:0.01 (0.89) 2021: 0.21 (0.17)	ICima: -0.20 (0.17) Sal: 0.01 (0.66)	1.39 (0.12)	**2.33 (0.005)**		**12.66 (<0.001)**	39.4	223
	Twilight	**0.79 (<0.001)**	-0.11 (0.06)	-0.05 (0.46)	2019: 0.05 (0.65) 2020: -0.04 (0.67) 2021: 0.20 (0.34)	ICima: -31 (0.12) Sal: 0.02 (0.80)	**4.21 (0.02)**	**2.49 (<0.001)**		**12.64 (<0.001)**	52.0	223
	Night	0.11 (0.36)	-0.04 (0.49)	-0.01 (0.91)	2019: -0.01 (0.92) 2020: -0.13 (0.11) 2021: 0.06 (0.76)	ICima: -0.09 (0.61) Sal: 0.08 (0.27)	3.31 (0.27)	**1.00 (<0.001)**	**1.83 (0.01)**	**14.77 (<0.001)**	61.1	223

S3. Effect of year and island on latitude, longitude and distance



S3. Effects of year and island on the latitude, longitude and distance of the centroid of tropicbird core non-breeding areas. Numbers indicate sample sizes.



Picture by Sarah Saldanha

Chapter 4. Repeatable and heritable phenology in a tropical marine top predator

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ABSTRACT

Carry-over effects, whereby events in one season affect individual success in subsequent seasons, often result in changes in phenology. In regions with pronounced seasonality, these adjustments can lead to mismatches between breeding timing and optimal environmental conditions, consequently reducing individual fitness. In tropical regions with less marked seasonal resource fluctuations, species may exhibit higher phenological flexibility, potentially buffering carry-over effects and enhancing their resilience to environmental changes. However, this hypothesis lacks substantiation, as it remains unclear whether the observed phenological variations in the tropics stem from individual-level plasticity or population-wide responses of non-plastic individuals. Using a combination of nest monitoring and GLS tracking, we examined the year-round breeding and migration phenology, breeding success, and recruitment of Red-billed Tropicbirds (*Phaethon aethereus*) in Cabo Verde from 2017 to 2024. Our aim was to investigate the underlying mechanism of phenological variability in tropicbirds to understand how they may cope with carry-over effects and future environmental change. Specifically, we investigated whether their phenology is 1) correlated between cyclical life-history events, 2) repeatable at the individual level, and 3) heritable. Our study involved the observation of repeated breeding, migratory, and recruitment events from 501, 45, and 27 adults, respectively, for two to six consecutive years. We found high population-level variability in breeding and migration timings, while individuals maintained remarkably consistent year-round phenology across subsequent years. Interestingly, the repeatability of migration was higher than that observed in species breeding in temperate climates. Despite some variability in the onset of migration, the timing of return to the colony was largely independent of the previous breeding success,

although it was delayed if a successful re-nesting event occurred (by 55.06±12.72 days). Moreover, the duration of the breeding interval did not affect subsequent success, but a delay in incubation date in respect to that of the previous year resulted in lower breeding success. Moreover, we found evidence of heritable phenology, with recruits returning to breed around the same time as when they fledged. Our findings suggest that long-lived tropical species may be more vulnerable to environmental change than previously thought, as population-wide responses cannot rely solely on individual-level plasticity.

INTRODUCTION

Understanding the drivers of phenology, the timing of life history events, and how phenological flexibility relates to individuals' fitness is crucial for predicting how populations will adapt to changing environmental conditions (Acácio et al., 2022; Gilroy et al., 2016; Lameris et al., 2018; Van Bemmelen et al., 2017). In animals this often requires an insight into how differences in behavior relate to individual fitness throughout the annual cycle (Acácio et al., 2022; O'Connor & Cooke, 2015). Events and processes experienced previously can have causal effects on individuals' fitness in subsequent seasons (Harrison et al., 2011; Norris, 2005; Norris & Marra, 2007). As such, unfavorable conditions during one part of the cycle may hamper an individuals' fitness in later parts of their cycle, despite the presence of seemingly favorable conditions (O'Connor & Cooke, 2015). These residual non-lethal effects, also known as ecological carry-over effects, have been shown to have surprisingly long-lasting repercussions, which may even persist after periods of apparent recovery (O'Connor & Cooke, 2015). Therefore, understanding the influence of carry-over effects on individual fitness and population dynamics is a key aspect of species ecology (Norris & Marra, 2007).

Carry-over effects have primarily been studied in migratory species, in which individuals experience and depend on a series of vastly different environmental conditions throughout their life cycle (Norris & Marra, 2007; O'Connor & Cooke, 2015). In these species, reproductive success may influence the timing and destination of subsequent migrations (Catry et al., 2013; Méndez et al., 2022; Mitchell et al., 2012), and conditions encountered during non-breeding periods may influence individuals' subsequent reproductive success

(Harrison et al., 2011; Norris & Marra, 2007). However, studies investigating these differences have almost exclusively focused on migratory birds breeding in temperate climates, leaving little known about the mechanisms of carry-over effects in species with primarily tropical distributions.

In species with non-tropical distributions, the seasonality of resources predominantly mediates the phenology of migration (Emmenegger et al., 2014; Monteith et al., 2011) and breeding of individuals (Lany et al., 2016; Meltofte et al., 2007). Conversely, tropical species rely on resources with less marked seasonal fluctuations compared to those found at higher latitudes (de Araujo et al., 2017; Nurul-Ain et al., 2017). For species that rely on less spatiotemporally predictable resources, individuals are expected to show higher levels of phenological flexibility (Franklin, et al., 2022a). Indeed, the breeding phenology of many tropical species is quite variable, with many species breeding asynchronously (e.g., Medrano et al., 2022; Oosthuizen et al., 2023) or even year-round (e.g., Franklin et al., 2022a; Stonehouse, 1962). In some extreme cases, phenology and seasonality are completely decoupled, with individuals breeding sub-annually once a particular quorum is reached (e.g., Reynolds et al., 2014; Stonehouse, 1962). If tropical species have higher flexibility in their phenology, they may be able to buffer, within physiological limitations, carry-over effects by adjusting their reproductive cycles according to experiences in the previous breeding seasons. In turn, this phenological flexibility may help them handle environmental changes, particularly those related to climate change. However, this hypothesis remains largely unconfirmed as it relies on whether the observed population-wide flexibility in phenology stems from individual adaptability. To gain insight into whether observed phenological variability in tropical systems is driven by individual plasticity or population level responses, individual repeatability, or the proportion of observed variance attributable to among-individual differences can be quantified (Stoffel et al., 2017). However, to date, there are very few studies on phenological repeatability in tropical species. A recent meta-analysis on the repeatability of avian migration phenology identified a single study site in the tropics out of 54 studies with suitable information on migratory timings (Franklin et al., 2022b). Moreover, two recent studies on tropical species have found very low individual phenological flexibility despite population-wide asynchrony in breeding (Franklin et al., 2022a; Oosthuizen et al., 2023), suggesting that individual repeatability of phenology might be more common in tropical systems than previously thought.

Understanding the underlying driver of phenological variability within a population may be particularly important considering climate change. In polar and temperate environments, prolonged periods of warming have advanced important life cycle events or shifted the geographical ranges of a wide array of animal species (Ambrosini et al., 2019; Gordo, 2007; Gunnarsson & Tómasson, 2011; Orgeret et al., 2022; Sydeman et al., 2015). Population-level phenological shifts arise from individual responses to changing conditions (individual plasticity, e.g. Przybylo et al., 2000; Sauve et al., 2019) and/or from or via changes in population structure that may then shape trait distributions (selection causing micro-evolutionary changes, e.g. Acker et al., 2023; Moiron et al., 2024). Whether these shifts are driven by individual plasticity or selection, they can impact the effectiveness of change. On the one hand, individual plasticity allows populations to adapt rapidly to change and may be beneficial in stochastic environments if the climatic cues for the event or conditions are loyal predictors of its occurrence (i.e., phenological sensitivity). On the other hand, individual plasticity cannot lead to the same level of efficiency as selection-induced specialization

(DeWitt et al., 1998). These mechanisms, however, are non-exclusive (Grenier & Litrico, 2016), and, in the face of climate change, individual plasticity is expected to buffer some of the effects of the fast-changing environment, while selection (a slower mechanism) eventually takes hold if the trait under selection is heritable. Moreover, individual plasticity can ensure that more genetic diversity is maintained after selection takes place, allowing species to continue to adjust rapidly to future changes (Gienapp et al., 2014). Identifying the mechanisms through which phenological shifts occur may be vital in predicting the effects of rapid environmental change on declining species (Knudsen et al., 2011). Therefore, examining phenology's repeatability and heritability give insights into how a species may respond to rapid change.

Here, we investigate the underlying mechanism of phenological variability in a tropical marine top predator, the Red-billed Tropicbird (*Phaethon aethereus*), to shed light on how this species may adapt to carry-over effects and changes in environmental conditions. By studying the year-round phenology, breeding success, and recruitment of Red-billed Tropicbirds using a combination of nest monitoring and GLS tracking, we determine whether phenology is 1) affected by connections between cyclical life-history events, 2) repeatable at the individual level, 3) a heritable trait.

Overall, the variability in breeding timing can enhance the resilience and adaptability of a population. However, if tropicbirds have low individual repeatability in their phenology, we expect that they will (at least initially) buffer carry-over effects and respond to environmental change with individual plasticity in behavior, which would, in theory, allow them to track climate change-induced shifts. Phenotypic plasticity may be especially important in long-lived species with low fecundity, such as Red-billed Tropicbirds since micro-evolutionary change is especially slow in species with longer generation times (Charmantier & Gienapp, 2014; Forcada et al., 2008; Gienapp et al., 2014). If tropicbirds exhibit high individual repeatability in phenology and this trait is heritable, they may lack the plasticity to buffer carry-over effects and environmental changes, implying that micro-evolutionary adjustments at the population level may occur.

METHODS

Study site

Data was collected in seven colonies, spread across two islands (Sal and Boavista) and two islets (Raso and Cima) in Cabo Verde, West Africa (Figure 1). At all sites, Red-billed Tropicbirds (Phaethon aethereus) were nesting in cavities in cliffs or under rock piles in areas with little or no vegetation cover. The climate at the study-sites is arid from December to June, with a wet season from July to November (Neto et al., 2020) with a peak in precipitation from August to October (Neves et al., 2017).

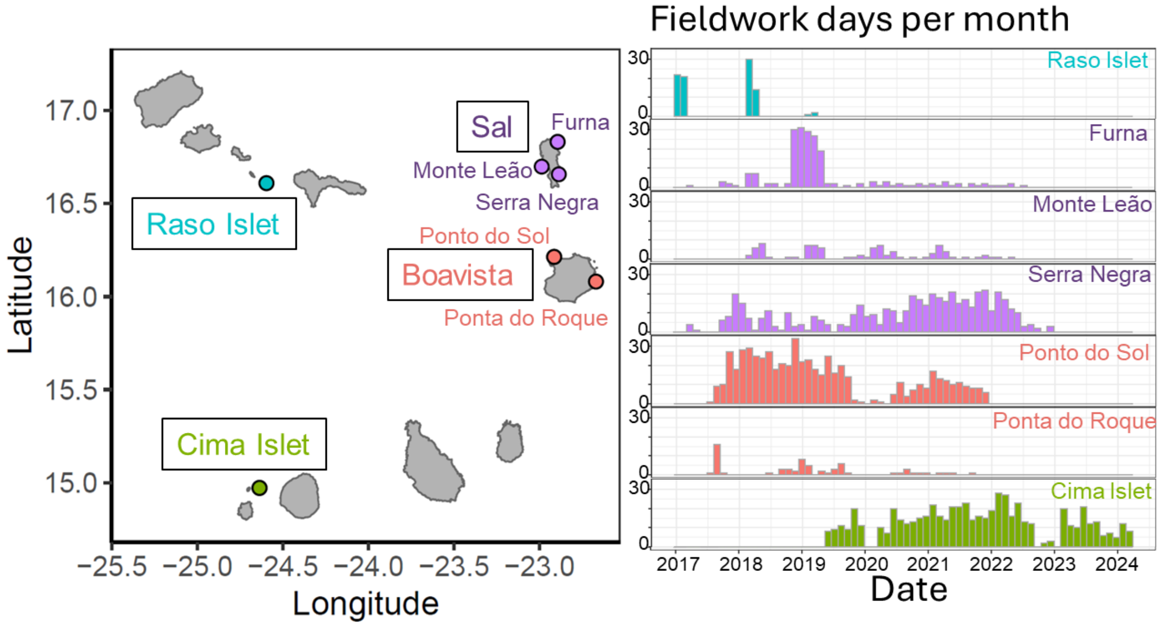
Fieldwork days per month

Figure 1. Study sites in Cabo Verde. Circles represent Red-billed Tropicbird colonies on Sal and Boavista islands and the uninhabited islets of Raso and Cima. Also shown are histograms of the number of fieldwork days per month per colony, as an indicator of nest monitoring effort. Note that the histograms do not include the fieldwork days related to the deployment and recovery of two geolocators in Raso in 2008 (both recovered in 2009).

