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Flexible foraging strategies of a tropical seabird in the western Atlantic Ocean

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ABSTRACT

Tropical oceans are typically oligotrophic but can feature productive environments, such as islands, which can promote high prey availability, influencing predators' foraging strategies in time and space. This study investigates interannual and sex-specific variations in the foraging ecology of the masked booby (Sula dactylatra) in the Fernando de Noronha Archipelago, western tropical Atlantic Ocean. During the 2017, 2018, 2019, and 2022 breeding seasons, blood from birds and muscle samples from regurgitated prey were analyzed for stable isotopes of carbon (δ^{13} C) and nitrogen (δ^{15} N). Simultaneously, birds were tracked with GPS devices and their dives were recorded by pressure sensors and later predicted by deep learning tools to estimate foraging areas. Tracking data revealed foraging areas eastward of the archipelago in all years, potentially driven by the Island Mass Effect. The δ^{13} C and δ^{15} N values varied significantly across the four years, but isotopic niches overlapped, except in 2022. Mixing models estimated the fourwing flying fish Hirundichthys affinis as an important prey source from 2017 to 2019, shifting to false herring Harengula clupeola in 2022. Simultaneously, foraging areas were closer to the archipelago in 2022, with shorter foraging trip duration and length. Stable isotope differences between sexes were occasional, with overlapping niches and foraging areas consistent across years. These findings showcase potential predictability in foraging areas, and also their interannual variability, suggesting shifts in prey availability and distribution around the archipelago. Our results highlight the ecological plasticity of masked boobies in tropical environments and their potential as monitors of fish community dynamics.

1. Introduction

Many areas of tropical oceans have unpredictable and patchy resources due to their limited primary productivity, which is considerably lower than temperate and polar oceans (Longhurst and Pauly, 1987). These factors pose challenges to different predators, which need to locate food efficiently and adapt to potential variations in its availability in time and space (Link, 2004; Watanuki et al., 2022). However, the topography around islands and seamounts can promote productive environments in tropical oceans by increasing nutrient concentrations near the surface (Gove et al., 2016). This process, known as the Island Mass Effect (Doty and Oguri, 1956), can benefit a wide range of marine organisms, such as small pelagic fish, which play a critical role in the energy transfer between basal and top trophic levels (Cairns, 1987; Montevecchi and Myers, 1996). Therefore, the distribution and availability of mid-level prey can directly influence the foraging strategies in time and space of top predators, such as large fish, marine mammals, and seabirds (Link, 2004; Staniland et al., 2006; Spitz et al., 2011; Cherel, 2020).

In the western tropical Atlantic Ocean, oceanographic features influence complex trophic webs in distinct layers of the water column (Campelo et al., 2019; Eduardo et al., 2023). The interaction of the South Equatorial Current (SEAc), the South Equatorial Undercurrent (SEUC), and the Equatorial Undercurrent (EUC) with the archipelagos of São Pedro and São Paulo, Fernando de Noronha, and Rocas Atoll generates eddies and turbulence (Araujo and Cintra, 2009). These

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hydrodynamic processes typically contribute to high productivity and biodiversity in these areas (Araujo and Cintra, 2009; Tchamabi et al., 2017). In Fernando de Noronha, the interaction between ocean circulation and island topography on the east side results in higher primary productivity on the west side (Tchamabi et al., 2017), which aligns with the Island Mass Effect. However, it is also hypothesized that the flow of particles and zooplankton from upwellings and incoming currents on the east side (windward) may serve as an essential energy source for planktivorous fish, leading to increased secondary and tertiary production eastward (Salvetat et al., 2022). Thus, these oceanographic processes likely enhance the predictability of fish distribution in the archipelago, potentially shaping the foraging strategies of their predators, such as tunas (*Thunnus* spp.), dolphinfish (*Coryphaena hippurus*), and seabirds (Santos et al., 2019; Martins et al., 2021).

Seabirds can play an essential role in the study of marine ecosystems as samplers of pelagic organisms. The group typically nest on continental coasts or islands and exploit resources around their colonies during the breeding season, acting as central place foragers (Schreiber and Burger, 2002). Some species can exhibit flexible foraging strategies that allow them to explore a wide range of prey, and adapt to spatiotemporal variations in their foraging areas (Sommerfeld et al., 2015; Castillo-Guerrero et al., 2016; Cerveira et al., 2020). Boobies (Suliformes: Sulidae) are seabirds distributed in subtropical and tropical regions, and have reverse sexual dimorphism (females larger and heavier than males) (Nelson, 1978), which can influence intersexual differences in foraging strategies during breeding and non-breeding seasons (Sommerfeld et al., 2013; Lerma et al., 2024; Roy et al., 2021). Their diet is based on schooling fishes such as flying fish (Exocoetidae), halfbeaks (Hemiramphidae), anchovies (Engraulidae), sardines (Clupeidae), jacks (Carangidae), tunas (Scombridae), and squid (Decapodiformes) (Zavalaga et al., 2007; Carboneras et al., 2020; Lerma et al., 2024; Mlodinow et al., 2024). Moreover, boobies demonstrate flexible foraging behaviors in response to spatial and temporal variations in prey availability and distribution around their colonies, which can be investigated through their movements (Weimerskirch et al., 2008; Sommerfeld et al., 2015; Soanes et al., 2021) and diet (Castillo-Guerrero et al., 2016; Donahue et al., 2020). Consequently, booby foraging strategies are potentially shaped by the conditions around their colonies (Gilmour et al., 2018; Jacoby et al., 2023), making them valuable indicators of local trophic dynamics in space and time.

