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RESUMO

Estratégias de forrageio de aves marinhas tropicais no arquipélago dos Abrolhos: As aves marinhas são *central-place foragers* durante a época de reprodução, o que reforça a competição ao redor da colônia, especialmente em ambientes oligotróficos, como os oceanos tropicais. Em resposta, as aves marinhas desenvolveram estratégias de forrageio, tais como estratégia de alimentação bimodal e/ou uso diferencial de recursos entre os sexos para evitar competição intraespecífica. Nas últimas décadas, as ferramentas de *biologging* proporcionaram importantes avanços na ecologia do movimento das aves marinhas. Por exemplo, a partir de conjuntos de dados obtidos com os receptores do Sistema Global de Navegação por Satélite (GNSS) é possível obter informações detalhadas e precisas sobre as viagens de alimentação das aves marinhas e segmentar as trajetórias para identificar comportamentos no tempo e no espaço usando ferramentas estatísticas, como os Modelos de Cadeias Ocultas de Markov (HMM). Os sistemas de posicionamento combinados com sensores de pressão fornecem informações sobre distribuição tridimensional, o que é particularmente útil para o estudo de estratégias de forrageio de aves marinhas mergulhadoras. Além disso, o uso de isótopos estáveis em carbono e nitrogênio fornece informações sobre a dieta das aves marinhas, estimando, por exemplo, um nicho isotópico bidimensional como um substituto do nicho trófico. Portanto, este estudo teve como objetivo caracterizar as estratégias de forrageio da ave marinha tropical rabo-de-palha-de-bico-vermelho *Phaethon aethereus* Linnaeus, 1758 (Aves: Phaethontiformes: Phaethontidae) em um espaço tridimensional e avaliar as diferenças no uso do espaço e dos recursos alimentares entre viagens curtas e longas, assim como as diferenças entre os sexos. Este estudo foi estruturado em dois capítulos: o primeiro apresenta uma avaliação do desempenho do HMM usando dispositivos GNSS e sensores de pressão para identificar áreas de forrageio quando são usadas baixas frequências de amostragem (ou seja, 1 localização a cada 15 min); e o segundo capítulo focalizou a aplicação de tais descobertas combinadas a isótopos estáveis para avaliar diferenças intersexuais em estratégias de forrageio dos rabo-de-palha-de-bico-vermelhos. A partir disto, demonstramos que o uso dos HMM a partir de dados somente de GPS é uma abordagem adequada para inferir áreas de forrageio a nível populacional, mesmo quando são usadas baixas frequências de amostragem. Além disso, este estudo evidenciou que os rabo-de-palha-de-bico-vermelhos realizam viagens bimodais de forrageio com duração de três dias e duas horas, mas não apresentam segregação sexual em relação ao uso do espaço e dieta durante a época de reprodução. Portanto, o presente estudo forneceu informações sobre a aplicabilidade de modelos de espaço-estado para segmentação de trajetórias em espécies de aves marinhas de baixa massa corporal que realizam longas viagens de forrageio e, portanto, precisam ser equipadas com equipamentos leves, com baixas frequências de amostragem. Finalmente, os resultados mostraram uma estratégia bimodal de forrageio e uma sobreposição intersexual quase completa de áreas de forrageio e aspectos dietéticos dos rabo-de-palha-de-bico-vermelho ao redor do arquipélago dos Abrolhos, onde está localizada a maior colônia das espécies no sudoeste do Oceano Atlântico.

Palavras-chave: Estimativas de densidade de Kernel com Autocorrelação; *biologging*; Modelos de Cadeias ocultas de Markov; rabo-de-palha-de-bico-vermelhos; isótopos estáveis.

ABSTRACT

Foraging strategies of tropical seabirds in the Abrolhos archipelago: Seabirds are central-place foragers during the breeding season which reinforces competition around the colony, especially in oligotrophic environments such as the tropical oceans. In response, seabirds developed foraging strategies, such as bimodal foraging strategy and/or differential resource use between sexes to avoid intraspecific competition. In recent decades, biologging tools have provided important advances in the movement ecology of seabirds. For example, from datasets obtained with Global Navigation Satellite System (GNSS) receivers it is possible to obtain detailed and accurate information about seabird foraging trips and to segment trajectories to identify behaviors in time and space using statistical tools, such as Hidden Markov Models (HMM). Positioning systems combined to pressure sensors provide information on three-dimensional distribution, which is particularly useful for studying foraging strategies of diving seabirds. In addition, the use of carbon and nitrogen stable isotopes provides information on the diet of seabirds by estimating, for instance, a bi-dimensional isotopic niche as a proxy of the trophic niche. Therefore, this study aimed to characterize the foraging strategies of the strictly marine red-billed tropicbird *Phaethon aethereus* Linnaeus, 1758 (Aves: Phaethontiformes: Phaethontidae) in a three-dimensional space and to assess differences in space and food resource use between short and long trips as well as differences between sexes. This study was structured in two chapters: the first presents an evaluation of the HMM performance using GNSS-only devices and pressure sensors to identify foraging areas when low sampling frequency (*i.e.* 1 fix each 15 min) are used; and the second chapter focused on applying such findings combined to stable isotopes to assess intersexual differences in foraging strategies of red-billed tropicbirds. From this, we demonstrated that HMM from GPS-only data is a suitable approach for inferring foraging areas at the population level even when low sampling frequencies are used. In addition, this study evidenced that red-billed tropicbirds perform bimodal foraging trips lasting three days and two hours, but do not present sexual segregation regarding space use and diet during the breeding season. Therefore, the present study provided information on the applicability of state space models for segmentation of trajectories in seabird species of low body mass which perform long foraging trips and thus need to be equipped with lightweight loggers set with low sampling frequencies. Finally, the findings indicate a bimodal foraging strategy and an almost complete intersexual overlapping of foraging areas and dietary aspects of red-billed tropicbirds around the Abrolhos archipelago, where the biggest colony of the species in the southwestern Atlantic Ocean is located.

Keywords: Autocorrelation Kernel density; biologging; Hidden Markov Models; red-billed tropicbird; stable isotopes

CONTENTS

INTRODUÇÃO GERAL

Em ambientes marinhos tropicais oligotróficos, a obtenção de recursos alimentares é um desafio para grandes predadores, dada a distribuição difusa das presas (Ballance et al. 1997; Weimerskirch 2007). Em resposta, predadores de topo, como as aves marinhas, desenvolveram estratégias de forrageio que lhes permite otimizar o ganho de energia (Charnov 1976; MacArthur e Pianka 1966). Isso é particularmente importante durante a época de reprodução, quando as aves marinhas devem encontrar um equilíbrio entre o fornecimento de alimento suficiente para o filhote e a manutenção de sua própria condição corporal (Orians e Pearson 1979). Durante este período, ambos os pais precisam usar estratégias para evitar competição e garantir sua própria sobrevivência e o sucesso do ninho.

As aves marinhas são *central-place foragers* durante a época de reprodução, período em que a competição por recursos já escassos e efêmeros aumenta ao redor da colônia (Orians e Pearson 1979; Boyd et al. 2014). Nesse contexto, a flexibilidade nas estratégias de forrageio funciona como um mecanismo adaptativo à variabilidade espaço-temporal na disponibilidade do alimento (Shaffer et al. 2003; Pettex et al. 2012), o que pode ser observado, por exemplo, a partir de variações na dieta (Navarro et al. 2009) ou de áreas de alimentação (Paiva et al. 2018). Tais variações podem ser observadas em temporalmente (Paiva et al. 2017), mas também entre sexos (Miller et al. 2018), classes etárias (Pettex et al. 2019), ou individualmente (Harris et al. 2020).

O uso diferencial de recursos entre sexos tem sido amplamente evidenciado em aves marinhas e tem sido atribuído, principalmente, à competição intersexual (Paiva et al. 2018; Clay et al. 2020; Miller et al. 2018). Isso pode ser intensificado quando as aves marinhas forrageiam em áreas pobres em nutrientes e/ou são obrigadas a usar áreas próximas à colônia, resultando na exclusão competitiva intraespecífica entre sexos (Ruckstuhl e Neuhaus 2005). Da mesma forma, a divisão intersexual dos recursos pode ser impulsionada pelo dimorfismo sexual de tamanho, de modo que o sexo maior é geralmente dominante e ganha mais acesso aos recursos quando esses são limitados (Phillips et al. 2004). Isso leva indivíduos do sexo não dominante a, por exemplo, explorar áreas de alimentação mais distantes (Rey et al. 2012; Granroth-Wilding e Phillips 2018) ou manter a sobreposição espacial e explorar diferentes recursos alimentares (González-Solís et al. 2005).

No nível do indivíduo, a estratégia bimodal de forrageio, na qual os pais alternam viagens longas e curtas, pode ser realizada durante o período de cuidado parental para garantir a alimentação do filhote e a alimentação própria, o que é particularmente importante em espécies que realizam viagens longas de alguns dias de duração (Chaurand e Weimerskirch 1994; Congdon et al. 2005). Em geral, as viagens longas são feitas pelo adulto que não é responsável por cuidar do ninho para encontrar áreas mais produtivas afastadas da colônia, visando a sua própria manutenção. Alternativamente, viagens curtas são feitas pelo adulto que está cuidando do ninho para áreas mais próximas da colônia para alimentar os filhotes (Granadeiro 1998). Tal dinâmica no atendimento ao ninho tem sido observada em várias espécies de aves marinhas, tais como Procellariiformes (Congdon et al. 2005; Shoji et al. 2015) e Phaethontiformes (Sommerfeld e Hennicke 2010; Campos et al. 2018).