Breeding phenology from nest monitoring

To monitor tropicbird breeding phenology, success, and recruitment, the contents of tropicbird nests were recorded between 2017-2024.Although many nests were visited every 1-3 days throughout the study period, some colonies were only visited monthly, and fieldwork on Raso was limited to the winters of 2008, 2009, 2017 and 2018. At each nest visit, the contents of the nest were recorded (empty, chick/egg, and whether there was an adult or not) and, upon first capture, we attached an individually numbered metal ring (identification ring) to the tarsus of adult and chick, for its later identification. Recruitment to the colony was identified by the recapture of an individual that was originally ringed as a chick post fledging. Whenever possible, 1ml of blood was also drawn from the tarsus of individuals, for molecular sexing (Griffiths et al., 1998). Since monitoring was inconsistent at certain times of the year and at more isolated nests, data on breeding phenology (laying, hatching and fledging date) and success (hatching success and fledging success) were only used in analysis when the window of uncertainty for these data was less than 30 days. When only one or two of the three breeding phenology dates were known, the unknown date(s) was(were) estimated based on adding/ subtracting the population means of incubation (41±5 days, n=27) or chick-rearing period (84±5 days, n=25) of nests with no uncertainty to/from the known phenological date with the smallest window of uncertainty.

Geolocation deployment and recovery

We deployed 133 Migrate Technology Ltd C330 and 2 Biotrack BAS_MK19 light-level geolocators (GLS) on 113 different individuals on Red-billed Tropicbirds breeding on Raso in 2008-2009 and at the remaining study sites between 2017-2021. Breeding individuals were captured whilst on the nest using noose-poles and GLS were attached with cable-ties to their metal identification ring. Devices were opportunistically recovered in subsequent years. The total tag weight of the GLS used was approximately 3.3g (0.5% of tropicbird mean tropicbird weight 630g±55, n=1297 individuals). During both deployment and recovery of GLS, birds were handled for the shortest time possible and immediately released back on to their nest after handling. Migrate Technology GLS recorded light intensities every minute, maximum light intensities every five minutes and conductivity (salt-water immersion data) every six seconds, while Biotrack GLS recorded both light intensity and wetness every 10 minutes. All GLS underwent at least one pre-deployment calibration near colony sites at an unshaded known location for a minimum of 3 days (Lisovski & Hahn, 2012). Upon recovery, a single post-deployment calibration at a known site was performed. Data from all available pre- and post-deployment calibrations were used to estimate the corresponding average zenith angle for each deployment, using the designated software IntiProc© from Migrate Technology Ltd. In cases for which post-recovery calibration was not possible, due to battery failure or technical issues with GLS, pre-deployment calibrations alone were used to calculate zenith angles (n=15). For devices which were deployed on birds for multiple years, each seasonal migration was analysed separately.

GLS data processing

We used the raw light-level data downloaded from recovered GLS to estimate the latitude and longitude of individuals each day, throughout the duration of the GLS deployment. This was done based on sunrise and sunset transitions identified with the function “preprocesslight”, using a light intensity threshold of 2, in the R package GeoLight (Lisovski et al., 2020; Lisovski & Hahn, 2012). This package was also used to visualise and manually repair sunrise and sunset transitions with evident interferences. A speed filter was applied to at-sea positions to remove points assumed to be erroneous due to speeds larger than the 95% percentile (Austin et al., 2003). For seasonal migrations, this corresponded to a speed of 17.19 km/h.

Breeding and migratory phenology from GLS data

For GLS, phenological dates and breeding success were extracted based on the birds' position according to the GLS tracks, in conjunction with raw light and wet-dry data. To do this, we first created and inspected interactive maps of track for each seasonal migration, using the package Shiny (Chang et al., 2015). The dates of initiation of outward migrations and arrival to Cabo Verde waters were defined based on directional movements outside of a 500 km radius around colony of origin. This 500km cut off was selected to exclude the foraging range of tropicbirds during the breeding seasons (although tropicbirds in Cabo Verde have been recorded to travel up to 803 km from their colonies, the mean foraging trip 66.67±sd 88.85 km is much smaller, this thesis Chapter 2) and based on the positional error associated with GLS tracks analysed with propGLS (~ 500 km for tropicbirds outside of equinox:(Halpin et al., 2021). If individuals did not undertake any directional movements, they were considered residents, and the non-breeding period was defined based on the last and first daytime burrow visit (n=2, Table 1). For individuals returning to or leaving the colony within 20 days of the spring and autumn equinoxes, longitudinal positions alone were used to determine directional movement and proximity to colony (Lisovski & Hahn, 2012).

The first and last day and night-time visits to the burrows, incubation bouts and the chick-rearing period were extracted based on the raw light and wet-dry data. Since tropicbirds in Cabo Verde breed in burrows, burrow visits were distinguishable dry and dark periods during the day, and long dry periods overnight (S1). The first/last daytime burrow visit was considered as the first/last dry and dark period over 1h after/before the individual's migration. The first/last night-time burrow visits were considered as the first/last night spent completely dry after-before migration. In cases for which no burrow visit was visible on the light-curve after the return migration, the day of GLS recovery was assumed to be the individuals' first day at the colony (n=6). Incubation bouts were classified as periods corresponding to a minimum of 48h of darkness in dry conditions (incubation shifts in tropicbirds last on average 6.04 ± 2.76 days; Beard et al. 2023). In cases in which additional incubation bouts were clearly visible in the wet-dry data but did not meet this set of criteria because of light infiltration into the burrow, the start and end of each incubation bout was added manually by inspecting each light-curve individually (S1). Individuals were assumed to be chick-rearing during the period between the last incubation bout and the last daytime visit at the colony.

Pre-breeding periods were calculated based on the number of days between the return to Cabo Verde waters and the first burrow visit. Similarly, post-breeding periods were calculated based on the number of days between an individuals' last daytime visit to the nest in each breeding season and the onset of the subsequent migration. The duration of the non-breeding period was calculated as the number of days between initiation of the outward migration and the first day in Cabo Verde waters. For further information on the extraction of phenological dates from GLS light curves see Table 1.

Table 1. Extraction criteria used for obtention of phenological dates from GLS light curves and corresponding sample sizes.

Phenological event	**Extraction criteria & sample size (n)**	**Observations**
Outward migration	Date individual starts directional movement away from colony, which is sustained for >3 consecutive days and followed by an absence from within a 500 km radius of the colony for >60 days (**n=156**).	For birds which did not migrate, the last day of nest activity was used to mark start of non-breeding distributions (n=2).
Arrival at non-breeding ground	Date individual ceases directional movement away from colony and sustains limited longitudinal and latitudinal shifts for >3 consecutive days, outside of a 500km radius around colony (**n=156**).	
Inward migration	Date individual starts directional movement towards the colony, which is sustained for >3 consecutive days and followed by a return to within a 500 km radius of the colony (**n=156**).	For birds which did not migrate, the first day at colony was used to mark the end of non-breeding distribution (n=2).
Arrival at breeding ground	Date individual returns to within 500km radius of colony (**n=151**). This date was also used to establish the season associated with the onset of the breeding period for individuals in any given year.	Battery failure meant that this date was missing for five migrations
First day at colony	Date of first daytime visit to burrow visible on light curve and wet-dry data, after return to within 500km radius of colony (**n=82**). This date marks the start of the pre-incubation period.	When missing, GLS recovery date used instead (n=7).
Onset of incubation	Date of first period of >48h of darkness in dry conditions associated with a given breeding attempt (**n=173**). This date also marks the end of individuals' pre-incubation periods and the start of their incubation period.	Some individuals re-nested after initial breeding attempts fails (n=37).

End of incubation	Date of last day of period of >48h of darkness in dry conditions associated with a given breeding attempt (**n=74**).	For attempts which fail at egg-stage, this equals the last day of nest activity (n=4)
Onset of chick-rearing	Date of first daytime visit to burrow visible on light curve, between the end of incubation and before the last day of nest activity for a given breeding attempt (**n=90**).	The existence of this date indicates hatching success.
Last night of nest activity	Date of last overnight stay in the burrow visible on light curve after the onset of chick-rearing for a given breeding attempt **(n=193).**	
Last day of nest activity	Date of last daytime visit to burrow visible on light curve after the onset of chick-rearing for a given breeding attempt (**n=193**). For attempts which failed at egg stage, this date equals the end of incubation.	Individuals may re-nest after initial breeding attempts fails (n=37).

Breeding success from GLS data

In the absence of nest monitoring data, we used GLS data to extract hatching success. Nests with GLS inferred incubation periods > 25 days followed by daytime nest activity, indicating chick-rearing, were deemed to have hatched successfully (n=7). The 25-day cut-off was derived from the Mean-2SD of GLS-derived successful incubation periods from nest with both monitoring and GLS data (40.93± 7.28, n=46). This is significantly shorter than the incubation period derived from the monitoring data for the same nests (44.75 ±6.64; paiRed-t=2.83, df=45, p-value=<0.0.1. mean difference=3.80 days), since the GLS only recorded incubation periods from one adult, and thus did not capture additional incubation bouts from the partner. Moreover, we also classified one GLS-derived incubation period which lasted for 60 days as unsuccessful, as we assumed the egg was infertile.

Similarly, we also used GLS data to extract hatching success in the absence of nest monitoring data. Nests with GLS inferred chick-rearing periods > 74 days were deemed to have fledged successfully (n=22). The 74-day cut-off was derived from the Mean-2SD of GLS-derived successful chick-rearing periods from nest with both monitoring and GLS data (84.50± 5.24, n=14). Again, this is significantly shorter than the chick-rearing derived from the monitoring data for these same nests (88.07±3.97; paiRed-t=2.35, df=13, p-value=0.04. mean difference=3.57 days) since chicks often fledged after the initiation of their progenitor's migration. Nests with chick-rearing periods >74 days were also deemed to be unsuccessful (n=33).

In all cases with both nest monitoring and GLS data, the breeding outcomes estimated based on calculated incubation and/or chick-rearing periods matched those recorded in the monitoring data.

Relationship between breeding success and the duration of life cycle events.

To evaluate the effects of breeding success on the duration of subsequent life cycle events, we created a series of General Linear Models (GLMs) relating the categorical variables breeding success (failed or successful) and re-nest (re-nest or no re-nest) to time within Cabo Vede waters, and the duration of the post-breeding, non-breeding, and pre-breeding periods. Since including individual ID in the model as a random intercept resulted in a singular fit, we randomly selected one life cycle event per individual to avoid pseudoreplication. Moreover, in a preliminary analysis, we found no sex-specific differences between the duration of life cycle events (S2), and therefore, sex was not included in the models as it greatly reduced sample size. To account for potential differences between islands, and year (year of initiation of migration), these variables were also included in the models as categorical co-variates.

Similarly, to evaluate the effect of breeding success on the subsequent breeding interval (period between two consecutive incubation periods, not including re-nesting attempts), we also created a series of GLMs relating the categorical variables breeding success (failed or successful) and re-nest (re-nest or no re-nest) of the first breeding attempt to the breeding interval. We analysed breeding intervals using two models: one based solely on GLS data and the other on nest monitoring data. We made this division because GLS data guarantees no missed nesting events, unlike monitoring data which lacks certainty in event capture. In both cases, including individual ID in the models as a random intercept resulted in a singular fit. Therefore, we randomly selected one breeding interval per individual To account for potential differences between islands, and year (year of initiation of migration), these variables were also included in the models as categorical co-variates.

Finally, to evaluate the effect of breeding interval on subsequent breeding success we also created a binomial GLM relating subsequent breeding success (success or failed) to the breeding interval. We analysed breeding intervals using two models: one based solely on GLS data and the other on nest monitoring data. We made this division because GLS data guarantees no missed nesting events, unlike monitoring data which lacks certainty in event capture. In both cases, including individual ID in the models as a random intercept resulted in a singular fit. Therefore, we randomly selected one breeding interval per individual. To account for potential differences between islands, and year (year of initiation of migration), these variables were also included in the models as categorical co-variates.

For all models, we started with the most complex model tested all possible combinations of the explanatory variables using the “dredge” function from the MuMIn package (Barton

2022) in R and compared their Akaike's Information criteria (AIC) values for model selection. The model with the lowest score was considered the best supported.