Studies focusing on foraging distribution and food resource use are typically interconnected and provide information on complementary dimensions of the ecological niche (Garvey and Whiles, 2016). Biologging techniques allow for remote observation of animal movements, enabling the identification of different behaviors through trajectory analysis and by employing multiple sensors (i.e. barometers, accelerometers) (Tremblay and Bertrand, 2016; Williams et al., 2020). Consequently, this information allows the characterization of space use strategies (Wilmers et al., 2015; Roy et al., 2022), which have been widely used in seabird studies (Machovsky-Capuska et al., 2016; Austin et al., 2021). Complementarily, stable isotope analysis allows the inference of trophic interactions through isotopic ratios of key elements. In ecological studies, the carbon isotopic ratio (δ^{13} C) is used as an indicator of foraging habitat, such as inshore/offshore areas (Cherel and Hobson, 2007), while the nitrogen isotopic ratio (δ^{15} N) provides information about the trophic level of predators (Fry, 2006). Thus, δ^{13} C and δ^{15} N are considered two dimensions of the ecological niche – or isotopic niche (Newsome et al., 2007; Jackson et al., 2011). Additionally, despite its potential biases in the marine environment, such as variations in baselines over time and space (Magozzi et al., 2017), stable isotope analysis is a relatively simple technique that allows for testing spatiotemporal variations in food resource use (Dalerum and Angerbjörn, 2005), and access the proportions of prev assimilated by a studied organism (Parnell et al., 2013). Therefore, combining biologging and stable isotopes can provide complementary information on foraging strategies and their variations through time and space, shedding light on

the ability to adapt to environmental conditions around colonies.

Fernando de Noronha is the archipelago with the greatest number of breeding seabird species in the southwestern Atlantic Ocean (Mancini et al., 2016). The foraging strategies of these species, including boobies, were investigated in a few studies that included interspecific and interseasonal (summer vs. winter) approaches using stable isotopes (Mancini et al., 2014). Tracking studies were also conducted to identify foraging areas of the white-tailed tropicbird *Phaethon lepturus* during a single breeding season (Campos et al., 2018; Santos et al., 2019) and to determine the year-round residence of masked boobies *Sula dactylatra* (Roy et al., 2021). Despite these efforts, the lack of interannual studies of predator foraging strategies in Fernando de Noronha prevents us from determining whether the use of areas where prey predictability is potentially enhanced by oceanographic processes, such as the Island Mass Effect, occurs and if is continuous over time.

In this context, the present study aims to characterize interannual foraging strategies of masked boobies around Fernando de Noronha and to identify if their foraging strategy remains stable across years considering the food resources promoted by the Island Mass Effect. For this, we analyzed biologging data obtained during foraging trips around the colony and stable isotope data of carbon and nitrogen from birds and their prey over four breeding seasons. Additionally, considering that seabird foraging strategies can be promoted by sex-specific responses to environmental variables (Gissi et al., 2023), we also analyzed data from males and females separately. Given the abundant and irregularly distributed food resources over time, without significant inter-annual variations.

2. Methods

2.1. Study area

The study was carried out on Meio Island (3°49'11.6" S; 32°23'35.4" W), a secondary islet belonging to the Fernando de Noronha Archipelago, located 360 km off the Brazilian coast (Fig. 1). The archipelago experiences two well-defined seasons, a rainy season from March to July and a dry season from August to January (Serafini et al., 2010), but these do not imply significant environmental variations, such as sea surface temperature, and fish distribution in the surrounding waters (Tchamabi et al., 2017; Salvetat et al., 2022). Meio Island holds the main colony of masked boobies in the archipelago (Gouvêa and Mello, 2017). Its area extends to approximately 0.16 km², mostly covered by herbaceous vegetation and exposed soil, where masked colonies nest (Gaiotto et al., 2022). Brown boobies Sula leucogaster and red-footed boobies S. sula also breed on the island, but the nests do not overlap spatially. The size of the population of the masked booby in Meio Island was estimated at 181, 388, 162, and 140 individuals respectively in 2017, 2018, 2019, and 2022 based on ground counts of incubating individuals and emancipated chicks. Before 2017, Meio Island had a population of black rats Rattus rattus, which preyed on eggs and chicks. However, between 2017 and 2018 these rats were eradicated from the island to favor the reproductive success of the boobies.