O conhecimento sobre o uso do espaço por aves marinhas avançou exponencialmente nas últimas décadas devido ao uso de ferramentas de *biologging* (Joo et al. 2022). A utilização de equipamentos fixados no corpo do animal permite a observação remota de deslocamentos, além de possibilitar a extração de informações comportamentais, fisiológicas e ambientais (Börger et al. 2020). Por exemplo, os receptores de sistemas globais de navegação por satélite (e.g. GPS) permitem estimar posições bidimensionais com acurácia de poucos metros (Tomkiewicz et al. 2010). Quando associados a sensores de pressão, viabilizam compreender o uso do espaço verticalmente, o que é particularmente importante para espécies que capturam suas presas através do mergulho.

O avanço na utilização das ferramentas de *biologging* demandou o desenvolvimento ou adaptação de técnicas estatísticas para extrair informações dos dados gerados. Nesse contexto, os Modelos de cadeias ocultas de Markov (HMM) têm permitido identificar os diferentes comportamentos realizados por uma ave durante a viagem de alimentação. Os HMMs assumem que as sequências de observações são geradas mediante uma sequência não observada de estados, e que cada estado depende do anterior (Rabiner 1989). Na prática, o movimento animal pode ser modelado através da identificação de estados identificados (*i.e. proxies* comportamentais) a partir de variáveis observadas, como *step-length* (distância entre dois pontos) e o *turning-angle* (mudança de ângulo entre dois *steps*) (e.g. Patterson et al. 2009). Adicionalmente, covariáveis medidas por outros sensores podem contribuir para a identificação de estados, gerando uma segmentação refinada mesmo em trajetórias com baixa frequência de amostragem (Michelot et al. 2016).

A partir da localização espacial dos estados de forrageio, é possível estimar o tamanho das áreas potenciais de alimentação e avaliar aspectos como, por exemplo, a segregação sexual no uso do espaço

(Miller et al. 2018). O método mais comumente utilizado para isso são as estimativas de densidade de Kernel (KDE), as quais são estimadores não paramétricos de funções de densidade de probabilidade. Os KDEs são aplicados sob o pressuposto de que os dados são distribuídos independentemente (Silverman 1986), mas os dados de rastreamento obtidos de dispositivos GPS apresentam uma autocorrelação espacial inerente, de modo que as áreas obtidas a partir dos KDEs podem ser subestimadas (Fleming et al. 2015). Para lidar com essa limitação, Fleming et al. (2015) propuseram uma metodologia derivada dos KDEs que considera explicitamente a autocorrelação (AKDE). Tal método é baseado principalmente na incorporação de efeitos de movimento por meio de uma função de autocorrelação derivada de um modelo de movimento ajustado. Assim, o uso de AKDEs poderia fornecer informações mais precisas sobre a localização e o tamanho das áreas de forrageio de aves marinhas.

A combinação de informações do movimento com técnicas de estudo da dieta permite uma compreensão mais refinada sobre a segregação de nicho entre sexos em aves marinhas. Nesse contexto, a análise de isótopos estáveis pode contribuir diretamente para o estudo do uso diferencial do espaço e dos recursos alimentares por machos e fêmeas (Kelly, 2000). Por exemplo, a análise de IE de carbono fornece informação sobre as áreas de alimentação dos predadores (e.g. nerítico *vs*. oceânico), enquanto os IE de nitrogênio fornecem informação sobre o nível trófico consumido (Boecklen et al, 2011). A partir dos dados de IE de carbono e nitrogênio, ainda é possível estimar o nicho isotópico (utilizado como *proxy* de nicho trófico) de cada grupo de indivíduos como um espaço bidimensional, o que proporciona testar diferenças de amplitude e sobreposição intersexual de nichos (Jackson et al. 2011). Embora o uso de ferramentas de *biologging* e isótopos estáveis tenha aumentado o conhecimento sobre a ecologia do forrageio de muitas espécies de aves marinhas, as informações sobre espécies de aves marinhas tropicais, como o rabo-de-palha-de-bico-vermelho (*Phaethon aethereus*), ainda são escassas.

O rabo-de-palha-de-bico-vermelho *Phaethon aethereus* (Aves: Phaethontiformes: Phaethontidae) é uma ave estritamente marinha de reprodução colonial, que apresenta distribuição pantropical (Orta 1992). Realiza viagens longas e solitárias de forrageio e captura, principalmente, peixes-voadores (Exocoetidae) ou lulas-voadoras (Ommastrephidae), os quais são capturados através do mergulho conhecido por *plunge-diving* (Orta 1992; Le Corre 1997). Para isso, o rabo-de-palha-de-bico-vermelho faz mergulhos superficiais (Le Corre 1997), atingindo cerca de dois metros de profundidade máxima (Castillo-Guerrero et al. 2011). A espécie apresenta dimorfismo sexual de tamanho, de modo que os machos são maiores do que as fêmeas (Nunes et al. 2013). Durante a época de reprodução, fêmeas e machos compartilham o cuidado do ninho e exploram áreas ao redor das colônias para procurar alimento, realizando longas viagens que duram cerca de dois ou três dias (Diop et al. 2018; Nunes et al. 2022). Embora ainda não tenha sido documentado para rabo-de-palha-de-bico-vermelho, rabo-de-palha-de-bico-laranja (*P. lepturus*) e rabo-de-palha-de-cauda-vermelha (*P. rubricauda*) utilizam uma estratégia bimodal de forrageio com pais alternando viagens longas (> dois dias) e curtas (< um dia) (Sommerfeld e Hennicke 2010; Campos et al. 2018).

No Atlântico Sudoeste, sua principal colônia está localizada no arquipélago dos Abrolhos, no litoral sul da Bahia, Brasil, e é composta por cerca de 600 indivíduos (Mancini et al. 2016). Em nível global, a espécie está categorizada como Pouco Preocupante (LC), mas tem apresentado declínio como tendência populacional, devido à introdução de espécies invasoras e expansão urbana em seus sítios de reprodução (Lee e Walsh-McGehe 2000; Sarmento et al. 2014). No Brasil, a espécie está categorizada como Em Perigo (EN) na Lista Nacional de Espécies Ameaçadas de Extinção (Portaria MMA 148/2022) devido à distribuição espacial limitada, pequeno tamanho populacional, e predação por ratos exóticos no arquipélago dos Abrolhos (Sarmento et al. 2014), e por gatos em Fernando de Noronha (Gaiotto et al. 2021). A erradicação de ratos em Abrolhos teve início em 2021 e as perspectivas quanto ao resultado são positivas para incremento no tamanho populacional de *P. aethereus* no arquipélago, mas a contaminação por metais pesados oriundos da barragem de Fundão pode levar a efeitos deletérios em nível populacional em médio e longo prazos (Nunes et al. 2022).

Equipamentos a serem fixados em aves devem respeitar o limite máximo de 3% da massa corporal dos animais (Phillips et al. 2003), o que possui implicações sobre o a vida de bateria dos equipamentos. Considerando que *P. aethereus* possui cerca de 600g, os indivíduos dessa espécie podem ser equipados com rastreadores de, no máximo, 18g, o que leva à necessidade de redução na frequência de amostragem para que o equipamento tenha bateria suficiente para registrar uma viagem de alimentação completa (i.e. 2 a 3 dias). No entanto, uma consequência da redução na frequência de amostragem é a baixa resolução da trajetória, visto que a frequência para registrar uma viagem completa de *P. aethereus* deve ser de 1 posição a cada 15 minutos. Nesse sentido, o objetivo da presente dissertação foi avaliar a performance dos HMMs para segmentar trajetórias obtidas com baixa frequência de amostragem, bem como avaliar as diferenças no uso do espaço e dos recursos alimentares entre os sexos de *P. aethereus*, durante o período reprodutivo no arquipélago dos Abrolhos. Para isso, a dissertação foi subdividida em dois capítulos, de modo que o primeiro buscou avaliar a eficácia dos HMMs em identificar áreas de forrageio a partir de dados de GPS obtidos com baixa frequência de amostragem, enquanto o segundo testou diferenças entre sexos e entre viagens curtas e longas em relação às estratégias de forrageio. Os capítulos estão apresentados ao longo desta dissertação através de anexos em forma de manuscritos preparados para publicação.

SÍNTESE DOS RESULTADOS

- Dados de receptores de GPS obtidos com baixa frequência de amostragem são aplicáveis para identificação de áreas de forrageio através de segmentação por HMMs, desde que interpretados em nível de grupos, como, por exemplo, população, sexos, e classes etárias;

- A alta sobreposição de áreas de forrageio e do nicho isotópico não evidenciou diferenças sexuais no uso do espaço dos recursos alimentares por *P. aethereus*, o que pode estar relacionado com uma alta produtividade ao redor do arquipélago dos Abrolhos devido à sua posição na plataforma continental;

- *P. aethereus* mostrou ser mergulhador superficial, explorando recursos nos dois primeiros metros da coluna d'água. Adicionalmente, as atividades de alimentação ocorrem, exclusivamente, durante o dia, tanto nas viagens curtas como nas longas;

- Viagens longas e curtas de rabo-de-palha-de-bico-vermelho não apresentaram diferenças em relação à profundidade de mergulho, o que sugere que não há diferença nas presas capturadas, embora isto deva ser mais explorado a partir da análise refinada do comportamento e da dieta em escala temporal mais fina;

- Embora a estratégia de forrageio bimodal pareça ter evoluído para favorecer o sucesso reprodutivo das aves marinhas, pode ser uma ameaça para a conservação desta espécie, visto que o filhote é deixado sozinho diariamente por um período aproximado de 2,5h;

- Embora a área de reprodução de rabo-de-palha-de-bico-vermelho esteja localizada dentro do Parque Nacional Marinho dos Abrolhos, os esforços de conservação para esta espécie poderiam ser estendidos para suas áreas de forrageio, além dos limites da área protegida, já que esta é a maior colônia do sudoeste do Oceano Atlântico e a espécie está ameaçada de extinção localmente.