Repeatability and the effect of breeding success

Repeatability (R) was calculated for the Day of Year (DOY) of phenological dates (incubation, hatching, fledging, last day of nest activity, initiation of migration, arrival at first non-breeding area, initiation of the last migration, return to Cabo Verde waters, the first daytime burrow visit, and the first overnight burrow visit of the season) with the R package rptR (Stoffel et al., 2017). For this, we used mixed-effects models with Poisson distributions and individual ring number as a random effect. We also included 1,000 bootstrap iterations to estimate confidence intervals (CIs)

To overcome the circular nature of dates, we modified the phenological dates of individuals who's consecutive phenological events spanned the first of January, by adding 365 to the second value. For example, for an individual with the onset of a first migration on the 31st of December (DOY=365), and of the second migration on the 1st of January (DOY=1), the latter was transformed to DOY=366. This modification had no significant impact on the estimated repeatability values.

To determine the effect of breeding success on the repeatability of breeding phenology (lay, and hatch date), we used Generalized Linear Mixed Models (GLMM) with a Gaussian distribution, with individuals' ring numbers defined as a random intercept and categorical variables for breeding success. Although we only considered the repeatability of phenology of the first breeding attempt per season, when there was a successful re-nesting event, we considered the breeding success between phenological events to be successful. To account for potential differences between sexes, years, and islands, these variables were also included in the models as fixed effects. For all models, we started with the most complex model tested all possible combinations of the explanatory variables using the “dredge” function from the MuMIn package (Barton & Barton, 2023) in R and compared their Akaike’s Information criteria (AIC) values for model selection. The model with the lowest score was considered the best supported.

Heritability of breeding phenology

Within the duration of our study, 67 individuals that were ringed as chicks were recaptured at the colonies at least once, and of these, we recorded 31 breeding events from 28 individuals for which there was less than one month of uncertainty in the breeding phenology of both the parents and offspring. Since we only had repeated breeding events from two individuals, only the first breeding attempt per chick was included in the models. This subsample was used to examine narrow-sense heritability in hatching or predicted hatching dates, since the data were not detailed enough to build pedigrees that would allow the genetic basis of phenological variation to be determined with ‘animal models’ (Kruuk, 2004). We therefore used parent-offspring regression to estimate narrow-sense heritability (h2) in hatch date, or, in case of failure at the egg stage, predicted hatch date. To correct for circularity, the day of the year of hatch and/or recruitment were modified by adding 365 days when the DOY of recruitment lapsed January 1st.

All analyses carried out as part of this study were performed in R. Values presented alongside averages represent the standard deviation (±SD) of the sample, unless specifically stated otherwise.

RESULTS

Phenology

From nest monitoring data, the mean incubation and chick-rearing periods for successful nests were 43.94±10.78 days (n=353), and 81.16±14.00 days, respectively (Figure 1).

Similarly, from GLS data, the mean incubation and chick-rearing periods for successful nests were 41.88±5.12 days (n=50), and 85.50±5.26 days (n=18), respectively (Figure 1). From the GLS data, we were also able to extract the mean post-breeding period (19.52±30.21 days (n=140), non-breeding period (166.64±25.39 days, n=151), the mean pre-incubation period (34.53±24.04, n=125) and, finally, the mean time spent in Cabo Verde waters, including the periods of pre-incubation, breeding and post-breeding (174.16±38.73 days, n=43).

During the pre-laying period, a departure from Cabo Verde waters was detected for 59 birds (19 females, 26 males and 14 of unknown sex) and interpreted as a pre-laying exodus as it often occurred after a first nest visit.

In successful breeders, individuals undertook 4.8±0.97 incubation bouts before hatching a chick (n=50). The mean number of bouts was greater in males (5.15±0.99) than in females (4.54±1.03; t=-2.16, df=42, p-value=0.04) but the time spent incubating (sum of all GLS-derived incubation bouts) did not differ significantly by sex (t=-1.15, df=42, p-value=0.25).

In 22 cases in the GLS derived phenology, individuals re-nested after failure to hatch (n=11), fledge (n=8) or at an unknown stage (n=3). The success of the re-nesting attempts was 37.5%success (n=16). For individuals which engaged in re-nesting attempts, the average number of days between the onset of the two subsequent incubations was 57.4 days (±17.9

days, n=22). Based on nest monitoring data, 75 cases of re-nesting were also identified (35.4% success, n=51).

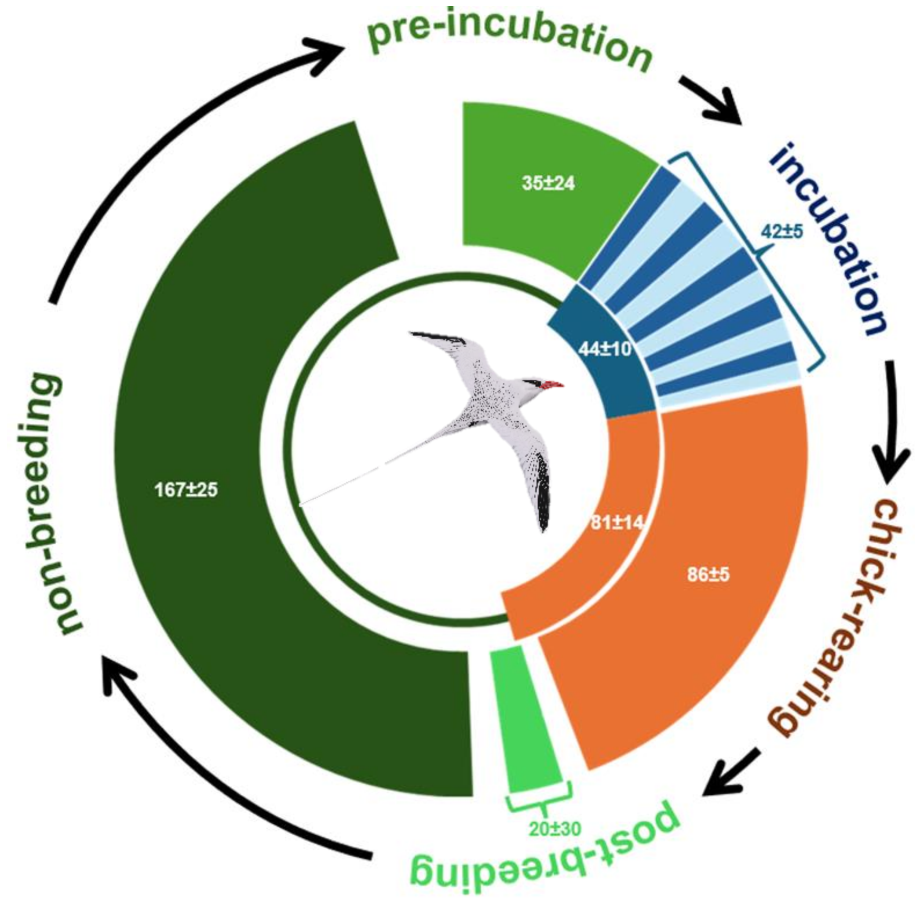

Figure 1. Mean duration and standard deviation of the durations in days of the different stages in the annual cycle of Red-billed Tropicbirds extracted from nest monitoring data (inner circle) and GLS data (outer circle) from successful breeders with only one breeding attempt per season. More while year-round information was extracted from the GLS data, only breeding phenology could be extracted from nest monitoring. Moreover, for the incubation period extracted from the GLS data, the mean duration of the incubation (dark-blue) and foraging bouts (light blue) are shown (5 bouts are shown since we recorded an average of 4.8±1.0 incubation bouts per individual). Failed breeders may engage in a re-nesting attempt, involving a second pre-laying, incubation, and chick-rearing period within a breeding season.

Relationship between breeding success and the duration of life cycle events

The best model to predict mean time spent in Cabo Verde waters, included a categorical variable for re-nesting (S3), with individuals that re-nested spending 39.08±16.39 (Estimate±SE) days longer in Cabo Verde waters than those that did not re-nest (p-value=0.02, Table 2)

The best model to predict the duration of the post-breeding period included categorical variables for re-nesting and island (S3). Individuals that re-nested spent 75.63±7.97 (Estimate±SE) days longer in the post-breeding than those that did not re-nest (p-value <0.001, Table 2)

The best model to predict the duration of the non-breeding period included a categorical variable for re-nesting (S3), with individuals that re-nested spending 17.64±7.94 (Estimate±SE) days less in the non-breeding period than those that did not re-nest (p-value=0.02, Table 2)

The best model to predict the duration of the pre-laying period included categorical variables for re-nesting, island, and year (S3). However, no relationships were significant (Table 2).

The mean breeding interval was 334.51±40.98 (n=49) based on GLS data and 343.32±49 (n=789) based on monitoring data. The best model to predict the breeding interval based on both the GLS and the nest monitoring data, included a categorical variable for breeding success, re-nesting, island, and year. In the model based on GLS data, the breeding interval of successful birds was 33.18±11.97 days longer than unsuccessful birds (p<0.01) and that of re-nesting birds was 55.06±12.72 days longer than those that did not re-nest (p<0.01). Similarly, in the model based on nest monitoring data, the breeding interval of successful birds was 32.77±5.90 days longer than unsuccessful birds (p<0.01) and that of re-nesting birds was 33.99±18.96 days longer than those that did not re-nest (p<0.01).

Finally, the best fit model to predict the effect of breeding interval on subsequent breeding success, only included the variable island, suggesting breeding interval does not have an important influence on subsequent breeding success (S2, table 2). The best model to predict subsequent success based on the difference in DOY of incubation, included a categorical variable for island, and year. Birds were more likely to be successful when their incubation started early in comparison to the previous year (p=0.05, S2, table 2).

Table 2. Model output of best AIC-selected General Linear Models relating the duration of different cyclical life stages to previous breeding success and re-nesting and Generalized Linear Models with binomial distribution relating cyclical life stage duration on subsequent breeding success.

Fixed effects	Estimate±SE	t-value	Lower CI	Upper CI	P-value
Duration in Cabo Verde waters ~ breeding success (n=29, R2=0.14)					
Intercept	209.75±13.94	15.04	181.14	238.36	<0.001
Re-nest re-nest)	39.08±16.39	2.39	5.46	72.70	0.02
Duration of post-breeding ~ breeding success (n=106, R2=0.48)					
Intercept	94.81±7.92	11.97	79.09	110.51	<0.001
Re-nest (re-nest)	75.63±7.97	9.49	59.8	1.44	<0.001
Island Boavista-Cima	-9.89±6.85	-1.44	-23.48	3.39	0.15
Island Boavista-Raso	-2.75±10.09	-0.27	-22.76	17.26	0.79
Island Boavista-Sal	-8.79±5.68	-1.55	-20.06	2.47	0.13
Duration of non-breeding ~ breeding success (n=112, R2=0.03)					
Intercept	149.73±7.54	19.85	134.78	164.68	<0.001
Re-nest (re-nest)	-17.64±7.94	-2.22	-33.38	-1.90	0.03
Duration of pre-incubation ~ breeding success (n=74, R2=0.02)					
Intercept	38.33±23.65	1.62	-8.91	85.57	0.11
Re-nest (re-nest)	11.24±7.66	1.47	-4.07	26.55	0.15
Island Boavista-Cima	1.03±8.54	0.12	-16.02	18.09	0.90
Island Boavista-Raso	18.41±16.99	1.08	-15.54	52.35	0.28
Island Boavista-Sal	-1.96±5.72	-3.34	-13.39	9.46	0.73
Year 2008-2017	-14.50±20.54	-7.06	-55.53	26.53	0.48
Year 2008-2018	9.50±20.54	0.46	-31.53	50.53	0.65
Year 2008-2019	19.44±22.22	0.88	-24.95	63.83	0.39