2.2. Sampling methods

Sampling was carried out in 2017, 2018, 2019, and 2022 during the chick-rearing period (March–April) of masked boobies (Serafini et al., 2024). Breeding individuals who brooded chicks at an early stage of development were captured by hand or with a nylon snare on the end of a fishing rod. Females and males were identified by differences in vocalization (Nelson, 1978). GPS tracking devices, igotU GT-120 (Mobile Action, Taiwan), or Axy-Trek Marine (TechnoSmart, Italy), weighting, respectively, 16 g (waterproofed) and 26 g, were attached to the central tail feathers of each individual using TESA® tape. On



Fig. 1. Meio Island, Fernando de Noronha Archipelago, tropical Atlantic Ocean, where is located the main colony of masked booby (Sula dactylatra) sampled and tracked from 2017 to 2022.

average, the males weighed \sim 1540 g while the females weighed \sim 1720 g, so the devices represented less than 3 % of their body mass (Phillips et al., 2003). Loggers were set to record a position every 10-15 s. The IgotU model devices only provided position information, while the Axy-Trek devices also featured pressure sensors. From 88 individuals fitted with loggers with recorded trips, the pressure was measured for 55 individuals, enabling the identification of diving bouts. After two to three days, birds were recaptured for logger retrieval and biological sampling. Blood samples (0.3 mL) were collected from the metatarsal vein from all tracked birds using sterile syringes/needles and stored in microtubes. During handling, spontaneous regurgitations of undigested material were collected, stored in plastic bags, and frozen at -20 °C. Subsequently, prey items were identified at the lowest possible taxonomic level, measured using a stop ruler when not partially digested, and muscle samples were collected and stored in microtubes with 70 % ethanol.

2.3. Stable isotope analysis

Prey samples were washed in a Soxhlet extractor for a 6 h cycle using a 2:1 chloroform:methanol solution as a solvent to remove lipids (Logan et al., 2008; Nunes et al., 2018). Lipids from blood samples were not extracted as they are typically present in low concentrations (Bearhop et al., 2002). Subsequently, all muscle and blood samples were lyophilized, grounded, and homogenized. Subsamples of ~0.7 mg were placed in tin capsules for stable isotope analysis (SIA) of carbon (δ^{13} C) and nitrogen (δ^{15} N) using an isotope ratio mass spectrometer at the *Pôle Spectrométrie Océan* of the *Institut Universitaire Européen de la Mer* (PSO-IUEM, France), and the *Centro Integrado de Análises* of the *Universidade Federal do Rio Grande* (CIA-FURG, Brazil). Differences between sample and standard ratios (Vienna Pee Dee Belemnite for δ^{13} C; atmospheric air for δ^{15} N) are expressed in δ notation in parts per thousand (‰). The accuracy of the measurements was checked by repeated analyses of internal samples of acetanilide at the PSO-IUEM and glutamic acid and caffeine at the CIA-FURG.

The mean and standard deviation of isotopic values between years were calculated using the FSA package version 0.9.6 (Ogle et al., 2025) in the R software version 4.4.2 (R Core Team, 2024). Subsequently, univariate differences between years were tested using the Kruskal-Wallis test (KW), followed by Dunn's test for post-hoc pairwise comparisons, with p-values adjusted using Bonferroni correction (Legendre and Legendre, 2012). The same approach (KW and Dunn's test) was applied separately for females and males to assess isotopic variation across years. To test differences between sexes within each year, KW was used. Additionally, the isotopic niches of females and males per year were estimated using a Bayesian approach that provides Standard Ellipse Areas (SEA), implemented in the SIBER package version 2.1.9 (Jackson et al., 2011). Finally, the contribution of each prey species to the diet of females and males was estimated with Bayesian mixing models in the simmr package version 0.5.1.217 (Govan and Parnell, 2023). The discriminant factors used in the mixing models were 0.5 \pm 0.3 ‰ for δ^{13} C and 1.7 \pm 0.6 ‰ for δ^{15} N, estimated for the Guanay cormorant Leucocarbo bougainvillii (Le Croizier et al., 2022). The prey species and family used in the models were the margined flying fish Cheilopogon cyanopterus (n = 4), the tropical two-wing flying fish Exocoetus volitans (n = 25), the fourwing flying fish Hirundichthys affinis (n= 24), halfbeaks Hemiramphidae (n = 4), the bigwing halfbeak Oxyporhamphus micropterus (n = 6), and the false herring Harengula clupeola (n = 3). These fish prey sources were chosen based on the main species of fish found in regurgitates (n = 33) from handled masked boobies, collected in 2017, 2018, and 2022 (Table S1).

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2.4. Biologging analysis

Avian trajectories were split into distinct central-place foraging trips. For this, we have considered trajectories whose maximum distance from the colony was greater than 500 m. Dive occurrences were detected from pressure sensors, specifically in situations where the estimated depth was below 1 m, given natural variations of the equipment records and atmospheric pressure.

The trajectories of individuals who did not have pressure sensors were segmented for the identification of dive bouts using a dedicated U-shaped deep neural network (Roy et al., 2022), which infers the diving behavior of seabirds solely based on the geometry of their flight paths, outperforming traditional approaches based on hidden Markov models (Patterson et al., 2009). Moreover, this method has the benefit of fine-tuning a pre-trained deep network with additional trajectory data. We followed this fine-tuning approach using our dataset and based on the pre-trained models using custom Python code (https://github.com/AmedeeRoy/BirdDL). Our model was trained, validated, and tested on distinct datasets with respectively 50 %, 30 %, and 20 % of the trajectories, and obtained above 91 % predictive accuracy on the test dataset.