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Suitability of GPS-only data obtained at low sampling frequency for estimating seabird foraging areas

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ABSTRACT

This study assessed the performance of Hidden Markov Models (HMMs) in classifying the foraging behavior of Red-billed tropicbird *Phaethon aethereus* tracked with GPS loggers set to record 1 location every 15 minutes at the trip and population levels. Foraging trips were segmented by HMMs and the location of “foraging” events were compared to location of dives, which were obtained from pressure sensors. Foraging areas were estimated using autocorrelation kernel densities (AKDE) both for the foraging (HMM) and dive datasets, and overlap was calculated to assess global accuracy. Here, we demonstrated that HMM is a suitable approach for inferring foraging areas from GPS-only data of low sampling frequencies at the population level. Despite being cheaper and lighter than multisensor platforms, GPS-only devices can provide accurate information about foraging activities for researchers looking at intra and interpopulation levels. In this context, studies targeting small/light seabird species, or even small-budget projects targeting larger species, can benefit from our findings to use GPS-only data and advance knowledge about avian movement ecology.

KEYWORDS

Biologging, Hidden Markov Models, Movement Ecology, *Phaethon aethereus*.

INTRODUCTION

The study of animal movement and behavior has presented unprecedented advances in the last decades due to the use of biologging tools and statistical techniques (Joo et al. 2022). This allowed the behavior of animals within their natural environment to be described at spatial and temporal scales which are not accessible through direct observation (Kays et al. 2015). For example, global navigation satellite systems (hereafter "GPS") have been used in studies targeting animal movement, with high accuracy and precision, resulting in a solid growth of the movement ecology discipline (Joo et al. 2022). The association of GPS with temperature and pressure sensors (TDR), accelerometers and video-cameras provide accurate information on foraging behavior (Patterson et al. 2019). However, the use of multi-sensor loggers generate increased costs and weight, restricting their use only to relatively small number of individuals and species of large body mass, as well as large-budget projects. In this context, GPS-only devices have been widely used, because they are more accessible due to their low costs (Smith et al. 2018) and because their reduced size and mass is suitable for small flying species (Hallworth and Marra 2015).

Due to the ethical consensus of using devices lighter than 3% of the avian body mass (Phillips et al. 2003), an important constraint of GPS loggers is its battery life, which can lead to a reduction of the sampling frequency to optimize the trajectory recording. In studies targeting light/small species performing long foraging trips (e.g. > 24 h), reducing the sampling frequency is a usual strategy to record the entire trip (e.g. Fayet et al. 2015). However, low frequency sampling results in low resolution tracks and low accuracy of statistical models used to infer foraging activities (e.g. flying, foraging, resting) from GPS data, such as Hidden Markov Models (HMMs) (Jonsen et al. 2013). HMMs have been widely used to study migration, habitat selection and foraging behavior in seabird species (Joo et al. 2022). Seabirds are considered sentinels of marine ecosystems and suitable models for movement studies due to their anatomical traits, high mobility and breeding philopatry. In addition, colonial breeding and central-place foraging facilitates deployment of biologgers to investigate foraging strategies (Boyd et al. 2014).

Identifying seabird foraging areas as accurately as possible is important for ecological and conservation purposes. However, differences in biology and foraging strategies among species represent is challenging since different GPS sampling frequencies need to be used for recording complete trips. For species performing long trips (e.g., wedge-tailed shearwater *Ardenna pacifica* – about 8 days, or wandering albatross *Diomedea exulans* – 30 days), frequencies of one position recorded every 10–15 or

25 min have been used to ensure the battery life lasts long enough to record the entire trip (Miller et al. 2018; Clay et al. 2020). In contrast, for species performing trips lasting less than one day (e.g. brown boobies *Sula leucogaster*, and black-legged kittiwake *Rissa tridactyla*), it is possible to increase the track resolution by recording up to one position every second (Nunes et al. 2018; Osborne et al. 2020). In this context, the use of low sampling frequencies may reduce the accuracy of HMMs to identify foraging behaviors, so the estimation of foraging areas can be unreliable.

In general, seabirds inhabiting tropical regions are exposed to an oligotrophic system and unpredictable distribution of food resources and thus can present variable foraging strategies (Schreiber and Burger 2001). Red-billed tropicbirds *Phaethon aethereus* are central-place foragers during breeding season and capture mostly fish in the topmost layer of the water column by plunge-diving (Nelson 2005). Tropicbirds present a body mass of less than 0.7 kg and makes long foraging trips (~3 days) so devices with low weights programmed at low sampling frequencies have been used to record the entire trajectory (Nunes et al. 2022). In this context, it is crucial to assess whether the classification of foraging behaviors based on HMMs is reliable for low sampling frequency data.

From foraging data, it is possible to estimate the size of potential foraging areas at the population level and to evaluate different aspects, such as sexual (Miller et al. 2018) or age segregation in space use (Pettex et al. 2019), or niche partitioning (Rayner et al. 2016). For this, kernel density estimates (KDE) are the most widely used non-parametric method to identify one or more areas of use within a range and are applied under the assumption that the data are independently distributed (Silverman 1986). However, tracking data obtained from GPS devices present an inherent spatial autocorrelation so that there is underestimation of areas by KDEs (Fleming et al. 2015). To deal with this limitation, Fleming et al. (2015) proposed a methodology derived from KDEs which explicitly considers autocorrelation (AKDE). Such method is mainly based on the incorporation of movement effects by means of an autocorrelation function derived from a fitted motion model. Thus, the use of AKDEs could provide more accurate information on the location and size of seabird foraging areas.

Therefore, the present study aimed to assess the performance of HMMs in classifying foraging behavior from GPS-only data obtained from red-billed tropicbirds breeding in the southwestern Atlantic Ocean at trips and population levels. For this, data from GPS and pressure sensors, which provide control information on diving activities, were used. It was expect that at least at the population level, HMMs can be used to estimate foraging areas with high accuracy.

METHODS

The Abrolhos archipelago is located in the southwest Atlantic Ocean (18°02'16"S; 38°40'02"W) under influence of the tropical climate and the Brazil Current (Muehe 1987). Abrolhos is a Brazilian protected area and hosts colonies of seven seabird species, including 600 red-billed tropicbirds (Mancini et al. 2016).

Tracking data on foraging trips of tropicbirds were obtained from February 2019 to August 2021 during the chick-rearing period. Birds were captured in the nest and fitted with GPS receivers combined with pressure sensors (model Axy-Trek Marine, Technosmart). The devices weighed 15 g, under the 3% body mass (Phillips et al. 2003). After one foraging trip, individuals were recaptured for device recovery. GPS was programmed with a frequency of one fix every 10 or 15 minutes and pressure sensors with a frequency of one fix every second (1 Hz).

GPS data (date, time, latitude, longitude) obtained were linearly interpolated at 15 min intervals. The interpolated data were used to fit Hidden Markov Models (HMMs) to estimate distinct behaviors or states. HMMs of two, three, four and five states were fitted from step length and turning angle values (estimated from the regularized GPS data) using the gamma and von Mises distributions, respectively (Michelot et al. 2016). The calculation of the step length and turning angle, as well as the fitting of HMMs were performed using the *moveHMM* package (Michelot et al. 2016). The initial values of the step length and turning angle distributions for the HMMs were determined by clustering analysis based on Gaussian mixture models (Scrucca et al. 2016). The selection of the best model according to the number of states was based on the fit of the angle and step residuals and the Akaike Information Criterion – AIC value. The model with the best fit of the residuals and the lowest AIC value, as well as the best biological explanation for the number of states, was selected.

Once the best model was defined, their performance in classifying foraging behavior was evaluated at three different levels: i) at the population level, for which all trips were taken and ii) at the level of each trip. To validate the foraging events projected by the HMM, data from pressure sensor were used to accurately identify and locate diving activities, a proxy for foraging activity. Pressure data were corrected to define sea surface level and transformed to depth (m) and a threshold of 0.3 m was considered to remove the sensor noise. To identify the depth threshold for dives, sensitivity tests were conducted based on the maximum depths of the dives within each trip (Roy et al. 2022). For each of the GPS locations used for the HMMs, 1 was assigned if the birds performed dives and 0 if they did not. Confusion matrices were constructed with the 'foraging' state and dive data obtained from the HMMs and pressures sensors, respectively. Then at trip and population level, 'precision', 'sensitivity', 'specificity' and 'accuracy' were calculated (Kuhn 2008). In this case, precision indicates the proportion of foraging states correctly classified; sensitivity was the proportion of dives that were identified as foraging states; specificity was defined as the proportion of non-dives identified as such by the HMM; and accuracy was the proportion of dives and non-dives that were correctly classified by the HMM (Fig 1).

To estimate potential foraging areas, AKDE was performed with the foraging state classifies by HMMs (HMM-AKDE) and diving data sets (dive-AKDE) for population level, considering kernel density contours of 50%, 75% and 95%. For model fitting and AKDE estimation, the *ctmm* package was used in R (Fleming and Calabrese 2017). Subsequently, the area and overlap of the HMM and dive AKDEs were calculated for the three established AKDE contours.