Year 2008-2020	21.46±22.46	0.96	-23.41	66.33	0.34
Year 2008-2021	13.24±24.100	0.55	-34.91	61.39	0.59
Interval of breeding (GLS data only) ~ breeding success (n=35, R2=0.56)					
Intercept	331.08±23.20	14.27	283.48	378.68	<0.001
Success between	33.18±11.97	2.77	8.62	57.75	0.009
Re-nest between	55.06±12.72	4.33	28.97	81.15	<0.001
Island Boavista-Cima	-49.65±23.75	-2.09	-98.38	-0.92	0.05
Island Boavista-Sal	12.84±11.67	1.10	-11.10	36.78	0.28
Year 2018-2019	15.28±18.58	0.82	-22.85	53.40	0.42
Year 2018-2020	29.06±16.29	1.78	-4.37	62.49	0.09
Year 2018-2021	51.19±20.20	2.54	9.75	92.63	0.02
Interval of breeding (nest monitoring) ~ breeding success (n=418, R2=0.14)					
Intercept	305.49±11.34	26.93	283.17	327.80	<0.001
Success between	32.77±5.90	5.55	21.16	44.38	<0.001
Re-nest between	33.99±8.96	3.80	16.40	51.60	<0.001
Island Boavista-Cima	-4.35±9.98	-2.44	-43.99	-4.71	0.02
Island Boavista-Raso	25.08±27.53	0.91	-29.07	79.23	0.36
Island Boavista-Sal	8.18±8.26	0.99	-8.05	24.42	0.32
Year 2018-2019	24.23±10.58	2.29	3.42	45.04	0.02
Year 2018-2020	17.45±10.40	1.68	-3.00	37.90	0.09
Year 2018-2021	20.16±9.90	2.04	0.69	39.63	0.04
Year 2018-2022	37.81±11.53	3.28	15.13	60.49	0.001
Year 2018-2023	39.32±14.10	2.79	11.60	67.05	0.006
Year 2018-2024	43.10±45.88	0.94	-47.16	133.35	0.34
Subsequent breeding success (0/1) ~ breeding interval (based on monitoring data, n=501)					
Intercept	0.56±0.36	1.55	-0.13	1.30	0.12
Island Boavista-ICima	0.84±0.42	1.99	-0.01	1.65	0.05
Island Boavista-Raso	0.13±1.27	0.11	-2.31	3.26	0.92
Island Boavista-Sal	-0.34±0.40	-0.85	-1.15	0.43	0.39
Subsequent breeding success (0/1) ~ difference DOY incubation (based on monitoring data, n=501)					
Intercept	-0.56±0.40	-1.40	-1.37	0.21	0.16
Diff DOY incubation	-0.00±0.00	-1.92	-0.01	-0.00	0.05
Island Boavista-ICima	0.86±0.41	2.12	0.08	1.69	0.03
Island Boavista-Raso	-14.23±0.809.16	-0.02	NA	91.11	0.98
Island Boavista-Sal	0.22±0.36	0.60	-0.48	0.96	0.55
Year 2018-2019	-1.30±0.52	-2.52	-2.33	-0.29	0.01
Year 2018-2020	-0.19±0.46	-0.41	-1.10	0.73	0.68
Year 2018-2021	-0.74±0.47	-1.58	-1.67	0.19	0.11
Year 2018-2022	-0.48±0.50	-0.96	-1.47	0.51	0.34
Year 2018-2023	-0.01±0.62	-0.03	-1.22	1.20	0.98
Year 2018-2024	-16.01±839.58	-0.02	NA	93.04	0.98

Repeatability of phenology

We recorded the laying phenology of 501 individuals in two or more subsequent years (two years: 313, three years: 107, four years: 64, five years: 15, and six years: 2). The 1,290 laying dates of this datasset were extracted from monitoring data (83.9%, n=1,082), GLS data (1.6 %, n=21), or from both GLS and nest monitoring (14.5%, n=187).

We recorded the hatching phenology of 325 individuals in two or more subsequent years (two years: 229, three years: 52, four years: 41, five years: 3). The 793 hatching dates of this datasset were extracted from monitoring data (81.0 %, n=642), GLS data (0.5%, n=4), or from both GLS and nest monitoring (18.5 %, n=147).

We recorded the fledging phenology of 175 individuals in two or more subsequent years (two years=89, three years=31, four years=8). The 303 fledging dates of this datasset were extracted from monitoring data (83.5 %, n=253), GLS data (0.3 %, n=1), or from both GLS and nest monitoring (16.2 %, n=49).

In total, 156 seasonal migrations were recorded by the recovered GLS, corresponding to 136 separate deployments on 113 different individuals. Of these, 103 GLS were recovered from birds after 1 year of deployment, 28 after 2 years and 8 after 3 years. From the GLS tracks, we recorded repeated phenological events in two or more subsequent years from 45 different individuals. The number of repeated events for each of the non-breeding phenological dates are summarized in Table 3.

We found that high repeatability in phenology in all breeding and migratory dates observed (Table 3, Figure 3). The timing of the return to Cabo Verde waters had the highest overall repeatability (0.94) while the lowest repeatability was associated with the laying date (0.63).

Both the repeatability of laying and hatching date were affected by breeding success. The best models to predict the repeatability of laying date included categorical variables for re-nesting and breeding success (S3). Individuals that were that breed successfuly and that re-nested had higher repeatability values then those that were unsuccessful (p<0.001) of that did not re-nest (p=0.002, Table 4, Figure 3, 4)

Similarly, the best model to predic the repeatability of hatching date included a categorical varibale for breeding success (S3). Individuals that breed successfully had a higher repeatability in their values than those that were unsuccessful (p<0.01, Table 4, Figure 3, 4).

Table 3. Repeatability estimates (R) from Red-billed Tropicbirds with repeated breeding and migratory phenologies (2-6 years). N.ind=Number of individuals, N.rep=Number of repeated measures. Darker green cells highlight higher levels of repeatability.

Event	N.ind	N.rep	R	SE	Lower CI	Upper CI	p-value
Laying date	501	1578	0.63	0.02	0.59	0.67	<0.001
Hatching date	325	936	0.73	0.02	0.68	0.77	<0.001
Fledging	128	350	0.80	0.03	0.73	0.85	<0.001
Last night at the burrow	30	74	0.86	0.05	0.75	0.93	<0.001
Last day at the burrow	45	106	0.71	0.07	0.54	0.82	<0.001
Initiation of outward migration	35	86	0.88	0.04	0.78	0.93	<0.001
Arrival at non-breeding ground	34	82	0.88	0.04	0.77	0.93	<0.001
Initiation of return migration	34	74	0.92	0.30	0.85	0.96	<0.001
Return to Cabo Verde waters	34	80	0.94	0.02	0.88	0.97	<0.001
First day at the burrow	33	76	0.91	0.03	0.82	0.95	<0.001
First night at the borrow	28	62	0.93	0.03	0.86	0.97	<0.001

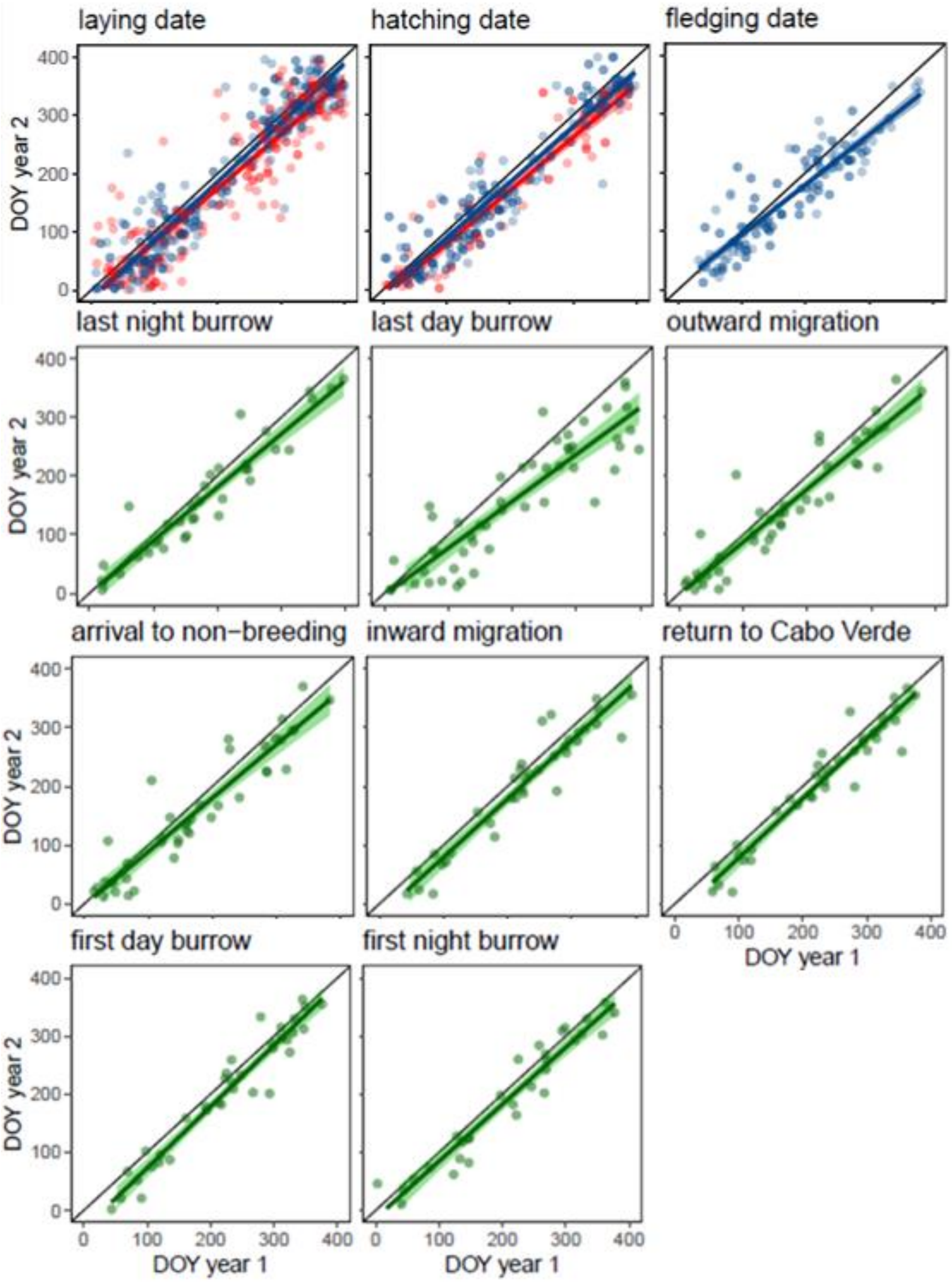

Figure 3. Regression of phenological dates in two subsequent years. For laying and hatching dates the relationship is seperated for failed (red) and successful breeders (blue). In green are GLS extracted phenological dates related to the non-breeding period.

Table 4. Model output of best AIC-selected Generalized Linear Mixed Models relating the repeatability of laying and hatching dates to prior breeding success and re-nesting (blue) and to the subsequent breeding success. Upper and Lower CI=Upper and lower 95% Confidence Interval, SE=Standard error. The sample size and the variance and standard deviation of the random effect individual ID is included in the title of each model.

Fixed effects	**Estimate±SE**	**t-value**	**Lower CI**	**Upper CI**	**P-value**
Repeatability of laying date ~ breeding success between (n=402, Variance of ID: 0.00, SD: 0.03)					
Intercept	0.89±0.01	112.50	0.88	0.90	<0.001
Breeding success	0.05±0.01	5.51	0.03	0.07	<0.001
Re-nest	0.05±0.01	3.07	0.02	0.07	0.002
Repeatability of hatching date ~ breeding success between (n=258, Variance of ID: 0.00, SD: 0.03)					
Intercept	0.91±0.01	119.50	0.90	0.93	<0.001
Breeding success	0.04±0.01	4.25	0.02	0.05	<0.001

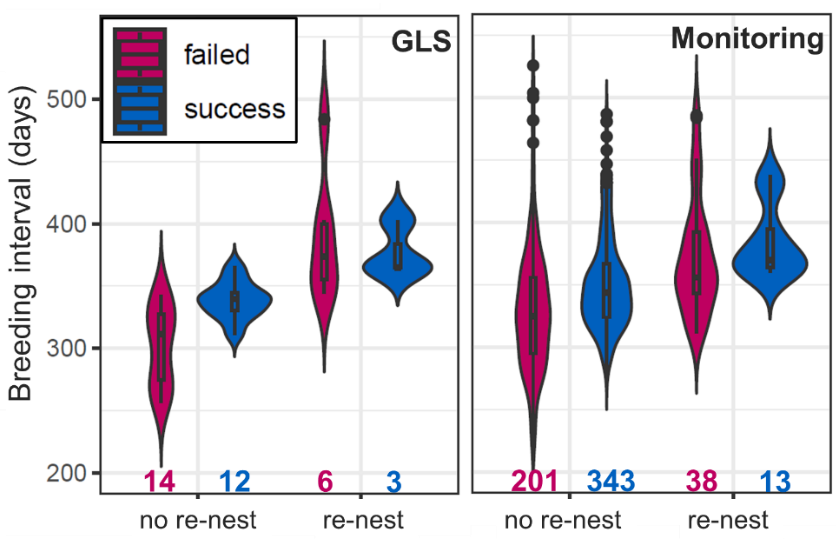

Figure 4. Violin plots of breeding interval (time between subsequent incubations) of Red-billed Tropicbirds after the first breeding attempt failed (red) or was successful (blue) and whether a re-nesting attempt occurred or not based on GLS (left) and nest monitoring (right) data. Note that for re-nesting birds, success refers to the success of the re-nesting attempt after initial failure. Numbers indicate sample size.