Finally, the observed and predicted dive occurrences were used to estimate foraging utilization distributions using a Gaussian Kernel Density Estimation (KDE), with bandwidth selection based on Scott's "rule of thumb", that produces a larger bandwidth, useful for estimating smooth distributions from auto-correlated GPS data (Scott, 1992). We evaluated the similarity between sex- and year-specific foraging utilization distribution using two metrics: the root mean squared error (RMSE) and the Bhattacharyya coefficient (BC). These two metrics are particularly effective at representing spatial differences between species distribution models (Wilson, 2011). The RMSE allows for measuring the differences in intensity between spatial distributions, and BC provides a more interpretable measure of "overlap" between two spatial distributions (Fieberg and Kochanny, 2010; Winner et al., 2018).

Additionally, for complete trips (i.e., first and last points recorded at the colony) of males and females, the following metrics were calculated: total distance traveled (D_{tot}, km), maximum distance from the colony (D_{max}, km), trip duration (T_{dur}, min), proportion of time (min) spent diving (P_{div}, %), and straightness index (ratio ranging from 0 to 1). The straightness index of a central-place foraging trajectory was defined as two times the quotient between the D_{max} and D_{tot} (Benhamou, 2004). To test variations of $D_{\text{tot}}, D_{\text{max}},$ and T_{dur} across years, we used Linear Mixed Models (LMM) with the *lmerTest* package version 3.1-3 (Kuznetsova et al., 2017). For the straightness index, we applied Generalized Linear Mixed Models (GLMM) via the glmmTMB package version 1.1.10 (Brooks et al., 2017), with a beta distribution and logit link function. For Pdiv, we used a zero-inflated beta model within the GLMM framework, ensuring compatibility with the continuous and proportional nature of the data. In all models, the individual was included as a random effect to account for multiple trips from the same bird. For multiple comparisons between years, we performed post-hoc Tukey tests using the emmeans package version 1.10.7 (Lenth, 2025). Additionally, to test sex-related differences within each year, we fitted separate models with sex as the fixed predictor, maintaining the same random effects and distributional

assumptions for each metric.

3. Results

3.1. Stable isotopes

Ninety-seven blood samples from masked boobies were analyzed, 43 from females and 54 from males (Table 1). The δ^{13} C mean values were lower in 2022 and higher in 2017 for females and males. The δ^{15} N mean values for females were lower in 2017 and higher in 2022 and, for males, the lower values were also observed in 2017, but the highest occurred in 2019 (Fig. 2, Table 1). Additionally, a total of 66 prey samples were analyzed (Table S1). The δ^{13} C mean values varied from -17.86 ± 0.05 ‰ (*H. clupeola*) to -17.13 ± 0.30 ‰ (*H. affinis*), and δ^{15} N values ranged from 7.66 ± 1.44 ‰ (*O. micropterus*) to 9.75 ± 1.55 ‰ (*C. cyanopterus*) (Table S1).

Considering all bird samples, significant differences between years



Fig. 2. Variations in δ^{13} C and δ^{15} N values in whole blood of males and females masked booby (*Sula dactylatra*) breeding in the Fernando de Noronha Archipelago, Brazil, from 2017 to 2022. *Significant differences between sexes.

Table 1

Mean \pm standard deviation (SD), minimum (Min) and maximum (Max) values of carbon (δ^{13} C) and nitrogen (δ^{15} N) isotopic values from blood samples of females and males of masked boobies (*Sula dactylatra*) from Fernando de Noronha Archipelago, tropical western Atlantic Ocean, during breeding season through sampling years.

	Fema	ales		Males										
	_	δ^{13} C (‰)			δ^{15} N (‰)				δ ¹³ C (‰)			δ^{15} N (‰)		
	n	$\text{Mean} \pm \text{SD}$	Min	Max	$\text{Mean} \pm \text{SD}$	Min	Max	n	$\text{Mean} \pm \text{SD}$	Min	Max	$\text{Mean} \pm \text{SD}$	Min	Max
2017	9	-16.58 ± 0.10	-16.80	-16.43	10.50 ± 0.24	10.05	10.84	21	-16.61 ± 0.08	-16.73	-16.44	10.34 ± 0.18	10.07	10.89
2018	21	-16.92 ± 0.16	-17.18	-16.55	10.71 ± 0.26	10.28	11.40	13	-17.01 ± 0.14	-17.30	-16.79	10.42 ± 0.10	10.25	10.55
2019	7	-16.62 ± 0.09	-16.75	-16.53	10.96 ± 0.38	10.58	11.72	5	-16.72 ± 0.06	-16.79	-16.64	10.80 ± 0.09	10.72	10.96
2022	6	-17.62 ± 0.04	-17.67	-17.55	11.02 ± 0.18	10.81	11.28	15	-17.66 ± 0.11	-17.91	-17.52	10.74 ± 0.14	10.44	11.01