RESULTS

For HMMs, 23 trips of 19 red-billed tropicbirds were used and the four-state model was selected, as it presented a better fit based on the step length and turning angle residuals and lowest AIC values. The state with the largest turning angle variance and the second lowest step length value was assumed as 'foraging' behavior ('state 2' in Fig. 2).

At the population and trip levels, indicators estimated values were similar, with the highest value for Sensitivity (around 0.65) and the lowest value for Precision (around 0.10). This low value for Precision indicates that most of the events classified as foraging were not dives. While the Accuracy and Sensitivity obtained values around 0.60 and 0.50, respectively (Table 1). In relation to forage areas estimated from foraging state from HMM and dives al population level, at 50, 75 and 95% KD contour, the overlap values were around 90% (Table 2 and Fig. 3).

DISCUSSION

The present study demonstrates that trips recorded at low sampling frequency with GPS-only loggers are suitable for predicting foraging areas of seabirds at population level. These findings illustrate the potential for studying movement strategies of small species performing long trips, which need to be equipped with devices of short battery life and thus with low sampling frequency for recording complete trips. Therefore, low resolution datasets are also useful for inter and intrapopulation comparisons, such as for testing intersexual differences, enabling progress on ecology and guiding conservation of small seabird species by indicating key foraging areas.

Although at the population level the foraging areas estimated from the foraging states of the HMMs showed a high accuracy, the indicators of the confusion matrices showed relatively low values, mainly the precision, reflecting an over-estimation of foraging states by HMMs. Unlike displacement activities which have long durations and can be identified with greater accuracy, diving events in tropicbirds are shallow and last a few seconds (Castillo-Guerrero et al. 2011). Previous studies with other seabirds obtained similar results, showing the disadvantages of applying HMMs to predict fine-scale behaviors such as dives on low resolution GPS data (Clay et al. 2020). Furthermore, most positions misclassified as foraging for tropicbirds were close to positions classified as resting, which suggests that resting state could have been misclassified as foraging. An alternative to deal with the over-estimation of foraging states in seabirds is the use of other classification techniques. For example, support vector machines and random forest can be used to successfully classify animal behaviors (Wang 2019; Joo et al. 2022). In addition, deep learning was also demonstrated to be efficient to identify foraging events of seabirds, but this was demonstrated only for GPS data of higher sampling frequency (Roy et al. 2022).

The identification of foraging areas at the group level allows intra and interspecific comparisons, which is particularly important when studying seabirds due to their high mobility and extension of areas used for foraging. Increasing the accessibility of biologging tools and statistical techniques for small species and study groups with small budgets will promote advances in knowledge seabird ecology, since the applicability of such tools is easier and cheaper for species of larger body mass. In this context, GPS loggers and trajectory segmentation using HMMs are still a more attractive and less complex option for dealing with low resolution, proving to be useful for estimating foraging areas with high accuracy.

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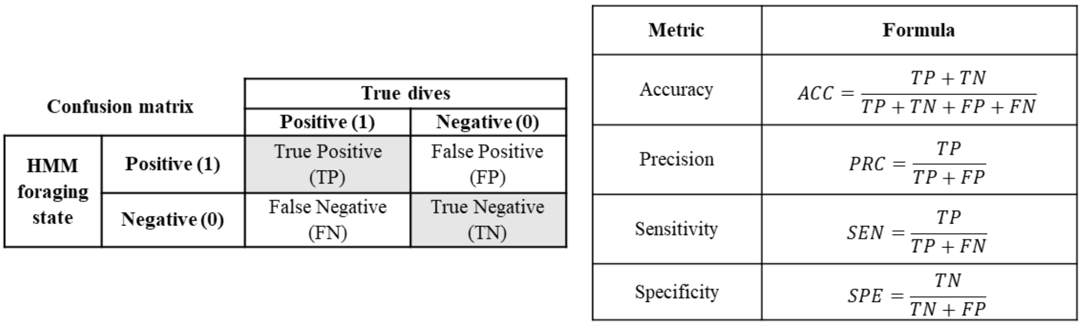
TABLE 1. Hidden Markov Models (HMM) performance indicators at population and trip levels for red-billed tropicbird *Phaethon aethereus* breeding on Abrolhos archipelago, Brazil.

Level	Accuracy	Precision	Sensitivity	Specificity
Population	0.60	0.10	0.51	0.69
Trip	0.59	0.09	0.53	0.66

TABLE 2. Estimated areas and overlap of Autocorrelation Kernel Density Estimations (AKDEs) of dives and Hidden Markov Models (HMM) by Kernel Density (KD) contour for red-billed tropicbird *Phaethon aethereus* breeding on Abrolhos archipelago, Brazil.

Source data	**Area (km^2) by KD contour**		
	95%	**75%**	**50%**
Dives	93683	41281	20758
HMM	91319	40783	20510
Overlap (%)	**92**	**96**	**90**



Confusion matrix		**True dives**	
		Positive (1)	**Negative (0)**
HMM foraging state	**Positive (1)**	True Positive (TP)	False Positive (FP)
	Negative (0)	False Negative (FN)	True Negative (TN)

Metric	**Formula**
Accuracy	$ACC = \frac{TP + TN}{TP + TN + FP + FN}$
Precision	$PRC = \frac{TP}{TP + FP}$
Sensitivity	$SEN = \frac{TP}{TP + FN}$
Specificity	$SPE = \frac{TN}{TN + FP}$

FIGURE 1. Classification performance metrics based on the confusion matrix

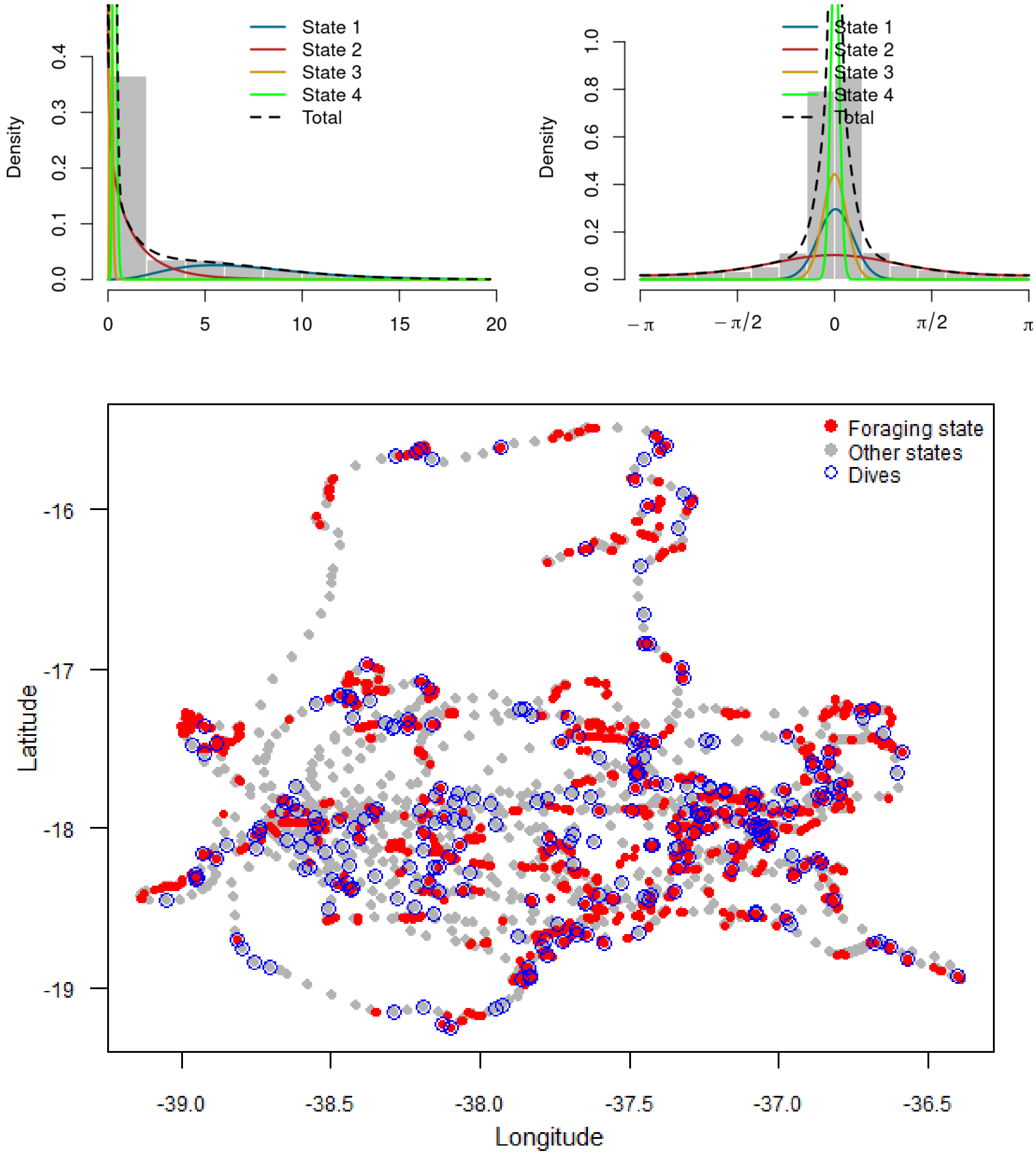


FIGURE 2. Step length (left) and turning angle (right) distributions (top) and trips with foraging states (red), other states (gray) and dives (blue) (bottom) for red-billed tropicbird *Phaethon aethereus* and for different states (colors) breeding on Abrolhos Archipelago, Brazil. Red represents the state considered as ‘foraging’.