Recruitment

Within the duration of our study, 67 individuals that were ringed as chicks were recaptured at the colonies at least once. Of these individuals, 41 (61%) were breeding when first observed (28 incubating and 13 chick-rearing), 18 (27%) were vagrants and the breeding stage of 8 individuals (12%) was not recorded. While some individuals were recorded to be breeding as soon as one year after hatching, most individuals were first recorded between 2-3 years after hatching (Figure 5). The recruits showed strong philopatry and most returned to the same colony in which they hatched (97%). However, there were 3 events in which individuals were recaptured at different colonies or even islands. One chick that hatched in the colony of Ponto do Sol (Boavista) was recovered in Ponto do Roque (Boavista), Moreover, one chick hatched in Cima islet was recovered in the neighbouring Rei islet, and in the biggest inter-island movement, one chick hatched in Ponto do Sol (Boavista) was recaptured in Cima islet.

Parent–offspring regression analysis indicated breeding phenology of recruits were significantly correlated to that of their progenitors (intercept: 89.47 days, slope=0.84, se=0.09, p<0.001, figure 4). Moreover, the amount of variation explained by the parent-offspring regression was high (R2: 0.77). The intercept of this model also suggests that individuals recruited to the colony slightly later then when they were hatched, around the time that they fledged (Figure 5).

Figure 5. A) Age of Red-billed Tropicbirds in years when first recaptured at the colony as non-breeders (red) and breeders (cyan). B) Parent-offspring regression of breeding tropicbirds ringed as chicks (intercept: 89.46 days, slope=0.84, se=0.09, p<0.001, R2: 0.77).

DISCUSSION

Although Red-billed Tropicbirds breed year-round in Cabo Verde, individuals maintained consistent breeding and migratory phenologies. The repeatability of phenology near the end of the non-breeding period (e.g., initiation of return migration, return to Cabo Verde waters, first day at the burrow, first night at the borrow) was greater than that for the phenological events during the breeding and post-breeding periods (e.g., laying, hatching, and fledging, last day at the colony), suggesting that individual adjust their migratory phenology by extending or shortening their non-breeding period in the case of nest failure or subsequent re-nesting events, respectively. Furthermore, we found that when incubation was delayed relative to the timing of incubation in the previous year, individuals had lower breeding success, suggesting that individuals who failed to adjust their phenology suffered fitness consequences. Moreover, tropicbird phenology appears heritable, with chicks recruiting to the colony around the same time of year as when they fledged. These results challenge the idea that tropical species can freely adjust their phenology throughout the year.

Benefits of GLS-derived phenology

This study combined GLS and traditional nest monitoring methods to gather information on individual breeding and migratory phenology. While both methods offer advantages, GLS provided precise data on non-breeding period events, such as the start of return migration and arrival in Cabo Verde waters. Additionally, GLS ensured no missed breeding attempts, unlike potential gaps in nest monitoring. However, GLS tracking is not foolproof and some re-nesting attempts may have been misidentified as initial attempts if GLS deployment or recovery occurred between incubation periods or due to inconsistent nest monitoring.

Nonetheless, this study supports previous findings that GLS devices are valuable for identifying individual migratory phenology (Franklin et al., 2022b).

Phenology and links between life cycle events

On average, tropicbirds were absent from the breeding colony for six months and were either breeding or in Cabo Verde waters for the remaining months of the year. This is similar to what has been recorded for this species breeding in Ascension (Stonehouse, 1962, mean non-breeding period of 166 days). As in previous studies, individuals who failed to fledge a chick in their first breeding attempt occasionally engaged in re-nesting attempts (Madden, 2019; Stonehouse, 1962). These events resulted in the individuals spending longer within Cabo Verde waters and later compensating for this by reducing their non-breeding period. By the time individuals reached their subsequent pre-laying period, the effect of the re-nesting was generally no longer significant.

However, GLS and nest monitoring results suggest that despite shortening the non-breeding period, the breeding interval was longer in re-nesting birds. We also found that the interval was more extended in successful and unsuccessful birds. This suggests that birds that failed to breed returned to the colony earlier unless they attempted to re-nest. This is consistent with the findings of other seabird studies, which recorded that failed breeders and non-breeders depart earlier from their colony in comparison to successful breeders (Phillips et al., 2005; Yamamoto et al., 2014). Interestingly, individuals who re-nested but were unsuccessful maintained a similar migratory and subsequent breeding phenology to those who were successful on their first try, potentially masking the relationship between breeding success and phenology. Moreover, we also found that birds that initiated incubation late in relation to the previous year had a lower breeding success than those that initiated incubation early, but that subsequent breeding success was not affected by the breeding interval. Therefore, the lack of phenological consistency and not the duration of time between breeding events resulted in lower breeding success. Altogether, these findings suggest that breeding failure has carry-over effects on subsequent migratory phenology, which individuals buffer to a certain extent by reducing the non-breeding period. However, if the lag persists into the breeding season, individuals suffer fitness consequences.

Repeatability

We found high individual repeatability in tropicbird phenology, ranging from 0.63 (laying date) to 0.94 (return to Cabo Verde waters). These indices of repeatability are higher than what was found in a recent review of avian migratory timings, which reported an average repeatability of 0.41 (CI: 0.3-0.5) across landbirds, waterbirds and seabirds (Franklin et al., 2022b). However, it is important to note that since tropicbirds breed year-round, the repeatability of phenology may be naturally inflated by the large population-wide variability (Franklin et al., 2022a). Indeed, a recent study on the repeatability of phenology in a group of tropical gadfly petrels, which breed year-round, also reported exceptionally high individual repeatability ranging from repeatability of 0.79 (CI: 0.70-0.85) for outward migrations and (0.81; CI: 0.72-0.88) for inward migrations (Franklin et al., 2022a). Other studies investigating individual variation in phenology in tropical species also noted important individual consistency (Leal & Bugoni, 2021; Medrano et al., 2022; Oosthuizen et al., 2023). For example, a study on Cape Verde Storm Petrels (*Hydrobates jabejabe*) found two peaks of breeding, with individuals rarely switching between the two, indicating that although repeatability was not explicitly measured, the species showed some levels of individual consistency (Medrano et al., 2022). Moreover, a recent study on asynchronously breeding southern elephant seals (*Mirounga leonina*) also found high individual repeatability in phenology (Oosthuizen et al., 2023), suggesting that consistent individual differences in migratory timings may be a more common feature in the migratory systems of tropical marine top predators than previously thought.

We also found that individual repeatability values were lowest for breeding phenology (i.e., incubation, hatching, and fledging dates) and highest for inward migration to Cabo Verde waters and that these values were higher for successful breeders. Although some of the lowest repeatability values in the breeding season may have resulted from the inherent uncertainty of the monitoring data, this pattern also occurred in the GLS-derived phenologies, indicating that this is not the only case. Instead, this suggests that individuals adjust non-breeding periods to compensate for breeding failure, re-nesting, or successful breeding; however, despite these adjustments, unsuccessful breeders still had lower laying and hatching repeatability values than successful birds. Similar patterns have been documented in previous studies investigating carry-over effects on migration phenology, where individuals with lower parental investment depart breeding colonies earlier, resulting in more extended non-breeding periods compared to successful counterparts (Bogdanova et al., 2011; Phillips et al., 2005; Yamamoto et al., 2014). Additionally, as seen in Black-legged Kittiwakes (Rissa tridactyla) and Cory's Shearwaters (*Calonectris borealis*), individual repeatability to the arrival to the breeding areas exceeds that of migration onset, indicating buffered carry-over effects from previous breeding attempts across subsequent post-breeding, non-breeding, and pre-breeding periods (Bogdanova et al., 2017; Ramos et al., 2018). This result suggests that repeatability in the arrival date to the breeding areas brings some advantages.

Repeatability in phenology may increase fitness through familiarity with the environment and/or by facilitating synchronous mate arrival (Fayet et al., 2017; Gunnarsson et al., 2006; E. D. Wakefield et al., 2009). Although tropicbirds breed year-round, there are seasonal differences in tropicbird behavior and environments encountered in both the breeding (this thesis, chapter 2) and non-breeding season (this thesis, chapter 3). By maintaining individually consistent phenologies, tropicbirds may benefit from familiarity with the resources and risks of a given season. Consistency in the migratory distribution and/or phenology in marine vertebrates is common, suggesting that both space use and phenology may offer more stable energetic rewards than plastic behavior in marine environments (e.g., Abrahms et al., 2018; Brown et al., 2021; Franklin et al., 2022b; Léandri-Breton et al., 2021; Pérez, 2019; Shimada et al., 2020; Studds & Marra, 2005; E. Wakefield et al., 2015). Different migration timing may result from individual foraging behavior and habitat quality, leading to varying optimal migration times (Studds & Marra, 2005). Moreover, consistency may also benefit tropicbirds through knowledge of the availability of nest sites and synchronous mate arrival, which may be particularly important in species with high nest-site competition, such as tropicbirds. Although the causes of nest failure were often challenging to determine in this study, intense inter and intra-species competition for sites has been recorded for tropicbirds (Semedo, 2020; Stonehouse, 1962). Moreover, it is even the primary cause of nest failure in certain colonies. For example, in Ascension, it has been suggested that the seasonal peaks in phenology in both White-tailed (*Phaethon lepturus*) and Red-billed Tropicbirds were regulated by both intra and interspecific competition, as indicated by higher failure when the highest number of individuals from both species were breeding (Stonehouse, 1962). Red-billed Tropicbirds are known to have high mate and nest fidelity (Madden, 2019), and since tropicbirds breed year-round, having highly repeatable phenology may enable them to synchronize with previous partners. Thus, maintaining consistent migratory phenology and behavior can significantly enhance tropicbird fitness by optimizing resource use, reducing risks, and facilitating mate synchronization, which is crucial in environments with high nest-site competition.

Heritability of phenology

We found high heritability of tropicbird phenology, with recruits returning to the colony around the same time of year as when they fledged. This finding is similar to previous results on Scopoli's Shearwater *Calonectris diomedea* (Pérez, 2019), which also found high repeatability and heritability of phenology between late and early breeders. Offspring regression is a simple model that does not account for other factors influencing phenotypes, such as non-genetic maternal effects and the environment, which may result in inflated heritability estimates (Charmantier & Gienapp, 2014). Nevertheless, in our study, tropicbirds were recruited to the colony between one to four years after fledging and at various times of year, likely minimizing the influence of environmental covariance. Moreover, this same variability in first recruitment time also makes it unlikely that the similarity in breeding phenology between progenitors and offspring results from a physiological constraint on reproductive timing dictated by an annual cycle and starting upon hatching.

CONCLUSIONS

In conclusion, our results indicate that tropical seabirds with year-round reproduction, despite having access to enough resources to breed at any time of the year, show high levels of individual repeatability in phenology. They exhibit limited flexibility in response to reproductive success, with birds buffering the carry-over effects of the previous breeding attempt during the non-breeding period in a way that ensures the arrival date to the breeding grounds is not affected. In failure to make these adjustments their phenology, late breeders suffered from lower subsequent breeding success. Understanding phenological constraints and how these relate to individuals' fitness is crucial for predicting how species will respond to changes in environmental conditions (Yamamoto et al., 2014). Since phenological flexibility has the potential to govern population dynamics and may be masked by re-nesting attempts in Red-billed Tropicbirds, further long-term research is needed to establish the degree to which shifts in phenology accumulate over time. Moreover, future studies on how these shifts relate to mate and nest site fidelity and subsequent breeding success may also shed light on the evolutionary drivers of phenological consistency (Bogdanova et al., 2011; Dubois & Cézilly, 2002; González-Solís et al., 1999).

The low individual phenological flexibility of tropicbirds and the apparent heritability of this trait suggests that tropicbirds are more susceptible to environmental change than previously thought (Franklin, et al., 2022a; Keogan et al., 2018). Since phenology is both repeatable and heritable, tropicbirds may only be able to respond to shifts in environmental conditions caused by global climate change by micro-evolutionary changes. As a long-lived species, these changes may not be fast enough to keep pace with the rapidly changing environment (Charmantier & Gienapp, 2014; Forcada et al., 2008; Gienapp et al., 2014). Moreover, if environmental conditions eventually drive selection for individuals to only breed during certain parts of the year, tropicbirds may eventually suffer from a loss of genetic diversity in the population (Visser & Gienapp, 2019). Due to the isolation and high philopatry of tropicbirds, they may already be genetically vulnerable (Varela et al., 2024). Therefore, future studies should try to measure whether seasonal patterns are consistent and how this is reflected in the genetic diversity of tropicbirds in Cabo Verde.

Our results indicate that tropical species with year-round reproduction may be at more risk than previously thought, as they may have a limited phenological flexibility despite not being constrained by seasonal fluctuations in resource availability. Since this may have a series of implications for ecology, evolution, and conservation, it is pivotal that such individual phenological constraints are explicitly considered and incorporated into management plans accordingly.

