



# Movement and diet of brown boobies in a remote protected area suggest temporal variations in foraging strategies

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## Abstract

Understanding tropical seabird foraging strategies is essential for evaluating ecosystem functioning within Very Large Marine Protected Areas (VLMAs). We investigated spatial and trophic behavior of brown booby (*Sula leucogaster*) at the Saint Peter and Saint Paul Archipelago (SPSP), a remote breeding site within a VMA in the equatorial Atlantic Ocean. Using GPS tracking from 207 individuals (706 trips, 2014–2015 and 2023–2024), stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) from 58 blood samples, and 49 regurgitated samples, we assessed variation in foraging effort and diet across sex, breeding stage, and temporal scales. Despite pronounced reversed sexual size dimorphism, no intersexual differences were detected in movement parameters. However, females exhibited significantly higher  $\delta^{15}\text{N}$  values, indicating subtle trophic segregation. Breeding stage showed minimal influence, suggesting that extreme nest density and continuous territorial defense override intrinsic reproductive demands. Pronounced interannual variation in foraging effort was detected, with 2023 showing nearly double the ranges compared to 2015. Seasonally, trip metrics did not differ, but time allocation shifted between austral winter and summer: traveling decreased (48.1% to 29.7%) while searching increased (40.3% to 58.4%), coinciding with dietary shifts from flying fish to margined flying fish (*Cheilopogon cyanopterus*) spawning. Daily foraging directions were highly variable, reflecting opportunistic responses to ephemeral prey distributions. The interannual increase in foraging effort coincided with recovery of large pelagic predators, though oceanographic mechanisms cannot be excluded. These findings demonstrate that colonial constraints override sexual dimorphism while positioning brown boobies as ecological indicator for adaptive management of remote VLMAs.

**Keywords** Biologging · Central-place foraging · Marine protected areas · Tropical seabirds · Sexual size dimorphism · Stable isotopes, Sulidae

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## Introduction

Seabird colonial central-place foragers provide unique opportunities to study behavioral responses to environmental variability across multiple temporal scales, from daily fluctuations in prey availability to decadal shifts in predator communities (Piatt et al. 2007; Grémillet and Boulinier 2009). Their repeated departures from fixed breeding sites allow direct comparison of foraging strategies across time while serving as integrative samplers of marine food web dynamics (Piatt et al. 2007). Long-term studies spanning multiple years are essential to disentangle these nested temporal effects, as short-term observations may miss critical ecosystem transitions that occur over longer time scales (Grémillet and Boulinier 2009). In remote oceanic environments where direct ecosystem monitoring is logistically

challenging, seabird foraging behavior becomes particularly valuable as a cost-effective proxy for detecting the effect of environmental changes on prey availability and identifying biologically important areas within large marine protected areas (Piatt et al. 2007; Trevail et al. 2024).

Foraging strategies within seabird populations are typically shaped by intrinsic factors such as sex, breeding stage, and individual experience, which influence energy requirements, physical capabilities, and risk tolerance (Lewis et al. 2005; Poli et al. 2017; Trevail et al. 2024). In particular, sexual size dimorphism (SSD) is widespread among seabirds and is commonly associated with spatial or trophic segregation during breeding, as morphological differences create distinct predictions for foraging niche partitioning (Phillips et al. 2011; Almeida et al. 2021). In the Sulidae (boobies and gannets), SSD follows a reversed pattern, with females being larger than males (Weimerskirch et al. 2006, 2009a, b). This reversed dimorphism has been documented to facilitate sexual segregation in several booby species: females and males exhibit different foraging ranges (Pontón-Cevallos et al. 2017; Miller et al. 2018a; Almeida et al. 2021), diving depths (Lewis et al. 2005; Zavalaga et al. 2007), temporal patterns of activity (Miller et al. 2018a), or prey preferences (Phillips et al. 2011; Mancini et al. 2023). Such segregation may arise through competitive exclusion, with larger females accessing superior foraging areas or prey types, or through differential energetic requirements and risk tolerance between sexes (Weimerskirch et al. 2006; Phillips et al. 2011).

However, the expression of sexual segregation and other individual differences can be strongly modulated by ecological constraints operating at the colony level (Weimerskirch et al. 2009b; Paiva et al. 2017; Reyes-González et al. 2021). When colonies face intense competition for limited nesting sites or when prey resources are highly concentrated near breeding areas, spatial or trophic partitioning between sexes may be suppressed despite pronounced morphological dimorphism (Weimerskirch et al. 2006, 2009b; Castillo-Guerrero and Mellink 2011). Studies comparing brown booby (*Sula leucogaster*) populations across different environmental contexts have revealed considerable flexibility in the expression of sexual segregation (Lewis et al. 2005; Castillo-Guerrero et al. 2016; Miller et al. 2018a), suggesting that local ecological conditions, particularly prey distribution patterns, and colonial density play a decisive role in shaping sex-specific foraging strategies.