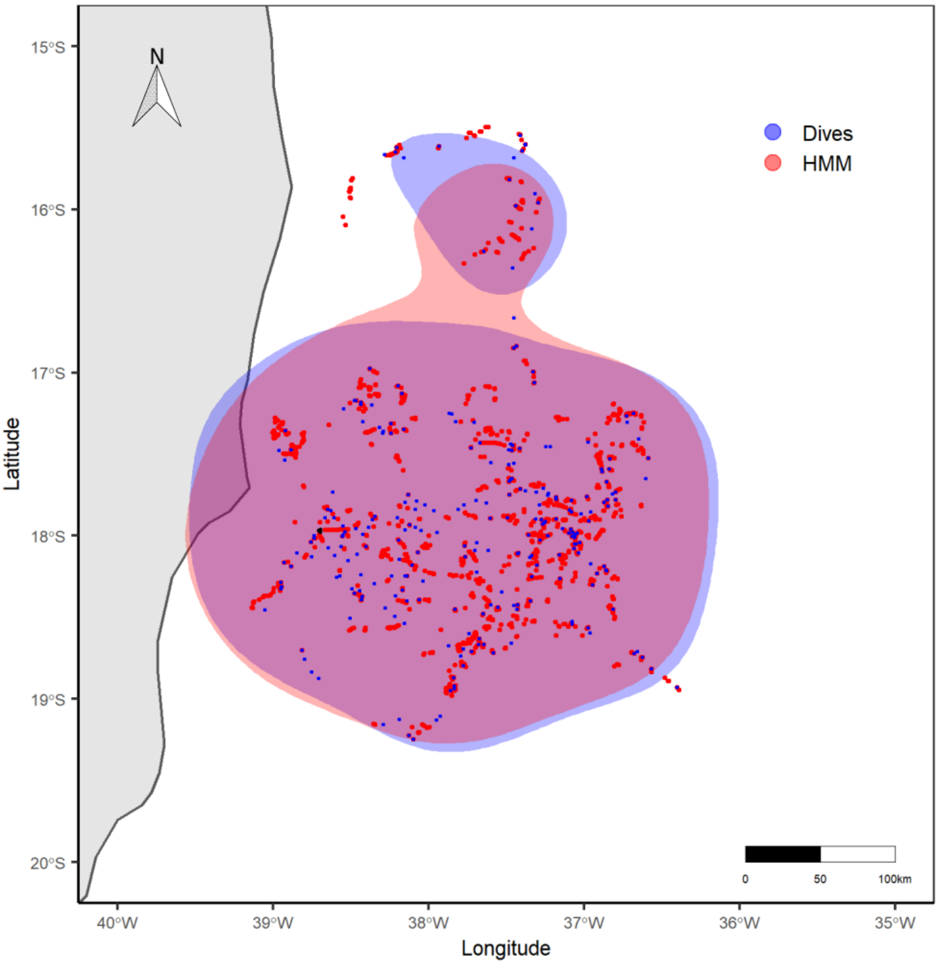


FIGURE 3. Autocorrelation Kernel Density Estimations at 95% Kernel density contour for red-billed tropicbird *Phaethon aethereus* at population level, and for dives (blue) and Hidden Markov Model results (red).

Three-dimensional foraging strategies of red-billed tropicbirds in the southwestern Atlantic Ocean

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ABSTRACT

Seabirds are central-place foragers during the breeding season, which reinforces competition around the colony, especially in oligotrophic environments as tropical marine waters. Thus, to avoid competition, seabirds may vary foraging strategies, such as differential niche use between the sexes, which could be favored by sexual size dimorphism (SSD). Likewise, both parents attend the nest and can use an intraindividual bimodal foraging strategy alternating long and short trips, for adult maintenance and to feed chicks, respectively. Red-billed tropicbird *Phaethon aethereus* is a pantropical seabird that exhibits SSD, with males larger than females, and its main colony in the southwest Atlantic Ocean (i.e. Abrolhos archipelago) which is considered an oligotrophic marine ecosystem. We expect to find sexual segregation of space use and diet in red-billed tropicbird since they exhibit SSD and breed in an oligotrophic environment. Therefore, in this study we aimed to characterize the foraging strategies of red-billed tropicbirds in a three-dimensional space, considering both short and long trips and to assess differential niche use between sexes. For this, GNSS receivers and time-depth recorders were used to track foraging trips and stable isotopes were used to estimate the trophic niche. The main findings evidenced that red-billed tropicbirds do not present sexual segregation of both horizontal and vertical distributions and diet during the breeding season, which may be associated with a high prey availability around the Abrolhos archipelago. Likewise, it was found that tropicbirds perform long and short trips lasting three days and two hours, respectively, but there was no difference in diving depths between long and short trips. In this context, SSD is suggested to be maintained in the population by another functional hypothesis besides differential niche use, such as sexual selection or fecundity selection.

KEYWORDS

Bimodal foraging strategy, Biologging, Differential niche use, *Phaethon aethereus*, Sexual size dimorphism, Stable isotope analysis.

INTRODUCTION

In tropical marine environments, which are typically oligotrophic (Longhurst 1995), foraging is a challenge for large predators, given the scattered distribution of prey (Ballance et al. 1997; Weimerskirch 2007). In response, predators such as seabirds have developed foraging strategies that allow them to obtain the greatest energy gain with the least amount of energy and time spent (Charnov 1976; MacArthur and Pianka 1966). This is particularly important during the breeding season, when seabirds must find a balance between providing sufficient food for the chick and maintaining their own body condition (Orians and Pearson 1979). During this period, both parents need to use strategies to avoid competition and ensure their own survival and the nest success.

Seabirds are central-place foragers during the breeding season and competition for already scarce and ephemeral resources increases around the colony during this period (Orians and Pearson 1979; Boyd et al. 2014). In this context, flexibility in foraging strategies works as an adaptive mechanism to spatiotemporal variability in prey availability and competition (Shaffer et al. 2003; Pettex et al. 2012). This can be observed from dietary changes for more accessible prey (Navarro et al. 2009), or even through the use of different foraging areas (Paiva et al. 2018). This difference in diet and areas used for foraging can be observed in relation to time (Paiva et al. 2017; Bourgeois et al. 2022), between sexes (Miller et al. 2018; Reyes-Gonzales et al. 2021), between ages (Pettex et al. 2019) or individual preferences (Harris et al. 2020).

Differential niche use between sexes has been evidenced in several groups of seabirds (e.g. petrel, albatross, boobies) and it has been attributed mainly to intersexual competition (Paiva et al. 2018; Clay et al 2020; Miller et al. 2018). This can be intensified when seabirds forage in nutrient-poor areas and/or are constrained to use areas close to the colony resulting in the competitive exclusion of one sex from the other (Ruckstuhl and Neuhaus 2005). Likewise, intersexual resource partition can be driven by sexual size dimorphism (SSD), so that the larger sex is generally dominant and gains more access to resources when these are limited (Phillips et al. 2004). This results on individuals of the non-dominant sex increasing the effort by exploring more distant feeding areas (e.g. Rey et al. 2012; Granroth-Wilding and Phillips 2018) or switching to different feeding resources in relation to the dominant sex (González-Solís and Croxall 2005).

Another foraging strategy employed by seabirds to supply these energy requirements is the bimodal foraging strategy, with parents alternating long and short trips (Chaurand and Weimerskirch 1994; Congdon et al. 2005). In general, long trips are made by the adult which is not in charge of caring for the nest to find more productive areas farther away from the colony for adult's maintenance. Alternatively, short trips are performed by the adult which is caring for the nest to areas closer to the colony to feed the chicks (Granadeiro 1998; Weimerskich 1998). Such dynamics in attending the nest has been observed in several seabird species, such as shearwaters (Congdon et al. 2005; Shoji et al. 2015), petrels (Chaurand and Weimerskirch 1994), and tropicbirds (Sommerfeld and Hennicke 2010; Campos et al. 2018).

In this context, biologging tools and stable isotopes analysis (SIA) have been demonstrated to be useful techniques for studying foraging strategies in seabirds, since they provide accurate information on spatial and trophic niches, respectively. For example, GNSS receivers ('GPS' hereafter) make it possible to identify the location of seabirds with high accuracy and to infer different behaviors for identifying foraging areas (Joo et al. 2022). The combination of GPS and pressure sensors provides information on spatial distribution in three dimensions, which is relevant when studying diving seabirds (Patterson et al. 2019). In addition, SIA provides information on dietary aspects and trophic niche (Boecklen et al. 2011). For example, carbon isotopic ratios can inform on the location of foraging areas, while nitrogen values can be used as a proxy of trophic position, so that a bi-dimensional isotopic niche can be estimated as a proxy of the trophic niche (Kelly 2000; Jackson et al. 2011). Although the use of biologging tools and SIA has greatly increased knowledge of the foraging ecology of several seabird species, information on tropical seabird species such as tropicbirds is still scarce.