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SUPPLEMENTARY MATERIAL

S1. Visualization of phenological date extraction based on GLS light and wet-dry sensors

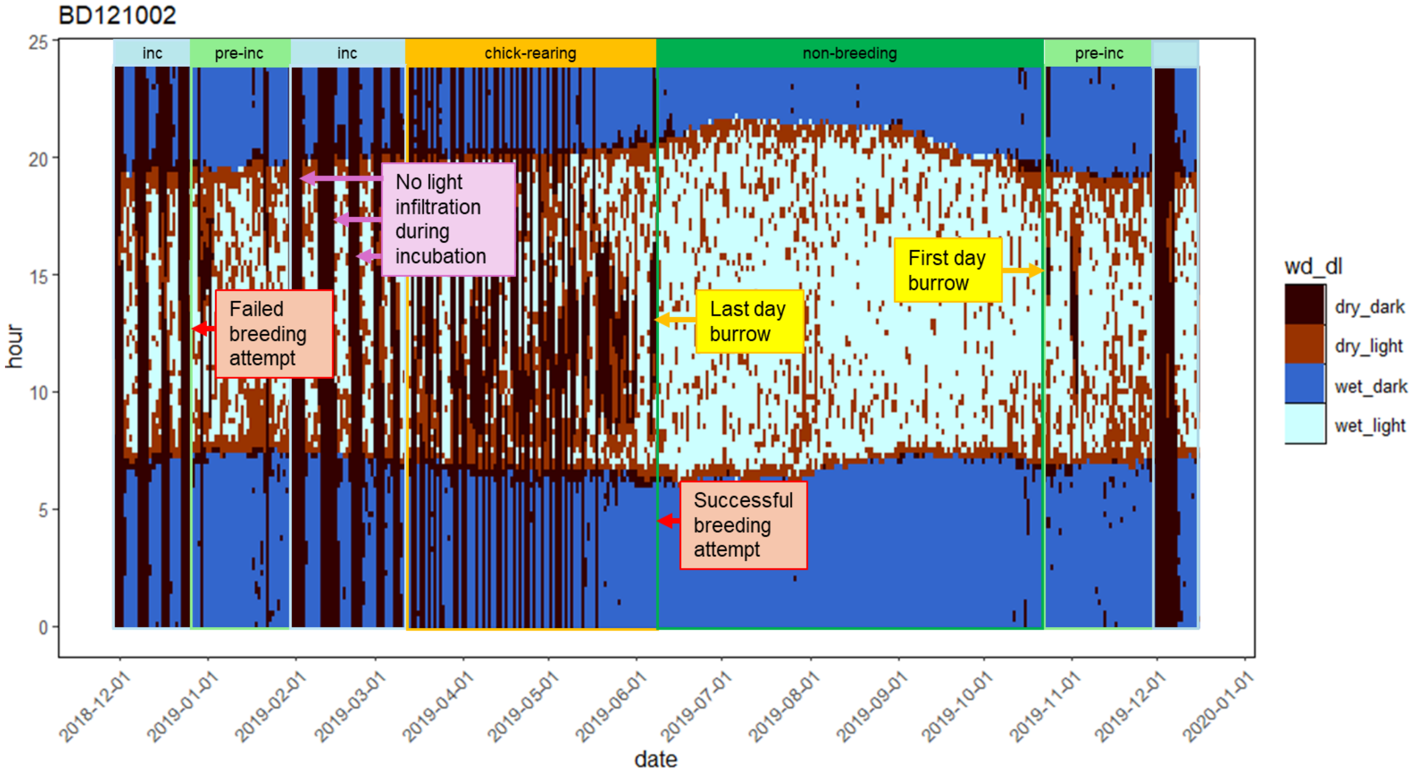

Figure 1. Visualization of phenological date extraction based on GLS light and wet-dry sensors deployed on a Red-billed torpicbird. Colours indicate whether the bird was mainly dry and light (interpreted as flying), dry and dark (interpreted as flying night or in burrow), wet and dark (interpreted as resting on the water at night) or wet and light (interpreted as resting on the water during the day), every 15 minutes throughout the tracking period. In this case, the individual failed to breed at the end of 2018 (whether it failed during incubation or chick-rearing is unclear), then re-nested successfully at the end of January 2019. It then migrated in June 2019, returning to Cabo Verde in October 2019. Once within Cabo Verde waters, it visited a burrow for several hours during the day on two occasions, and finally started incubation in December 2019.

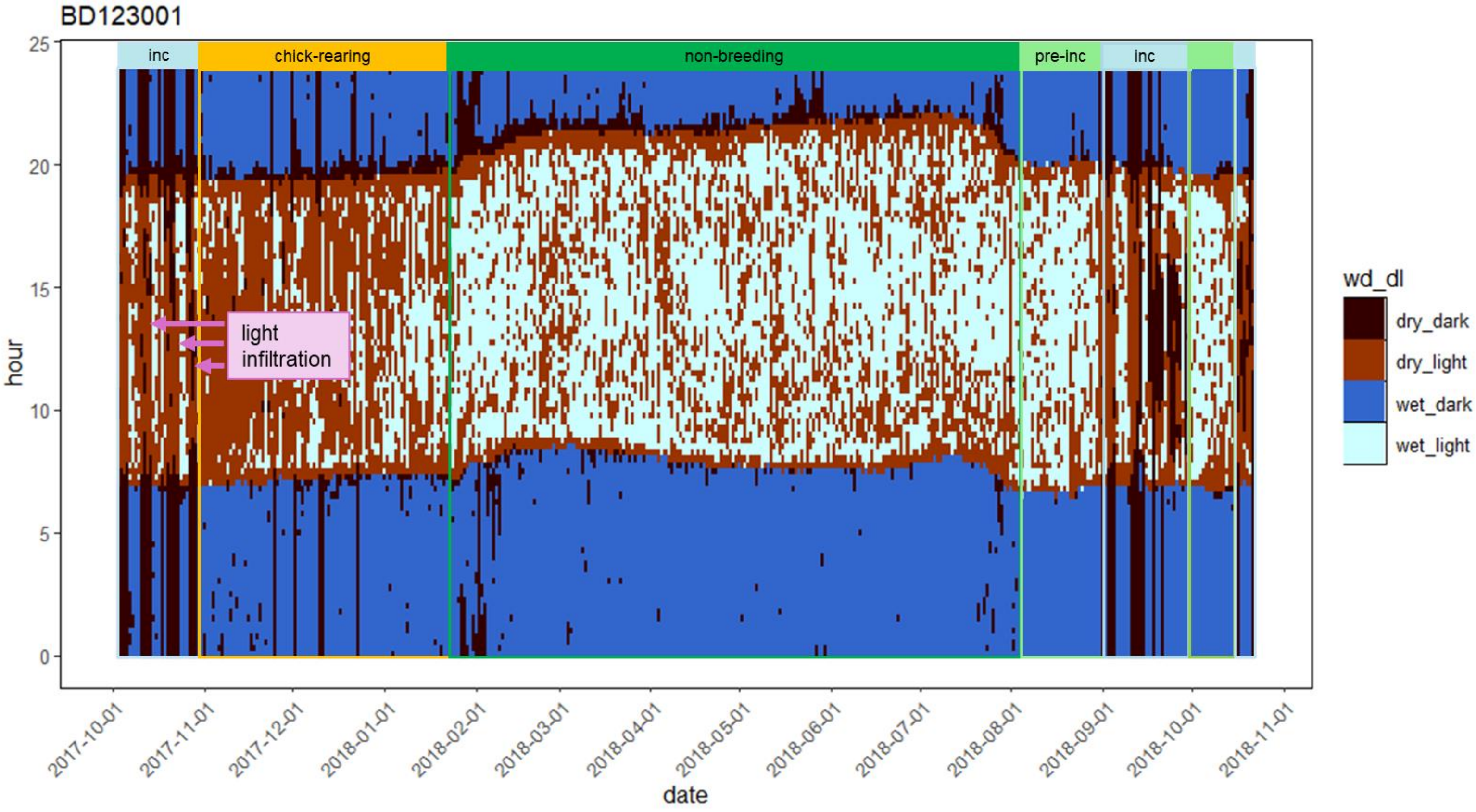

Figure 2. Visualization of phenological date extraction based on GLS light and wet-dry sensors deployed on a Red-billed Tropicbird. Colours indicate whether the bird was mainly dry and light (interpreted as flying), dry and dark (interpreted as flying night or in burrow), wet and dark (interpreted as resting on the water at night) or wet and light (interpreted as resting on the water during the day), every 15 minutes throughout the tracking period. In this case, there was light infiltration into the burrow during the day, and therefore, incubation bouts were measured as periods of >48h of dry only. This individual breed successfully in January 2018, migrated, and returned to Cabo Verde waters in August 2018. In September 2018, the individual started incubation, however this appears to be an unsuccessful attempt, failing in October 2018.

S2. Analysis of whether there are sex-specific differences in phenology

Table.1 Preliminary analysis of whether there are sex-specific differences in the duration of cyclical life history events.

Test	Mean Male	Mean Female	t-value	df	p-value
Breeding by Sex	46.37	44.67	0.38	72.53	0.70
Post-breeding by Sex	18.78	21.94	-0.54	109.82	0.59
Non-breeding by Sex	166.08	167.03	-0.21	126.27	0.83
Breeding interval by Sex	172.92	184.39	-0.69	22.48	0.50

S3. Model selection

Table 1. General(ized) Linear Model (GLM) selection for measuring the effect of breeding success and re-nesting on the duration of cyclical life stages (blue), the breeding interval based on GLS and nest-monitoring data (yellow) and of breeding interval and diff in the day of year of incubation on subsequent breeding success (green). Shown are all models with a cumulative weight > 0.95. The best model is in bold. Link functions for each model are shown in parentheses. df=degrees of freedom, LogLik=Loglikelihood, AIC=Akaike Information Criterion, ΔAIC=delta AIC.

Model	Intercept	df	LogLik	AIC	ΔAIC	weight
Effect of renesting and success on the duration in Cabo Verde waters (Gaussian)						
renest (0./1)	**228.0**	**3**	**-114.86**	235.7	0.00	0.38
renest (0./1) + island	216.0	5	-113.43	236.9	1.14	0.22
renest (0./1) + success (0/1)	228..0	4	-114.85	237.7	1.98	0.14
renest (0./1) + success (0/1) + island	215.5	6	-113.38	238.8	3.03	0.08
renest (0./1) + year	219.3	5	-114.66	240.8	3.60	0.06
renest (0./1) + year +island	213.8	7	-113.41	241.1	5.10	0.02
renest (0./1) + success (0/1) + year	216.7	6	-114.55	241.10	5.38	0.03
Effect of renesting and success on the duration of post-breeding (Gaussian)						
renest (0/1) + island	**75.96**	**6**	**-304.04**	**620.1**	**0.00**	**0.45**
renest (0./1)	67.37	3	-307.86	621.7	1.65	0.20
renest (0/1) + previous success (0/1) + island	76.08	7	-304.03	622.1	1.99	0.17
renest (0./1)+ previous success (0/1)	67.31	4	-307.86	623.7	3.65	0.07
renest (0./1) + year	72.31	6	-306.31	624.6	4.56	0.05
Effect of renesting and success on the duration of the non-breeding period (Gaussian)						
renest (0/1)	**143.0**	3	**-327.78**	**661.6**	**0.00**	**0.27**
renest (0/1) + year	138.8	6	-325.06	662.1	0.56	0.20
renest (0/1) + previous success (0/1)	144.8	4	-327.08	662.2	0.60	0.20
renest (0/1) + previous success (0/1) + year	142.1	7	-324.48	663.0	1.40	0.13
renest (0/1) + year + island	134.1	9	-323.36	664.7	3.16	0.06
null	162.6	2	-330.58	665.2	3.60	0.04
renest (0/1) + previous success (0/1) + year+ island	136.2	10	-323.22	666.4	4.88	0.02
year	163.2	5	-328.43	666.9	5.29	0.02
Effect of renesting and success on the duration of pre-breeding (Gaussian)						
renest (0/1) + island + year	**59.61**	**9**	**-185.06**	**388.1**	**0.00**	**0.19**
renest (0/1) + island	66.03	6	-188.14	388.3	0.18	0.17
renest (0/1) + year	58.25	6	-188.31	388.6	0.50	0.14
renest (0/1)	64.25	3	-191.56	389.1	1.00	0.12
renest (0/1) + previous success (0/1) + year	55.55	7	-187.57	389.1	1.02	0.11
renest (0/1) + previous success (0/1) + island + year	57.98	10	-184.88	389.8	1.65	0.08
renest (0/1) + previous success (0/1) + islandd	65.09	7	-188.03	390.1	1.94	0.07
renest (0/1) + previous success (0/1)	63.02	4	-191.29	390.6	2.47	0.05

Breeding interval based on GLS data (Gaussian)						
renest (0/1) + success between (0/1) + island + year	**331.1**	**9**	**-163.85**	**345.7**	**0.00**	**0.51**
renest (0/1) + success between (0/1) + island	377.3	6	-167.90	347.8	2.11	0.18
renest (0/1) + success between (0/1)	376.6	4	-169.96	347.9	2.23	0.17
renest (0/1) + island	387.4	5	-169.70	349.4	3.70	0.08
renest (0/1) + success between (0/1) + year	349.4	7	-168.04	350.1	4.38	0.06
Breeding interval based on nest monitoring data (Gaussian)						
renest (0/1) + success between (0/1) + island + year	**305.5**	**13**	**-1819.89**	**3665.8**	**0.00**	**0.74**
Effect of breeding interval on subsequent breeding success (0/1) based on monitoring data (binomial)						
island	**0.56**	**4**	**-191.64**	**391.3**	**0.00**	**0.54**
Island + breeding interval	1.58	5	-191.10	392.2	0.93	0.34
Island + year	0.42	9	-188.91	395.8	4.55	0.06
Effect of DOY difference in incubation on subsequent breeding success (0/1) based on monitoring data (binomial)						
Diff DOY + island + year	**-0.56**	**11**	**-302.14**	**626.3**	**0.00**	**0.60**
Island + year	-0.47	10	-304.05	628.1	1.81	0.24
Diff DOY + year	-0.53	8	-307.09	630.2	3.89	0.09

Table 2. General Linear Mixed Model (GLMM) selection for prediting the repetability of breeding phenology. All models included a random effect for individual ID.Shown are all models with a cummulative weight > 0.95. The best model is in bold, Link functions for each model are shown in parentheses. df=degrees of freedom, LogLik=Loglikelihood, AIC=Akaike Information Criterion, ΔAIC=delta AIC.