were found for δ^{13} C (KW, chi-squared = 78.64, p < 0.01) and δ^{15} N (KW, chi-squared = 42.11, p < 0.01). Paired differences were significant between all years for both elements, except between 2017 and 2019 for δ^{13} C, and between 2019 and 2022 for δ^{15} N (Table 2). Differences between years for females were significant for δ^{13} C (KW, chi-squared = 30.73, p < 0.01) and δ^{15} N (KW, chi-squared = 16.24, p < 0.01). Paired differences were significant between all years for δ^{13} C, except 2017 vs. 2019 and 2018 vs. 2022 (Table 2). For δ^{15} N, differences were significant between 2017 vs. 2019, 2017 vs. 2022, and 2018 vs. 2022 (Table 2). For males, differences between years were also significant for $\delta^{13}\mathrm{C}$ (KW, chisquared = 46.61, p < 0.01) and δ^{15} N (KW, chi-squared = 32.75, p <0.01). Paired significant differences were observed for δ^{13} C between 2017 vs. 2018, 2017 vs. 2022, and 2019 vs. 2022. For δ^{15} N, significant differences were found between all years except 2017 vs. 2018 and 2019 vs. 2022 (Table 2). The isotopic niches of all years overlapped for both sexes, except the one from 2022 (Fig. 3a).

Regarding intersexual variations per year, no significant differences were identified for δ^{13} C in any year (KW, p > 0.05), and for δ^{15} N there were significant differences in 2017 (KW, chi-squared = 4.43, p < 0.05), 2018 (KW, chi-squared = 11.454, p < 0.01) and 2022 (KW, chi-squared = 8.53, p < 0.01) (Fig. 2). There was a partial overlap of isotopic niches between sexes in all years (Fig. 3b, Table S2), with males having a narrower niche than females. However, this pattern was reversed in 2022 when males presented a wider niche compared to females and also with male niches from previous years (Fig. 3b, Table S2).

Mixing models demonstrated annual variations in the contribution of each prey to the diet of males and females. The most important prey source for females during 2017, 2018, and 2019 (from 25.1 % to 30.7 %) was *H. affinis*, as well as for males in 2017 and 2019 (40.7 % and 22.3 %, respectively). In contrast, in 2022, its contribution decreased to 13.5 % for females and 6.8 % for males (Table S3, Fig. 4), and there was an increase in importance for *H. clupeola* representing the prey item with the highest contribution to the diet of both sexes (27.9 % for females and 61.4 % for males) (Fig. 4, Table S3).

3.2. Foraging areas

From the 88 birds tracked, 42 were females and 46 were males, resulting in 235 complete foraging trips, 116 from females, and 119 from males (Table 3). Among these, 146 trips included dive data, while 89 did not, leading to a total of 2739 dives observed and 1485 dives predicted.

The mean D_{tot} (km) was lower in 2022 for females and males and higher in 2018 for females and in 2019 for males (Fig. 5, Table 3). The D_{max} (km) had the lowest averages in 2022 for females and males and the highest in 2018 for females and in 2019 for males (Fig. 5, Table 3). Similarly, T_{dur} (min) was shorter in 2022 for both sexes and longer in 2019 for females and in 2018 for males (Fig. 5, Table 3). The P_{div} varied from 0.010 % (2019) to 0.015 % (2017) for females and from 0.013 % (2019) to 0.020 % (2018) for males (Table 3).

The LMM and GLMM indicated significant differences ($p \le 0.05$)



Fig. 3. (a) Bayesian ellipses of δ^{13} C and δ^{15} N values from whole blood samples of females and males of masked booby (*Sula dactylatra*) during breeding seasons in the Fernando de Noronha Archipelago; (b) Bayesian ellipses of δ^{13} C and δ^{15} N of males and females in each sampling year.

between years for all metrics: D_{tot} ($F_{3,77} = 7.94$), D_{max} ($F_{3,74} = 5.43$), T_{dur} ($F_{3,55} = 6.54$), P_{div} , and straightness index. D_{tot} was lower in 2022 compared to 2017 (t = 3.48), 2018 (t = 3.46), and 2019 (t = 3.64), while D_{max} was also lower in 2022 compared to 2017 (t = 3.0), 2018 (t = 3.11), and 2019 (t = 2.65). T_{dur} was lower in 2022 compared to 2018 (t = 2.61) and 2019 (t = 3.97). P_{div} in 2019 was slightly lower than in 2017 (z = 2.71) and 2022 (z = -2.7), and the straightness index was higher in 2022 than in 2018 (z = -3.18) and 2019 (z = -2.58) (Fig. 5). The LMMs showed no significant differences in D_{tot} , D_{max} , and T_{dur} between sexes in any sampled year (p > 0.05) (Fig. S1, Table S4). Similarly, the GLMMs for straightness index and P_{div} found no significant sex differences in most years, except in 2017, when female trips exhibited slightly higher straightness than males (z = 1.98) (Fig. S1, Table S4).

Table 2

Results of Dunn's test for multiple comparisons of isotopic carbon (δ^{13} C) and nitrogen values (δ^{15} N) from blood samples of masked boobies (*Sula dactylatra*) from Fernando de Noronha Archipelago across sampled years. The values presented correspond to the Z score and the Bonferroni-adjusted *p*-value (P.adj). Analyses were performed for all individuals (all birds) and separately for females and males. Significant differences are marked in bold.