Red-billed tropicbird *Phaethon aethereus* (order Phaethontiformes) is a colonial and strictly marine bird and presents a small pantropical population occurring in the western Pacific, Atlantic and northern Indian Oceans (Orta 1992). Regarding its foraging ecology, this species makes long and solitary foraging trips and usually forage in association with other sub-surface predators (e.g. tuna or dolphins), foraging mainly on flying fish or squid, which are caught by plunge-diving (Orta 1992; Le Corre 1997). Likewise, red-billed tropicbird performs shallow dives (Le Corre 1997), reaching around one meter as maximum depth (Castillo-Guerrero et al. 2011). In addition, this species presents sexual size dimorphism (SSD), where males are larger than females (Nunes et al. 2013). During the breeding season, females and males share the care of the nest and explore areas around colonies for foraging, performing long trips which last about two or three days (Ndiop et al. 2018; Nunes et al. 2022). Although it has not yet been documented for red-billed tropicbirds, white-tailed and red-tailed tropicbirds use a bimodal foraging strategy with parents alternating long (> two days) and short (< one day) trips (Sommerfeld and Hennicke 2010; Campos et al. 2018). So far, studies about foraging strategies of red-billed tropicbirds have focused on evaluating differences between breeding stages (Ndiop et al. 2018) or environmental conditions (Castillo-Guerrero et al. 2011). However, differential niche use between sexes during breeding season has not been evaluated, considering that this species exhibits SSD as well as bimodal strategy foraging.

In this context, in this study we aimed to characterize the foraging strategies of red-billed tropicbirds in a three-dimensional space, considering both short and long trips, as well as to evaluate differences in the use of space and diet between sexes. To identify the foraging areas and the activities performed during foraging trips, miniaturized GPS loggers were used to estimate the distribution in a two-dimensional plane, while pressure sensors were used to identify and characterize the dives. Stable isotopes of nitrogen and carbon were also used to estimate the extent of their trophic niche. We expected to find similarities in the long and short trips characteristics of red-billed tropicbirds with those reported for white-tailed and red-tailed tropicbirds. Since red-billed tropicbirds exhibit SSD and are in an oligotrophic environment, we expect to find segregation in space use and diet between the sexes.

METHODS

Study area and species

The Abrolhos archipelago is located in the southwest Atlantic Ocean (18º02'16"S 38º40'02"W) and is characterized by a tropical climate influenced by the Brazil Current, which has a surface temperature between 24.5ºC and 27.5ºC and wind speeds between 13 and 16 knots (Muehe 1987). Abrolhos is a Brazilian protected area and hosts colonies of seven seabird species, including red-billed tropicbirds *Phaethon aethereus*, which has an estimated population size of 600 individuals (Mancini et al. 2016).

Although the breeding colony of red-billed tropicbirds is within a protected area, this species is categorized in the Brazilian Red List as ‘Endagered’ (MMA, 2022). This is due to the small population size and the tendency of decline caused mainly by the introduction of invasive species (e.g. rats, cats and lizards) which reduce its breeding success (Sarmento et al. 2014). In addition, studies conducted in Abrolhos have shown that the tropicbird population presents low genetic diversity, which makes them more vulnerable to extinction (Nunes et al. 2017), and that these birds are contaminated by heavy metals after the collapse of the Fundão dam (Nunes et al. 2022).

Biologging

Tracking data from foraging trips of red-billed tropicbirds were obtained in February, March, April and June 2019, February 2020 and August 2021. Tropicbirds with chicks of less than 30 days old were captured at their nests and fitted with GPS receivers combined with pressure sensors (model Axy-Trek Marine, Technosmart, Italy) or GPS-only devices (i-gotU GT-120/GT-600, Mobile Action, Taiwan). The devices weighed 15 g, respecting the 3% body mass limit of the individuals (Phillips et al. 2003). After one long foraging trip or four days (for tropicbirds only performing short trips), individuals were recaptured for device recovery. GPS were set with a frequency of one fix every 10 or 15 minutes (Axy-Trek Marine) and of one fix every 10 minutes (i-gotU) and pressure sensors were programmed at a frequency of one fix every second (1 Hz).

GPS data (lat, long) obtained from Axytreks and Igot-U devices were linearly interpolated at intervals of 15 min. Only complete trips were used to calculate total distance traveled (D), maximum distance to the colony (Dmax), trip duration, and sinuosity, which was calculated as D/2Dmax. Trip statistics were calculated for all data, for males and females and for long and short trips. Trips lasting less than 12 hours were considered short trips (Fig. 1).

The regularized GPS data were used to fit Hidden Markov Models (HMMs) to identify distinct behaviors or states. HMMs were fitted from step length and turning angle values estimated from the regularized GPS data, using the gamma and von Mises distributions, respectively. The calculation of the step length and turning angle, as well as the fitting of HMMs were performed using the *moveHMM* package (Michelot et al. 2016). The initial values of the step length and turning angle distributions for the HMMs were determined with clustering analysis based on Gaussian mixture models (Scrucca et al. 2016). Locations interpreted as ‘foraging’ from HMMs were used to estimate potential foraging areas from males and females. For this, autocorrelation kernel densities (AKDE) were applied using the *ctmm* package in R (Fleming and Calabrese 2017) and overlap was calculated considering the 50%, 75% and 95% Kernel Utilization Distribution (Kernel UD) contours.

Pressure data obtained from pressure sensors were corrected to define sea surface level and transformed to depth (m). Depth values higher than 0.3 m were considered as dives. The number of dives per trip, mean dive depth, maximum dive depth and the distance of first dive from colony were calculated. Dive statistics were calculated for all data, for males and females and for long and short trips.

Stable isotopes

Whole blood samples were obtained for red-billed tropicbirds within the scope of the *Programa de Monitoramento da Biodiversidade Aquática – Rede Rio Doce Mar* (PMBA–RRDM). Samples were dried and stored in plastic tubes. In the laboratory, samples were lyophilized, homogenized, weighed (1 mg) in tin capsules for stable isotope analysis (SIA) of carbon and nitrogen in an Isotope Ratio Mass Spectrometer (IRMS) coupled to elemental analyzer. Standards applied for carbon and nitrogen were Vienna Pee Dee Belemnite and atmospheric air (N_2), respectively. Isotopic ratios (R) of each element ($^{13}C/^{12}C$ and $^{15}N/^{14}N$), represented in delta notation (δ) and expressed in per mil (‰), were obtained through the equation from Bond and Hobson (2012). From $\delta^{13}C$ and $\delta^{15}N$ isotopes values were estimated the two-dimensional isotope niche range for males and females and the overlap of the isotope niche was calculated through Bayesian ellipses using the SIBER (Stable Isotope Bayesian Ellipses) package in R (Jackson et al. 2011). Likewise, from $\delta^{13}C$ and $\delta^{15}N$ isotopes values univariate differences between sexes were tested using the non-Parametric Mann-Whitney test (Bauer 1972).

Both biological samples and biologging data were obtained after licenses provided by SISBIO (No. 64234-6) and the ethics committee of UFRGS (CEUA/UFRGS; Project No. 37905).

RESULTS

A total of 55 trips corresponding to 34 individuals were used to estimated trip statistics. In general, total distance traveled was 303 ± 337 km, maximum distance from the colony was 101 ± 103 km, duration was 38 ± 47 hours, and sinuosity was 1.28 ± 0.4. From a total of 373 dives recorded in 46 trips, average number of dives per trip was 8, average dive duration was 2 s and mean and maximum depth of dives were 0.67 ± 0.28 and 0.91 ± 0.31 m, respectively. Likewise, tropicbirds only performed diving activities from 5 to 18 h (i.e. in daylight), mainly around 6 a.m. in the morning and around 5 p.m. in the afternoon. A total of 29 and 26 trips were used to analyze long and short foraging trips. Average trip duration was around 69 hours for long trips and 2 hours for short trips which can be between one or two trips per day, while total distance travelled and maximum distance from the colony were 174 ± 93.2 and 20.3 ± 20.1, respectively. Tropicbirds performed similar dive depths in both long and short trips (Table 2 and Fig. 2)

A total of 11 and 8 trips from 11 females and 5 males, respectively, were obtained, and both sexes presented similar strategies in foraging trips (Table 1 and Fig. 3). The overlapping values of foraging areas between females and males were around 80% when considering 50, 75 and 95% of the data (Fig. 4). A total of 100 and 73 dives were obtained from 9 female and 9 male trips, respectively. Similar to the results obtained for the foraging trips, dives presented similar characteristics in both sexes (Table 1). Likewise, the distribution of the density of dives in relation to depth was similar in both sexes and the maximum depth of dives was 1.68 m for females and 1.18 m for males (Fig. 2). Finally, isotopic niche area was similar between female and males, with overlap of 99% considering 95% of the data (Fig. 4). In relation to δ13C isotopes ratios, values of -17.5 ± 0.32 and -17.4 ± 0.32 were obtained for males and females, respectively. While, for δ15N isotopes ratios, values of 10.0 ± 1.28 and 10.1 ± 1.6 were obtained for males and females, respectively. As expected, δ13C (W = 886.5; p = 0.17) and δ15N (W = 771.5; p = 0.85) isotopes values did not differ significant between sexes.

DISCUSSION

As expected, the present study evidenced that red-billed tropicbirds do not present sexual segregation of space use, behavior and diet during the breeding period. This disagrees with the hypothesis that sexual segregation can occur in oligotrophic environments as a strategy to reduce intersexual competition and that it can also be favored by the SSD. In relation to the bimodal foraging strategy of red-billed tropicbirds, it was found that short trips present similar characteristics to those reported for the two other species of tropicbirds (e.g. white-tailed and red-tailed tropicbirds). However, in the present study we characterized the short trips also in a vertical plane, finding no differentiation in diving depth between long and short trips.