Model	Int	df	LogLik	AICc	Δ AICc	weight
Repeatability of laying date (Gaussian)						
Breeding success +re-nesting	**0.89**	**5**	**392.99**	**-776**	**0.00**	**0.58**
Breeding success	0.90	4	391.62	-775.2	0.74	0.40
Repeatability of hatching date (Gaussian)						
Breeding success	**0.91**	**4**	**356.14**	**-704.1**	**0.00**	**0.75**
Breeding success +re-nesting	0.92	5	355.82	-701.4	2.72	0.19

Picture by Marcos Hernández-Montero

General Discussion

General Discussion

This thesis aimed to understand the effects of seasonality on marine tropical ecosystems, through the study of the foraging and migratory ecology of Red-billed Tropicbirds, a poorly studied pantropical species that breeds year-round in Cabo Verde. We adopted a multidisciplinary approach, combining multiple years of biologging (with GPS, GLS, wet-dry data, TDR, and accelerometry) and nest monitoring data with diet analyses to assess seasonal differences in habitat use, foraging behavior, activity patterns and diet throughout the annual cycle. In the process, we evaluated and fine-tuned the use of Hidden Markov Models for the classification of behavioral states in opportunistic foragers such as Red-billed Tropicbirds and used spatial modelling to track seasonal changes in habitat use. We also uncovered the underlying mechanisms behind the population-wide variability observed in tropicbird phenology, finding that phenology is not only repeatable at the individual level but also heritable. By uncovering consistent seasonal patterns and relating these pattens to fitness metrics (both immediately and as carry over effects) and environmental conditions, we shed light on the seasonal selective pressures acting on this tropical species throughout its annual cycle. Specifically, across the four chapters of this thesis, we investigated the effects of seasonality on Red-billed Tropicbird foraging and migratory ecology, links between cyclical life-history events and finally, the potential evolutionary consequences of seasonality on this species.

Effect of seasonality on tropicbird foraging ecology

To assess how tropicbirds respond to seasonal changes in oceanographic conditions and resource availability at the breeding grounds, we first evaluated and fine tuning the use of

Hidden Markov Models for inference of behavioral states from GPS-tracks in **Chapter 1**. Then, in **Chapter 2**, we used the developed methodology in the spatial analysis of foraging movements during the breeding season.

In **Chapter 1**, we found that, even a at small proportions, semi-supervising HMMs with auxiliary sensors, such as accelerometer, TDR, and wet-dry sensors can dramatically improve a state-space model's global accuracy in the classification of GPS tracking data into behavioral states. Despite this overall increase in accuracy, the foraging state was poorly identified in our dataset. This suggests that tropicbirds may not use area restricted search while foraging, but rather forage opportunistically throughout their trips, and underlines the difficulties in the classification of this behavior in homogeneous and unpredictable environments. Although some previous studies have reported difficulties in inferring foraging behavior from GPS tracks in other tropical species (e.g. Adams et al., 2020; Diop et al., 2018; Patrick & Weimerskirch, 2014), this is the first study to directly evaluate whether semi-supervision in these models can improve behavioral classification. By doing so, our results provide valuable insight into how to approach the study of foraging behavior in tropical species.

If not addressed, the low sensitivity and precision of foraging in these models can have important implications in conservation and management decisions. Foraging areas are often the target of spatial management plans because of their ecological importance for species, and therefore their correct identification is critical (Allen & Singh, 2016; Lascelles et al., 2016; Wakefield et al., 2009). In our models, we found both low sensitivity and low precision, indicating that many foraging positions were undetected, and that positions classified as foraging should have been assigned to other behavioral states (resting or travelling). As a result, these models may both, underestimate and incorrectly define the total foraging range. To improve the behavioral classification of these models in future studies, it may be necessary to collect movement data at higher resolution or include additional auxiliary sensors to the full dataset. Higher resolution GPS data may give more insights into individual behavior (Roy et al., 2022). Moreover, auxiliary devices have been used in combination with GPS data to identify foraging behaviors in many seabirds and seals, which may otherwise be impossible (e.g. Bentley et al., 2021; Berlincourt et al., 2015; Carneiro et al., 2022; Viviant et al., 2010). If the use of higher resolution GPS-fixes and/or additional auxiliary data is not possible, we suggest taking a more conservative approach and considering all non-resting GPS positions as potential foraging areas.

In **Chapter 2**, we identified how tropicbirds adapt to seasonal changes in environmental conditions and resource availability during the breeding season. Using a large GPS dataset of 907 foraging trips, year-round nest monitoring and a combination of both traditional and stable isotope diet analysis, we found consistent seasonal patterns in nest occupancy, foraging patterns, diet, fitness components and local environmental conditions, which together represent changes in both intrinsic and extrinsic pressures that individuals face throughout the year.

We found that the annual cycle in Cabo Verde can be divided into a dry season (December to June) marked by cooler water temperatures, low rainfall, high windspeeds, and wave heights, and a wet season (July to November) with increased rainfall, warmer water temperatures and visibility. Breeding primarily occurs during the dry season, one to five months after a peak in primary productivity, which is similar to patterns in nest occupancy at other breeding colonies in Senegal (Diop et al., 2018) and Mexico (Hernández-Vázquez et al., 2018).

Foraging behavior, diet, body condition, and breeding success vary seasonally, with tropicbirds foraging over larger areas and consuming more squid during the dry season, leading to higher breeding success. In contrast, the wet season sees fewer breeders, with more sinuous foraging trips closer to colonies, and more consumption of planktivorous fish. Despite slightly better adult body condition during the wet season, chick condition is notably higher during the dry season. While the dry season appears preferable for breeding, advantages of the wet season, such as reduced competition, may partially offset these disadvantages for some individuals. In fact, the slightly better adult body condition during the wet season, may indicate a trade-off between adult survival and reproduction during this period. However, further long-term mark-recapture studies would be needed to evaluate the effect of seasonality on adult survival. These seasonal variations in behavior, diet, and breeding success result from seasonal changes in prey availability, nest site suitability, weather conditions, and competition, highlighting tropicbirds' ability to adapt to environmental fluctuations (Hernández-Vázquez et al., 2018).

Our findings in **Chapter 2** provide novel insights, not only in the foraging ecology of tropicbirds, but resource fluctuations in this tropical system in general. We suggest that the peak in consumption of squid during the end of the dry season, mirrored by increased foraging activity during twilight and the repeated use of more distant foraging areas, stems from the seasonal abundance of squid species, such as the European Flying Squid *Todarodes sagittatus*, known to spawn in April in the Canary Current and to be a significant prey for seabirds in Cabo Verde (Almeida et al., 2021; Piatkowski et al., 1998). If this is the case, then we may expect seasonal fluctuations in the diets of other local seabird species, such as Brown Boobies and Cape Verde Shearwaters, although this has yet to be measured. Alternatively, the shift to cephalopod consumption might be prompted by local depletion of planktivorous fish near colonies due to natural prey cycles or competition (Ashmole, 1971; Thiaw et al., 2017). Although competition-induced resource depletion is generally reserved for much larger seabird colonies, tropicbirds, as solitary foragers specialized on finding prey in nutrient poor and unpredictable environments, may be highly sensitive to both intra and inter specific competition (Ashmole, 1971; Spear & Ainley, 2005; Stonehouse, 1962; Thiaw et al., 2017).

The patterns in tropicbird breeding reproductive success, chick body condition, and foraging behavior described in **Chapter 2** also suggest weather-induced seasonal changes in nest site suitability. Increased temperatures and precipitation during the wet season, may increase thermoregulation and foraging costs in Cabo Verde, potentially leading to lower reproductive success (Danielson-Owczynsky, 2022; Streker et al., 2021). Moreover, extreme rainfall events could directly impact nest survival. Rain-induced nest failures have been recorded at other tropicbird breeding colonies (Danielson-Owczynsky, 2022), and in other seabirds, such as Cape Verde Storm Petrels (*Hydrobates jabejabe*) breeding on Cima Islet in Cabo Verde (Medrano et al., 2022). Together, these patterns in fitness metrics suggest seasonal resource fluctuations in Cabo Verde waters and may impact other seabirdts and marine life which inhabit the region.

In **Chapter 2**, we underline the importance of understanding seasonal variation in foraging behavior of tropical seabirds, highlighting the impact of small shifts in environmental conditions and nest occupancy on tropicbird fitness. Tropicbirds exhibited flexibility in foraging behavior, but environmental shifts translate into differences in fitness metrics, indicating season-specific in selective pressures. Our results also shed light on how this species may be expected to modify its behavior in relation to climate change (Campioni et al., 2023; Orgeret et al., 2022).

Effects of seasonality on tropicbird migratory ecology

In **Chapter 3,** we investigated how seasonality affects the non-breeding distribution and migratory ecology of tropicbirds. For this, we tracked 149 non-breeding periods from 111 individuals using GLS loggers and identified individual and seasonal patterns in tropicbird migration, non-breeding areas and daily activity. We related these seasonal shifts in non-breeding areas to differences in environmental conditions to identify whether shifts are driven by season-specific environmental niche tracking between the breeding and non-breeding period or population-wide tracking of preferred conditions.

We identified seasonal patterns in the non-breeding areas used, with dry season breeders favoring the central Atlantic to the north of Cabo Verde, while wet season breeders occupied a more westerly area in relation to Cabo Verde. These patterns were independent of sex, island, year, breeding success and bird size. Additionally, tropicbirds spend a higher proportion of time active during twilight in the dry season, than in the wet season during both migration and non-breeding, suggesting potential seasonal differences in foraging behavior or that individuals compensate for the shorter day length in the dry season by foraging more during twilight. The distance to non-breeding areas did not differ between seasons but was on average 1693±567 km over the entire year. We propose that these shifts in non-breeding areas allow tropicbirds to mitigate seasonal extremes in sea surface temperature and air density, indicating population-level habitat preferences throughout the year. By modifying their non-breeding areas seasonally, tropicbirds appear to remain within a preferred range of

SST (from ~ 21-28 °Celsius) and air density (~1.16- 1.20 kg/m3) during both the breeding and non-breeding period. Both, sea surface temperature (SST) and air density are known to influence the thermal and foraging costs of seabirds (e.g., Orgeret et al., 2022; Shepard et al., 2023). However, these factors are strongly negatively correlated, complicating the analysis of their individual effects. As such, we focused on the effects of SST for discussion. Our finding that SST may be driving the shifts is consistent with previous studies which highlight the importance of this variable in the ecology and movement patterns in other marine vertebrates (e.g. Favilla& Costa 2020; McMahon & Hays, 2006). In a changing environment, the ability of tropicbirds to shift their non-breeding areas to track ideal conditions may enhance their adaptability. However, as central place foragers during the breeding season, a strict SST thermal range may eventually limit the breeding season in Cabo Verde (Orgeret et al., 2022). Although the SST surrounding other breeding colonies where tropicbirds breed year-round generally falls within the range of our study (Diop et al., 2018; Madden et al., 2022), in Mexico, breeding stops during summer months, when SST reaches over 30°C (Hernández-Vázquez et al., 2018).

Links between cyclical life-history events

In both **Chapter 3** and **Chapter 4** we investigated carry over effects between breeding success and tropicbird migratory ecology, and vice versa.

In **Chapter 3**, we focused on how previous breeding success affects the non-breeding distribution and activity patterns. We found that breeding success could not predict the non-breeding distribution, but it did influence tropicbird activity patterns during the non-breeding period, with successful breeders spending more time active than unsuccessful breeders.