Years	All birds				Females				Males				
	δ^{13} C		δ^{15} N		δ^{13} C		δ^{15} N		δ^{13} C		δ^{15} N		
	Z	P.adj											
2017-2018	5.29	<0.01	-2.93	< 0.05	3.44	<0.01	-1.70	0.54	3.83	< 0.01	-1.24	1.00	
2017-2019	0.84	1.00	-5.00	< 0.01	0.29	1.00	-2.89	< 0.05	1.24	1.00	-3.82	< 0.01	
2017-2022	8.30	< 0.01	-5.56	< 0.01	4.78	< 0.01	-3.59	< 0.01	6.64	< 0.01	-4.98	< 0.01	
2018-2019	-3.10	< 0.01	-2.90	< 0.05	-2.81	< 0.05	-1.79	0.44	-1.39	0.98	-2.78	< 0.05	
2018-2022	3.73	<0.01	-3.06	=0.01	2.48	0.08	-2.63	=0.05	2.36	0.11	-3.29	=0.01	
2019-2022	5.74	<0.01	0.35	1.00	4.26	< 0.01	-0.78	1.00	3.15	=0.01	0.42	1.00	



Fig. 4. Sankey diagram representing proportions (%) of prey contribution estimated by stable isotopes mixing models (*Cheilopogon cyanopterus, Exocoetus volitans, Hirundichthys affinis, Oxyporhamphus micropterus, Harengula clupeola*, Hemiramphidae) for male and female of masked booby (*Sula dactylatra*) during breeding seasons (March–April) in the Fernando de Noronha Archipelago. The width of the connections represents the proportion of the prey's contribution to the diet in each year.

Table 3

Trip metrics (mean \pm standard deviation) of females and males of masked booby (*Sula dactylatra*) tracked in the Fernando de Noronha Archipelago during the breeding season by year and the number of trips for each sex and year. N_b: total number of birds tracked; N_t: total number of complete trips recorded; D_{tot}: total distance traveled (km); D_{max}: maximum distance from the colony (km); T_{dur}: trip duration (min); P_{div}: proportion of time diving (%); SI: straightness index.

	Females								Males							
	N _b	Nt	D _{tot}	D _{max}	T _{dur}	P _{div}	SI	N _b	Nt	D _{tot}	D _{max}	T _{dur}	P _{div}	SI		
2017	10	20	154.3 ± 78.9	$\begin{array}{c} 61.3 \pm \\ 31.1 \end{array}$	335.0 ± 239.2	0.015	$\begin{array}{c} 0.8 \pm \\ 0.1 \end{array}$	18	29	$\begin{array}{c} 163.7 \pm \\ 100.1 \end{array}$	$\begin{array}{c} 56.5 \pm \\ 35.4 \end{array}$	$\begin{array}{l} 437.4 \pm \\ 428.9 \end{array}$	0.016	$\begin{array}{c} \textbf{0.7} \pm \\ \textbf{0.2} \end{array}$		
2018	10	22	170.4 ± 119.5	$\begin{array}{c} 65.9 \pm \\ 51.6 \end{array}$	386.9 ± 332.5	0.014	$\begin{array}{c} 0.6 \pm \\ 0.2 \end{array}$	5	7	165.9 ± 75.7	$\begin{array}{c} 50.1 \pm \\ 25.0 \end{array}$	594.8 ± 693.2	0.020	$\begin{array}{c} 0.5 \pm \\ 0.1 \end{array}$		
2019	7	24	162.2 ± 95.6	$\begin{array}{c} 60.2 \pm \\ 49.5 \end{array}$	$\begin{array}{c} 512.6 \ \pm \\ 439.3 \end{array}$	0.010	0.7 ± 0.2	5	18	$\begin{array}{c} 198.0 \pm \\ 147.2 \end{array}$	$\begin{array}{c} 59.8 \pm \\ 39.9 \end{array}$	585.1 ± 723.1	0.013	$\begin{array}{c} 0.6 \pm \\ 0.2 \end{array}$		
2022	15	50	104.2 ± 46.8	$\begin{array}{c} \textbf{38.8} \pm \\ \textbf{18.4} \end{array}$	241.9 ± 121.4	0.013	$\begin{array}{c} 0.8 \pm \\ 0.1 \end{array}$	18	65	101.3 ± 50.2	$\begin{array}{c} \textbf{37.3} \pm \\ \textbf{19.4} \end{array}$	$\begin{array}{c} \textbf{242.4} \pm \\ \textbf{131.9} \end{array}$	0.015	$\begin{array}{c} \textbf{0.7} \pm \\ \textbf{0.1} \end{array}$		

The foraging areas of masked boobies were concentrated eastward of Meio Island in all years for both sexes (Fig. 6). For both males and females, the smallest overlaps (i.e., the highest dissimilarities) in foraging areas were observed between 2022 vs. 2019, followed by 2022 vs. 2018, considering the Bhattacharyya coefficient, and between 2022 and the remaining years when considering the RMSE (Fig. 7).