The high overlap of foraging areas and isotopic niche evidenced no spatial or dietary sexual segregation in red-billed tropicbirds. Considering that sexual segregation is a strategy to reduce competition for resources, we could suggest that there is a higher food availability around the colony located in the Abrolhos archipelago in comparison to oceanic colonies (Oppel et al. 2015). Although the Abrolhos archipelago is surrounded by an oligotrophic marine ecosystem, it can present a higher productivity due to its location on the continental shelf, where primary production is increased through, for instance, river plumes, seafloor nutrient resuspension, and shelf fronts. Also, during brooding stage, parents can be constrained to make trips with less duration and explore feeding areas closer to the colony which could result in the use of similar foraging areas (e.g. Poupart et al. 2020). Other studies have shown that sexual segregation in seabirds can manifest out of the chick-rearing season (Gorman et al. 2014) and, therefore, studying red-billed tropicbirds during the incubation period or even the non-breeding period could provide more comprehensive information on differential niche use between sexes.

Trip metrics and dive depths of red-billed tropicbirds in the Abrolhos archipelago were similar or slightly different in comparison to other populations or congenerics, although long trips and shallow dives have been observed worldwide. For example, the total distance traveled, maximum distance to the colony, and trip duration, were similar to those already reported in two colonies of the same species in Senegal (Diop et al. 2018). Similarly, trip duration of red-billed tropicbirds in this study were also similar to those obtained for a congeneric, the red-tailed tropicbird (Sommerfeld and Hennicke 2010). Trip durations were also long for the white-tailed tropicbirds in the Fernando de Noronha archipelago, but six days on average and thus slightly longer (Campos et al. 2019). Shallow dives observed in the present study were also consistent with that reported in normal environmental conditions in the Gulf of California, although tropicbirds can dive deeper during El Niño southern oscillations (Castillo-Guerrero et al. 2011). A maximum diving depth of about one meter was also reported for red-tailed tropicbirds (Sommerfeld and Hennicke 2010), which was even shallower than that reported for red-billed tropicbirds. Therefore, red-billed tropicbirds are superficial divers exploring food resources in the first two meters of the water column, such as flying fish and squids (Orta 1992).

Interestingly, we found that the diving activities of the red-billed tropics are restricted to daylight hours. Although Diop et al. (2018) and Sommerfeld and Hennicke (2010) reported foraging and/or commuting activities at night for red-billed and red-tailed tropicbirds, respectively, their results are based solely on GPS data. Although the use of segmentation models based on GPS data allows inferring foraging activities, the use of low sampling frequencies may decrease their accuracy so that it may not be possible to accurately identify fine-scale behaviors such as dives. On the other hand, the use of pressure sensors in this work allowed us to obtain more precise information on the diving activities of red-billed tropicbirds and no nocturnal activity was reported. In this sense, and taking into account that this species feeds by diving, we can conclude that during the chick-rearing period and long trips red-billed tropicbirds do not forage at night.

The bimodal foraging strategy presented by red-billed tropicbirds has already been studied in the red-tailed and white-tailed tropicbirds and similar results were found (Sommerfeld and Hennicke 2010; Campos et al. 2018). Studies in other seabird species suggest that long trips generate body reserves in the parents, which are spent during the period when the adult is incubating or taking care of the chick (Congdon 2005; Weclker et al. 2012). During long trips, adults have more time to increase their selectivity in capturing prey, while on short trips, capture could be more opportunistic due to the need to return and attend the nest. However, in the present study long and short trips of red-billed tropicbirds did not present differences regarding dive depth, which coincided with those reported for the species *Alle alle* (Brown et al. 2012). Therefore, we found no difference in prey captured by breeding adults between short and long trips, although this should be further explored from fine-scale behavioral and dietary studies.

Although the breeding area of red-billed tropicbirds is located inside the Abrolhos Marine National Park, conservation efforts for this species could be extended to their foraging areas beyond the limits of the protected area, since this is the largest colony in the southwestern Atlantic Ocean. In general, in recent decades the population of red-billed tropicbirds has shown a significant decline (BirdLife International 2022) and in Brazil the species is categorized in the Brazilian Red List as ‘Endangered’ (MMA, 2022). Red-billed tropicbirds breeding in Abrolhos show high concentrations of heavy metals as a consequence of the tailings released from the Fundão dam (Nunes et al. 2022), low genetic diversity in comparison to other threatened seabird populations (Nunes et al. 2017), and nest predation by invasive species (e.g. rats) (Sarmento et al. 2016). In addition, short foraging trips during the chick-rearing period, as described in this study, represent a window of opportunity for nest predation by rats. Although the bimodal foraging strategy seems to have evolved to favor the breeding success of seabirds, it may be a threat to the conservation of this species, under a scenario of invasive species that have easy access to nests. Therefore, the present study combines complementary techniques to provide valuable information to be considered by managers when planning buffer zones or redefining the limits of the protected area.

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TABLE 1. Mean ± standard error of the total distance traveled (D), maximum distance to the colony (Dmax), trips duration (h), sinuosity, number of dives per trip, depth of dives (m) and distance of first dive from colony (km) by females and males red-billed tropicbirds *Phaethon aethereus* nesting on Abrolhos archipelago, Brazil.

Variable	**Females**	**Males**
D (km)	553 ± 385	376 ± 267
Dmax (km)	178 ± 97	142 ± 105
Duration (h)	74 ± 51	43 ± 31
Sinuosity	1.4 ± 0.4	1.3 ± 0.2
Dives per trip	11 ± 8	8 ± 8
Dive depth (m)	0.64 ± 0.28	0.66 ± 0.24
Distance of first dive from colony (km)	39.1 ± 44.2	37.4 ± 47.6

TABLE 2. Mean ± standard error of the total distance traveled (D), maximum distance to the colony (Dmax), trips duration (h), sinuosity, number of dives per trip, depth of dives (m) and distance of first dive from colony (km) by long and short foraging trips of red-billed tropicbirds *Phaethon aethereus*.

Variable	**Long trips**	**Short trips**
D (km)	534 ± 317	45.5 ± 50.1
Dmax (km)	174 ± 93.2	20.3 ± 20.1
Duration (h)	69.5 ± 44.4	2.4 ± 2.2
Sinuosity	1.52 ± 0.3	1 ± 0.3
Dives per trip	12.7 ± 9.1	2.4 ± 2
Dive depth (m)	0.67 ± 0.28	0.64 ± 0.23
Distance of first dive from colony (km)	43.3 ± 40.9	9.8 ± 6.5

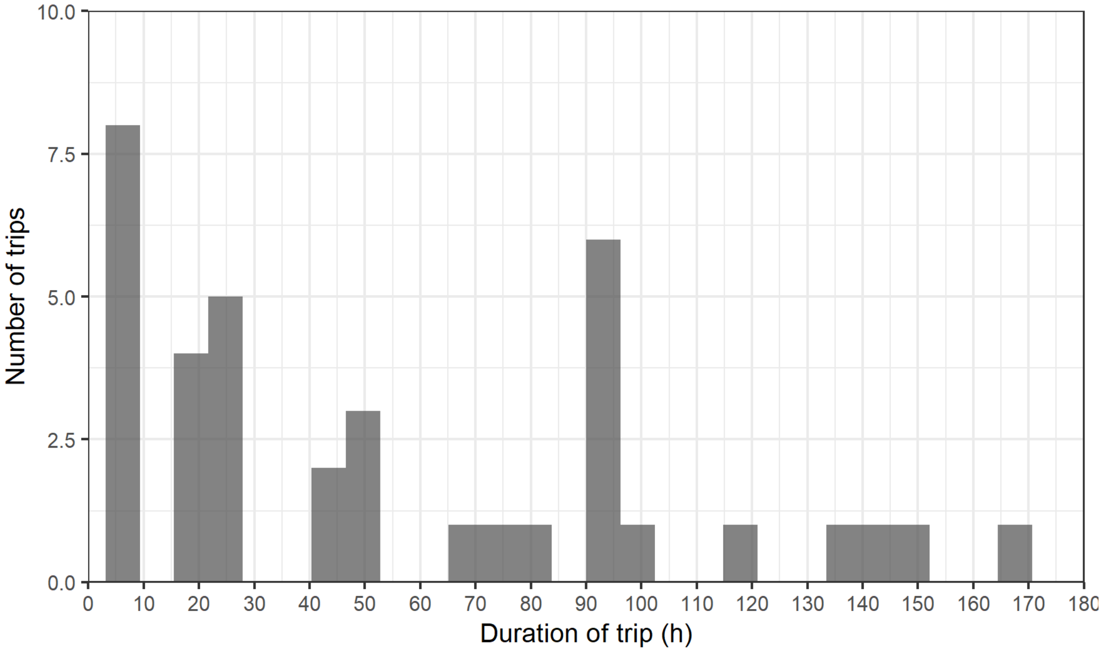

FIGURE 1. Number of trips in relation to trip duration of red-billed tropicbirds *Phaethon aethereus* sampled during the breeding period in the Abrolhos archipelago, Brazil, from 2019 to 2021.