However, this result may stem from the seasonal differences in breeding success, with higher failure during the wet season.

In **Chapter 4**, we found that previous breeding success affected tropicbird migratory phenology, but that these changes only influenced subsequent breeding success when they resulted in a delay in incubation. Consistent with earlier research (Madden, 2019; Stonehouse, 1962), individuals failing to fledge a chick in their initial breeding attempt sometimes initiated re-nesting efforts. These endeavors prolonged their stay within Cabo Verde waters, subsequently leading to a compensatory reduction in their non-breeding period. This is consistent with previous seabird studies which found that individuals adjust the duration of their non-breeding periods to compensate for breeding failure (Bogdanova et al., 2011; Phillips et al., 2005). Despite this shortened non-breeding period, previous breeding success affected the breeding interval. Birds that failed to breed had shorter breeding intervals, unless they attempt re-nesting, in which case they return to the colony later than individuals which breed successfully the first time. This finding aligns with research on seabirds, which shows that failed breeders and non-breeders depart colonies earlier than successful breeders (Yamamoto et al., 2014). Furthermore, we found that when incubation was delayed relative to the timing of incubation in the previous year, individuals had lower breeding success, suggesting that individuals who failed to adjust their phenology suffered fitness consequences. Thus, our study highlights how breeding failure and re-nesting can influence subsequent migratory phenology, although these effects ony impact subsequent breeding success if they result in a delay in incubation.

Together the results of **Chapter 3** and **Chapter 4** suggest that carry-over effects related to previous breeding success affect phenology, but no non-breeding distribution, as reported for other seabird species (Catry et al., 2013; Fayet et al., 2016; Schultner et al., 2014; Shoji et al., 2015).

Spatial consistency of breeding and non-breeding movements and repeatability and heritability of phenology

Chapter 2 and **Chapter 3**, we investigated the spatial consistency of the movement of tropicbirds both during both the breeding and non-breeding period, and, in **Chapter 4,** we investigated the repeatability and heritability of phenology.

In **Chapter 2**, we found higher overlap in subsequent trips from the same individuals than different individuals, suggesting some individual consistency in the areas used, despite population-wide variability in foraging distribution. Although this pattern was greater within a given season than among seasons, it also persisted between seasons and was highest during the dry season. This suggests that, although resources are generally patchily distributed in the waters surrounding Cabo Verde, familiarity may increase tropicbird foraging success, especially during the dry season when individuals travel further to forage on squid (Carroll et al., 2018; Pettex et al., 2010).

In **Chapter 3**, we revealed that Red-billed Tropicbirds exhibit consistency in their choice of non-breeding areas over consecutive years, and individuals migrating at similar times tend to utilize similar regions. This observation parallels findings in a recent study on asynchronously breeding tropical Gadfly petrels, indicating individual repeatability in non-breeding area selection (Franklin et al., 2022a). This suggests that in tropical environments characterized by patchy and unpredictable resources, familiarity with non-breeding areas may confer important fitness benefits (Carroll et al., 2018; Weimerskirch, 2007).

In **Chapter 4**, we investigated the individual repeatability and heritability of phenology using a combination of GLS tracking and nest monitoring. We found that individuals maintained remarkably consistent year-round phenology across subsequent years and that phenology appears to be heritable, with recruits returning to breed around the same time as when they fledged.

This high individual repeatability in phenology aligns with findings in other tropical seabirds, such as gadfly petrels and Cape Verde Storm Petrels, indicating more consistent individual differences in phenology in tropical systems than previously thought (Franklin et al., 2022a; Medrano et al., 2022). With the absence of large seasonal fluctuations in environmental conditions, we suggest that repeatability is selected as is favours synchronous mate arrival, which is particularly crucial in migratory species like tropicbirds, in which mates do not spend the non-breeding season together and face a high nest-site competition at their arrival to the breeding grounds (Fayet et al., 2017; Gunnarsson & Tómasson, 2011). Future research on the impact of phenological variability, divorce rates and subsequent breeding success would be needed to verify this claim. Moreover, since this high repeatability in phenology is also matched with individual spatial consistency in their movements, both during the breeding and non-breeding periods. We suggest that it may also be favoured by familiarity with the environment during this period of the year (Carroll et al., 2018; Pettex et al., 2010). Further investigation is needed to understand whether the differences in diet, activity patterns and areas used by breeding individuals indicate individual specialization (Medrano et al., 2022) did not find niche specialization in Cape Vede Storm Petrels that breed at different times of year.

Moreover, our study revealed high heritability of tropicbird phenology, with recruits returning to the colony around the same time of year as when they fledged. This finding is similar to results on other seabird species, indicating a genetic component to phenological patterns (Pérez, 2019), and are in line with the high repetabilities we found. However, the potential overestimation of trait heritability through offspring regression should be considered (Charmantier & Gienapp, 2014). Despite this, the variability in recruitment age and high philopatry among tropicbirds, highlight the complex interplay of genetic and environmental factors shaping phenological traits (Antaky et al., 2020; Varela et al., 2024; Zhang et al., 2015). Therefore, further long term ecological and genetic studies may be needed to understand the heritability of phenology and the gene flow between seasonal populations.

The high individual repeatability and heritability of phenology suggest that tropicbirds are more susceptible to environmental change than previously thought (Franklin, et al., 2022a; Keogan et al., 2018). Climate change and habitat loss pose significant threats to seabird populations, and understanding the genetic basis of phenological traits can help predict their responses to environmental shifts (Visser & Gienapp, 2019). Typically, species can adapt to climate change through individual plasticity by shifting the timing of breeding or through a micro-evolutionary response. However, since climate change is occurring rapidly, within just a few generations of tropicbirds, natural selection may not have sufficient time to act. The lack of plasticity in individual phenologies may prevent these birds from rapidly adapting to new circumstances by adjusting their breeding timing. Additionally, the observed repeatability of phenology may be mediated by ecological interactions such as competition and mate fidelity, and potentially uncoupled from the annual cycle, as seen in other tropical seabirds (Reynolds et al., 2014; Stonehouse, 1962).

Conservation implications

The findings of this thesis not only significantly advance our understanding of Red-billed Tropicbird foraging and migratory ecology but can also contribute to the understanding and conservation of tropical marine systems as a whole. The spatial data provided, which offers insights into seabird ecology from both behavioral and spatial perspectives, may be used to help inform management strategies for this species throughout its annual life cycle. Moreover, as marine top predators, tropicbirds can be used as sentinels for monitoring marine ecosystems (Hazen et al., 2019).

By studying the effects of seasonality during both the breeding and non-breeding periods, this thesis sheds light on the selective pressures acting on tropicbirds throughout their annual life cycle. Understanding the drivers of spatial, behavioral and phenological variability is crucial, especially in the context of climate change. Phenological shifts in polar and temperate environments have been well-documented, driven by individual responses to changing conditions and/or changes in population structure (Gordo, 2007; Gunnarsson & Tómasson, 2011; Orgeret et al., 2022; Sydeman et al., 2015). However, information in tropical oceans is far less complete (Sydeman et al., 2012). Although it has been hypothesized that the behavioral and phenological population-wide variability of tropical seabirds may buffer shifts in environmental conditions, recent studies on tropical species, including this thesis have found significant individual consistency in spatial habitat use and phenology (Franklin et al., 2022a, b). Furthermore, we showed that at least part of this consistency, breeding phenology, is actually heritable. The low individual flexibility of tropicbirds and the apparent heritability of this trait (Chapter 4) suggests that tropicbirds are more susceptible to environmental change than previously thought. Although tropicbirds breed year-round, there are seasonal differences in tropicbird behavior in both the breeding (Chapter 2) and non-breeding season (Chapter 3), which, in turn, result in seasonal differences in breeding success and fitness metrics (Chapter 2). Since individual tropicbird phenology is repeatable, individuals which breed during the wet season (which had the lowest breeding success), may continue to do so, potentially resulting in negative selection if no significant year to year variability in conditions occurs. Moreover, since phenology is heritable, this selection should lead to an evolutionary response (Visser & Gienapp, 2019).

Moreover, our study also provides valuable insights into how individual behavior changes with seasonality. Since changes in animal behavior, and spatial ecology have emerged as valuable indicators of ecosystem changes, often surpassing traditional metrics like abundance or distribution (Berger-Tal et al., 2016), they may be early indicators of the effects of climate change on species survival. Behavior fluctuations can serve as early warnings, offering insights into environmental shifts, especially when there's a robust understanding of the model species. Through continuous monitoring facilitated by tracking devices and advanced analytic algorithms, behavior assessment becomes both feasible and cost-effective (Berger-Tal & Saltz, 2016). Leveraging biologging or remote telemetry to track seabirds, along with behavioral inference, amplifies their role as effective ocean sentinels. The large diversity in spatial habitat use and phenology may make tropical species more adaptable to varying environmental conditions. The findings reveal diverse spatial habitat use and this diversity likely helps them adapt to varying environmental conditions to find food effectively (Soanes et al., 2021; Weimerskirch et al., 2005; Zango et al., 2020). However, at the same time, this diversity makes traditional methods of spatial conservation management inefficient for the protection of tropical species at sea.

Despite being Least Concern, populations in Cabo Verde are declining, raising concerns about genetic risks due to isolation and limited dispersal as in other tropicbird colonies (Varela et al., 2024). The Cabo Verde population is relatively isolated compared to other Atlantic populations. In fact, after seven years of intensive monitoring and ringing over 3,500 tropicbirds in Cabo Verde, along with some parallel efforts in the nearest colony in Senegal, no rings from other populations were ever found. Understanding these dynamics is crucial for predicting species responses to climate change and informing conservation efforts (Orgeret et al., 2022). Due to their movements across national boundaries during breeding, wintering, and migration, international cooperation is crucial for the conservation of pelagic seabird species (Jodice & Suryan, 2010; Louzao et al., 2012). The transboundary nature of these birds poses significant challenges for conservation, emphasizing the need for ecosystem-based management (Jodice & Suryan, 2010).

While our dataset's timeframe wasn't sufficient to explore climate change-induced shifts in tropicbird foraging behavior, phenology, and fitness (Orgeret et al., 2022), understanding how this species adapts to seasonal variations in bottom-up and top-down pressures offers insights into its potential response to climate change. Despite significant plasticity in their foraging behavior and diet, changes in environmental conditions and prey availability across seasons influenced tropicbird body condition and breeding success. This suggests that environmental and ecological changes resulting from climate change may have notable effects on their populations.

Our results provide some of the first in-depth knowledge on seasonal variation in foraging behavior of a tropical seabird species, suggesting seasonality in tropical systems may be a stronger driver of the movements of top predators than previously thought. We found that even small changes in environmental conditions and resource availability can have important repercussions on tropicbird foraging ecology, and although this species displayed some plasticity in foraging behavior, these effects translated into differences in fitness metrics throughout the year. This flexibility may give us insight into the adaptability to climate change and the importance of understanding the seasonal variability in behavior.

Picture by Sarah Saldanha

General Conclusions

General Conclusions

About the response of tropicbirds to seasonal changes in oceanographic conditions and resource availability during the breeding season

- In this thesis, we identified seasonal patterns in tropicbird foraging ecology, leading to variations in nest occupancy, space use, diet, activity patterns, and fitness metrics throughout the year. We conclude that these seasonal patterns are driven by changes in resource availability, particularly fluctuations in squid abundance, and nest site suitability, which decreases due to rainfall and high temperatures during the wet season, impacting the breeding success.

About how seasonal changes in oceanographic conditions affect the distribution and migratory ecology of tropicbirds during the non-breeding season.

- We identified seasonal patterns in the non-breeding distribution, activity patterns and migratory ecology of tropicbirds and suggest that these changes are driven by population wide habitat requirements of SST and air density during the non-breeding season.

About the links between cyclical life-history events, and whether there are carry over effects on phenology, spatial ecology and breeding success.

- We identified links between breeding success and subsequent migratory phenology, with individuals that re-nested shortening their non-breeding period in order to maintain a similar breeding phenology. If incubation was delayed despite these adjustments, tropicbirds suffered from lower breeding success. We did not find any evidence of carry over effects between migratory ecology and subsequent breeding success.

About the underlying mechanism driving spatial and phenological variability, and whether phenology is heritable.

- We identified that despite population-wide variability in foraging and migratory distribution and phenology, tropicbirds displayed consistency in the areas used and repeatable and heritable phenology, suggesting their plasticity in these traits is more limited than previously thought.

Our findings suggest that tropicbirds may be more susceptible to environmental change than previously thought. Even small seasonal changes in environmental conditions significantly affected their foraging and migratory ecology, resulting in seasonal patterns in fitness metrics. Combined with the high repeatability and heritability of their phenology, these results lead us to conclude that tropicbirds may lack sufficient individual plasticity to buffer against rapid environmental changes.

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