4. Discussion

This study revealed interannual stability in the location of foraging areas of masked boobies breeding at Fernando de Noronha. Nevertheless, we found interannual variation in their foraging strategies, especially in 2022 when the foraging areas were located nearer to the colony alongside an increase in the consumption of false herring(*H. clupeola* and a decrease of the four-winged flying fish *H. affinis*. This suggests that the prey availability and distribution around the colony can be one of the factors playing an important role in shaping the foraging strategies of masked boobies. Additionally, intersexual differences in foraging strategies were not substantial, with low spatial and isotopic niche segregation, even though females showed higher nitrogen values than males.

The interannual stability of foraging areas east of Fernando de Noronha can be linked with the spatial distribution of prey, which could be shaped by the oceanographic dynamics around the archipelago. While the Island Mass Effect in Fernando de Noronha enhances primary productivity westward (leeward), fish tend to concentrate eastward due to the flow of upwelling particles (Tchamabi et al., 2017; Salvetat et al., 2022). Thus, the Island Mass Effect should promote certain predictability of areas with abundant resources, providing familiar foraging sites, which are less risky than exploring new areas and contribute to saving time and energy during the breeding season (Wakefield et al., 2015; Regan et al., 2024). Masked boobies from Dog Island in the Caribbean, for example, forage more predictably than other booby species (Soanes et al., 2021), and the specific use of areas with increased productivity was observed in boobies in the central and eastern Pacific Ocean (Gilmour et al., 2018) and in the Caribbean Sea (Wilkinson et al., 2020). These findings suggest that local conditions that ensure stable food availability can reinforce foraging patterns and promote local adaptation and site fidelity.

Interannual variations in foraging strategies can be associated with the plastic behavior of boobies, which can reflect the changes in prey composition and distribution around the colony. Seabirds with flexible foraging behavior can adapt to shifts in prey availability (Montevecchi et al., 2009; Garthe et al., 2011). During the chick-rearing period they face higher time and distance constraints on their foraging trips due to nest attendance demand (Weimerskirch et al., 1997). In 2022, the isotopic values were significantly different and the isotopic niche of masked boobies did not overlap with those from previous years. This coincided with an increase in the proportion of H. clupeola in the diet and a consequent decrease in H. affinis importance. Additionally, the time spent foraging, and total and maximal distances of foraging trips, were significantly lower in 2022 compared with previous years, resulting in foraging areas concentrated nearer the colony. Moreover, the overlap between foraging areas observed in 2022 and the remaining years was the lowest. Such variations may indicate that prey patches were nearer the archipelago in 2022, favoring foraging with lower energy costs. This proximity of prey could be driven by changes in the ocean currents intensities that interact with the archipelago, which can influence oceanographic characteristics such as sea surface temperature, nutrient availability, and consequently zooplankton biomass (Campelo et al., 2019; Costa da Silva et al., 2021). Eventually, this can alter the



Fig. 5. Trip total distance traveled (D_{tot}, km), trip maximal distance from the colony (D_{max}, km), trip duration (T_{dur}, min), proportion of time diving (P_{div}, %) and straightness index (SI) of the foraging trips of masked boobies (*Sula dac-tylatra*) during the breeding seasons in the Fernando de Noronha Archipelago by year. *Significant differences between linked years; ***Significant differences between the year below and all the linked years.

prey distribution, considering that flying fish are associated with warm and low productivity waters, while *H. clupeola* has a wide tolerance to variations in temperature and salinity (Munroe et al., 2015; Michael et al., 2025). However, the spatial distribution of epipelagic fish schools, especially flying fish is very difficult to study (Churnside et al., 2017; Pierucci and Suaria, 2023), especially on small spatial and temporal scales, limiting other potential explanations related to oceanographic conditions. Alternatively, changes in the distribution of small pelagic fish could influence the foraging areas of pelagic predators, such as sharks and tunas, with which seabirds associate to catch their prev (Balance and Pitman, 1999; Miller et al., 2018). Thus, the observed inter-annual variation in foraging areas of masked boobies may reflect their pursuit of feeding areas of pelagic predators, reducing foraging costs during the chick-rearing period, as observed in the masked booby in Australia (Sommerfeld et al., 2015) and other booby species in Peru (Zavalaga et al., 2007, 2010). Therefore, the prey availability near the colony in 2022 could have triggered the switch to prey that could be captured during shorter trips, requiring less time and energy.