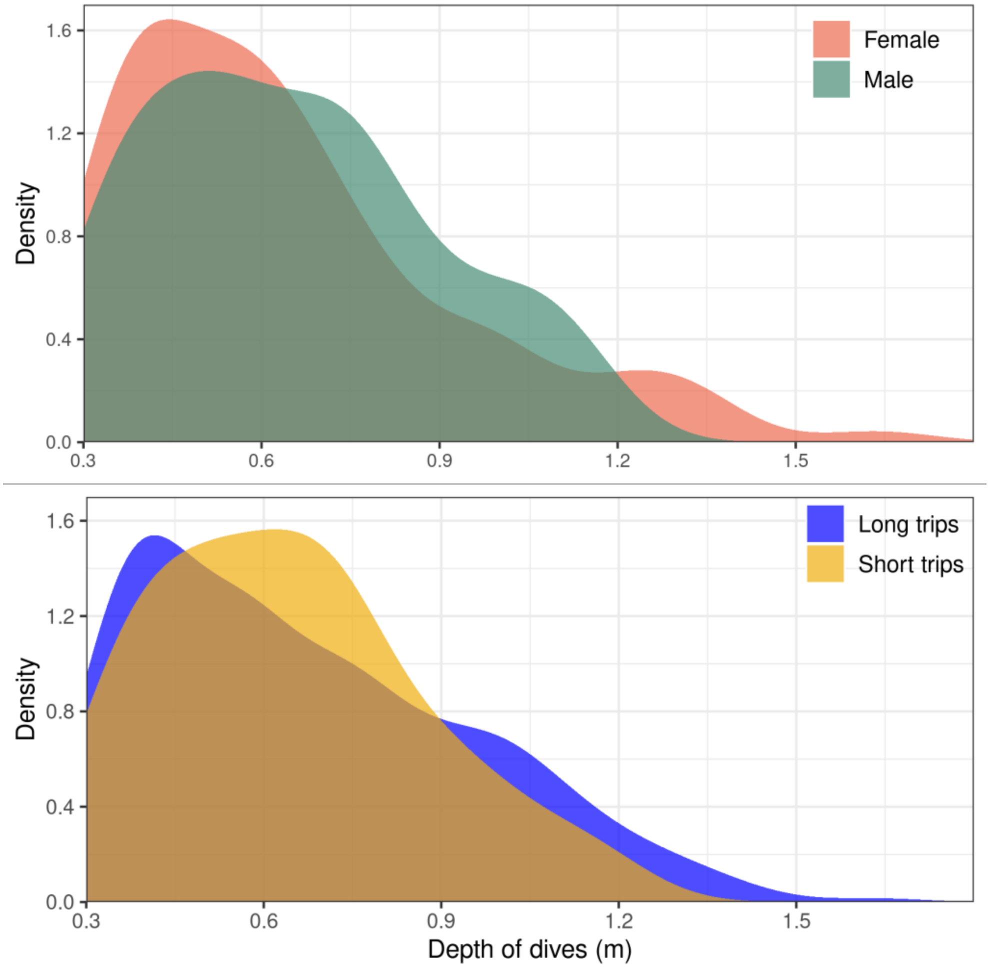

FIGURE 2. Density of number of dives in relation to depth by females and males (top) and long and short trips (bottom) of red-billed tropicbirds *Phaethon aethereus* sampled during the breeding period in the Abrolhos archipelago, Brazil, from 2019 to 2021.

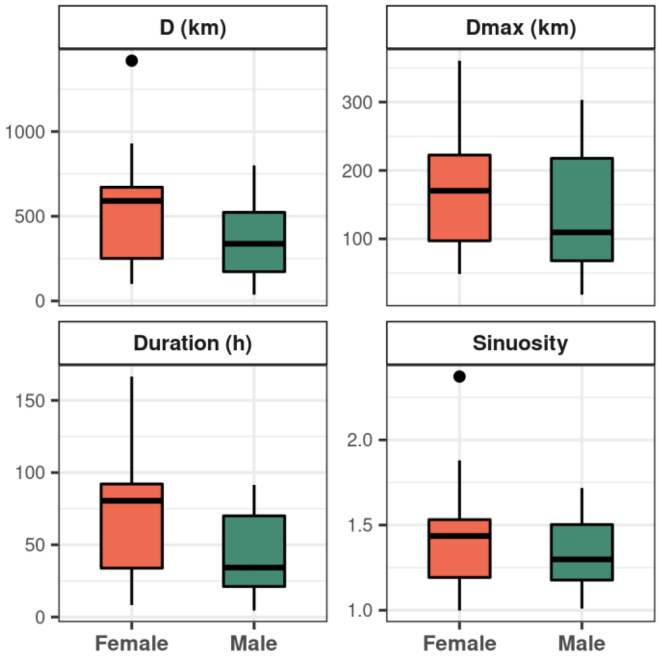

FIGURE 3. Metrics of foraging trips of red-billed tropicbirds *Phaethon aethereus* sampled during the breeding period in the Abrolhos archipelago, Brazil, from 2019 to 2021. D = total distance traveled; Dmax = maximum distance from the colony; h = trip duration; and sinuosity = 2Dmax/D.

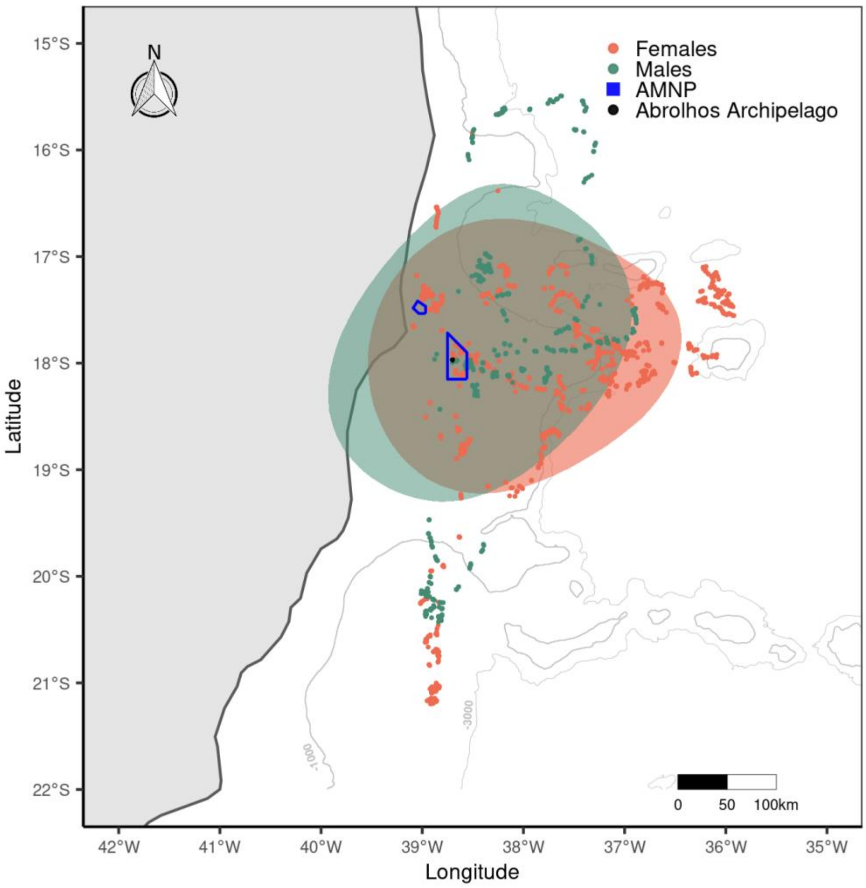

FIGURE 4. Foraging areas obtained by kernel analysis from the positions classified as "foraging" state by the HMMs for females and males (75% kernel UD) of red-billed tropicbirds *Phaethon aethereus* sampled during the breeding period in the Abrolhos archipelago, Brazil, from 2019 to 2021. AMNP = Abrolhos Marine National Park.

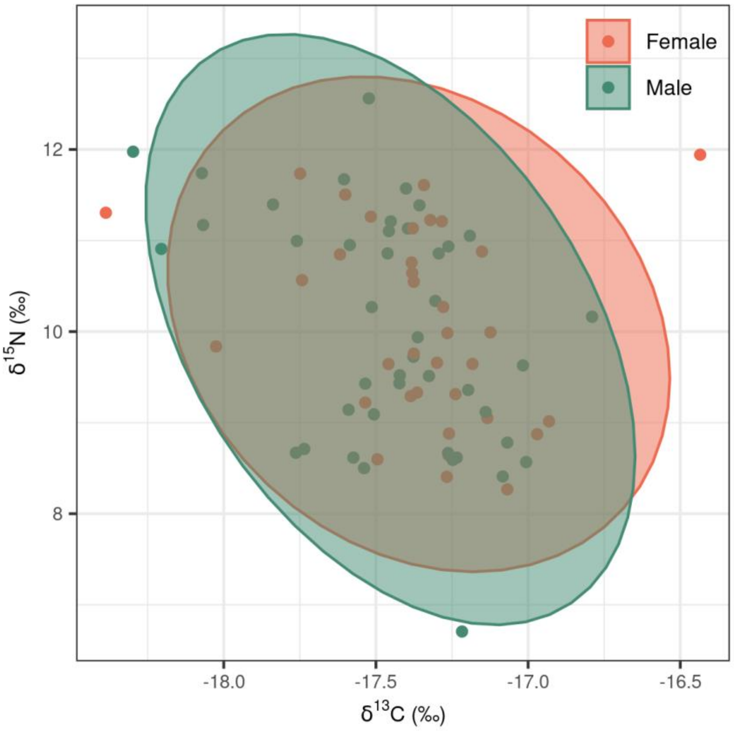

FIGURE 5. Isotopic niches estimated trough Bayesian ellipses using 95% carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values from female and male of red-billed tropicbirds *Phaethon aethereus* sampled during the breeding period in the Abrolhos archipelago, Brazil, from 2019 to 2021.