At Fernando de Noronha we found weak sexual segregation in isotopic niches and foraging areas as found for other masked booby populations elsewhere (Young et al., 2010; Kappes et al., 2011; Mancini et al., 2013; Oppel et al., 2015; Poli et al., 2017; Soanes et al., 2021). This may be associated with the high availability of food resources around the archipelago. Although located in the typically oligotrophic tropical ocean, the colony surroundings are influenced by oceanographic processes which increase local productivity (Campelo et al., 2019). This could contribute to reducing sexual competition, as observed in brown boobies (*Sula leucogaster*) in the São Pedro and São Paulo Archipelago (Nunes et al., 2018). Additionally, the surrounding waters provide abundant resources for large pelagic predators including ten other breeding seabird species (Mancini et al., 2016), and the yearround presence of masked boobies in the colony (Roy et al., 2021). Despite being weak, the significant difference in nitrogen values

between sexes may be related to factors not mutually exclusive, such as the larger body size and mass of females, allowing them to dive deeper and explore a greater variety of prey sizes and trophic levels, which may also be related to the wider isotopic niches compared to males in most years (Bearhop et al., 2006; Sommerfeld et al., 2013; Mancini et al., 2014). It could also be explained by the physiological peculiarities of females, considering specific demands of egg laying and chick-rearing during the breeding period (Castillo-Guerrero et al., 2016; Lerma et al., 2024). Additionally, such slight isotopic differences in the absence of segregation of foraging areas can also result from inherent methodological reasons, as stable isotopes from blood represent foraging over the previous four to six weeks (Hobson, 2005; Clark et al., 2021). Therefore, such findings suggest that a tropical archipelago with high food availability can contribute to reducing sexual competition, as predicted by fundamental theories of ecological niche and competitive exclusion (Hutchinson, 1957).

The use of complementary techniques such as stable isotope analysis and biologging provides a better picture of foraging strategies. However, the interpretations need caution, considering the inherent limitations of the methods and small sample sizes. Stable isotopes in marine environments are influenced by variations in baselines over time and space (Graham et al., 2010; Magozzi et al., 2017). In this sense, temporal variations in ocean circulation around the Fernando de Noronha Archipelago can influence oceanographic parameters such as temperature (Costa da Silva et al., 2021), and productivity, which could potentially influence isotopic baselines (Graham et al., 2010). Also, the use of similar prey (i.e., flying fish), which share similar feeding habits (Collette et al., 2019), and variable sample sizes in the mixing models may bias the proportion of contribution to diet between years. However, with the integration of tracking data, it was possible to observe interannual differences in bird movements similar to those observed in isotopic data, such as the differences observed in 2022 compared to previous years. Therefore, the complementarity of the techniques used was essential for confirming patterns and temporal variations in the foraging strategies of the birds, reducing potential misinterpretations of the results.

In the present study, we identified interannual stability in the foraging areas of a seabird in a tropical archipelago, which suggests the occurrence of regions with predictable prey availability. Meanwhile, the interannual approach was also key to identifying temporal variations in the extent of foraging areas and species consumed. This suggests that even strongly influenced by the Island Mass Effect, other environmental features less predictable (e.g. sea surface temperature, chlorophyll-a, water column stratification) should influence the surrounding resources (Poli et al., 2017; Gilmour et al., 2018). These findings reinforce the role of seabirds as important indicators of variations in the spatiotemporal distribution of the pelagic fish community composition around colonies, as they respond to such variations through trophic plasticity. Local conditions around colonies are known to influence genetic structure in seabirds through differentiation by local adaptation (Nunes and Bugoni, 2018; Muraro et al., 2024). Thus, physical-chemical alterations in the ocean promoted by climate changes could influence prey distribution and composition, leading to potential variations in the observed foraging strategies of seabirds (Regan et al., 2024). In current and future scenarios associated with the impacts of climate change in tropical oceans (Cooley et al., 2022), using organisms that predominantly depend on a specific resource as samplers of a known marine region can provide rapid insights into the consequences of environmental modification through interannual sampling.

CRediT authorship contribution statement

Júlia Jacoby: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Amédée Roy:** Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data



Fig. 6. Foraging distributions obtained by Kernel Density Estimation using 25 %, 50 %, 75 %, and 90 % contours of the kernel utilization distribution based on observed and predicted dives of males (M; blue) and females (F; orange) of masked booby (*Sula dactylatra*) during breeding seasons at the Fernando de Noronha Archipelago in 2017, 2018, 2019 and 2022. n = number of foraging trips. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Fig. 7. Interannual pairwise overlaps in foraging areas of masked boobies (*Sula dactylatra*) around Fernando de Noronha Archipelago based on the Bhattacharyya coefficient (left), which quantifies the overlap of foraging areas, ranging from 0 (no similarity) to 1 (complete overlap), and the Root Mean Squared Error (RMSE, right), measures differences in the intensity of spatial distributions (0 = no differences). Darker shades represent higher similarity, while lighter shades indicate lower similarity. Males are represented above the diagonal (bluish tones), while females are below the diagonal (orange tones). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

curation. **Sophie Lanco:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition. **Christophe Barbraud:** Writing – review & editing, Investigation. **Karine Delord:** Writing – review & editing, Investigation. **Leandro Bugoni:** Writing – review & editing, Resources, Project administration, Funding acquisition. **Guilherme T. Nunes:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used *ChatGPT* (hsttps://chatgpt.com) and *Deepl* Translator (https://www.deepl.com) to improve the readability and language. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2025.152099.

Data availability

All data and the R script from stable isotope analysis and trip metrics models are publicly available through the GitHub repository: https://github.com/SeabirdEcologyUFRGS/SIA_FdN. Pre-trained models and Python code are available at https://github. com/AmedeeRoy/BirdDL.

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