In oligotrophic tropical oceanic waters, where prey communities are less diverse and more ephemerally distributed compared to coastal habitats, sexual segregation in foraging areas are particularly constrained (Paiva et al. 2017).

Similarly, the typical variation in foraging effort across breeding stages, with frequently longer trips during incubation and shorter trips during chick-rearing (Mendez et al. 2016; Almeida et al. 2021), may be constrained by the need for continuous nest defense in high-density colonies where territorial competition is intense (Castillo-Guerrero et al. 2016).

Disentangling these multiple interacting factors requires integrated methodological approaches that combine movement ecology with trophic analysis across complementary temporal scales (Austin et al. 2021). GPS tracking reveals fine-scale spatial patterns and foraging effort, while stable isotope analysis integrates diet information over weeks to months, and direct dietary sampling captures immediate prey ingestion (Bearhop et al. 2002; Miller et al. 2018b). This multi-method approach is particularly powerful for detecting environmental responses, as diet and movement can respond differently to the same environmental shift, providing complementary and non-redundant information on foraging ecology (Miller et al. 2018a; Austin et al. 2021). Combined datasets allow robust hypothesis testing about both intrinsic drivers (sex, breeding stage) and extrinsic (seasonal variation, interannual change) shaping foraging behavior (Pontón-Cevallos et al. 2017; Almeida et al. 2021).

Such integrated approaches are particularly valuable in remote oceanic systems like the Saint Peter and Saint Paul Archipelago (SPSP), a small equatorial Atlantic archipelago influenced by current systems that generate enhanced local nutrient retention (Viana et al. 2009; Melo et al. 2012). SPSP represents a unique natural laboratory for studying seabird responses to environmental change under conditions of extreme colonial constraint. The archipelago supports a genetically distinct population of approximately 500 brown boobies. This species is diurnal, typically leaving the colony at dawn to forage offshore over long distances, and feeds primarily on small pelagic fish and squid by plunge-diving (Weimerskirch et al. 2009a). In SPSP, brown boobies breed year-round within a restricted nesting area of 200 m<sup>2</sup> (Nunes and Bugoni 2018), one of the most density-constrained colonial environments documented for tropical seabirds. Likewise, birds from SPSP display pronounced reversed sexual size dimorphism, with females being 5.2% larger in wing length and 21.9% heavier than males (Nunes et al. 2017), yet a previous study found no spatial segregation between sexes, attributing this behavioral convergence to intense competition for limited nesting sites combined with concentrated prey resources near the colony (Nunes et al. 2018). Whether this pattern persists under varying environmental conditions remains untested.

Importantly, SPSP has experienced significant environmental changes over the past decade, including the recovery of large pelagic predators such as silky sharks (*Carcharhinus falciformis*) and Galapagos sharks (*C. galapagensis*) following fishing restrictions (Queiroz et al. 2021), and concurrent fishing pressure on flying fish populations that may have reduced prey availability near the colony (G.T. Nunes, pers. obs.). Pronounced seasonal variation in prey availability is also driven by the spawning cycles of margined flying fish (*Cheilopogon cyanopterus*) during austral summer months (Lessa et al. 1999). As diurnal plunge-divers targeting epipelagic prey such as flying fish and squid, a key taxon for energy transfer to top predators in the region (Mancini and Bugoni 2014), boobies exploit a facilitating foraging strategy whereby the recovering subsurface predators (e.g., sharks, tunas, dolphinfish) drive prey schools toward surface waters, making them accessible to surface-foraging seabirds (Ashmole and Ashmole 1967; Au and Pitman 1986; Miller et al. 2018b). This dependence on predator-facilitated foraging suggests potential links between decade-long changes in pelagic predator abundance and seabird foraging success (Heithaus et al. 2008; Grémillet and Boulinier 2009), as studies in sulids demonstrate that foraging associations with subsurface predators drive movement patterns and increase prey capture success (Tremblay et al. 2014; Cansse et al. 2020). Multiple mechanisms could explain how predator recovery affects booby foraging: intensified competition for prey resources, spatial redistribution of prey patches, or altered prey behavior and accessibility (Heithaus et al. 2008; Miller et al. 2018a; Afonso et al. 2022), with opposing predictions for booby foraging effort depending on which mechanism dominates.

Since 2018, SPSP has been encompassed by two Very Large Marine Protected Areas (VLMPAs): the Environmental Protection Area (APA, in Portuguese), which allows sustainable resource use including fishing, and the Natural Monument (MONA), with stricter protection (Francini-Filho et al. 2018). Despite their extensive coverage, both areas face significant governance challenges, including spatial mismatches between protection boundaries and key biological features, e.g. the 200 m<sup>2</sup> breeding area of the brown booby colony falls outside MONA limits (Neves et al. 2015; Mancini et al. 2016), and documented increases in fishing activity following designation (Devillers et al. 2015; Magris 2021). In this context, seabird biologging and dietary data can play a critical role in adaptive management by providing cost-effective, continuous insights into ecosystem dynamics across vast oceanic areas where direct monitoring is logistically and economically prohibitive.

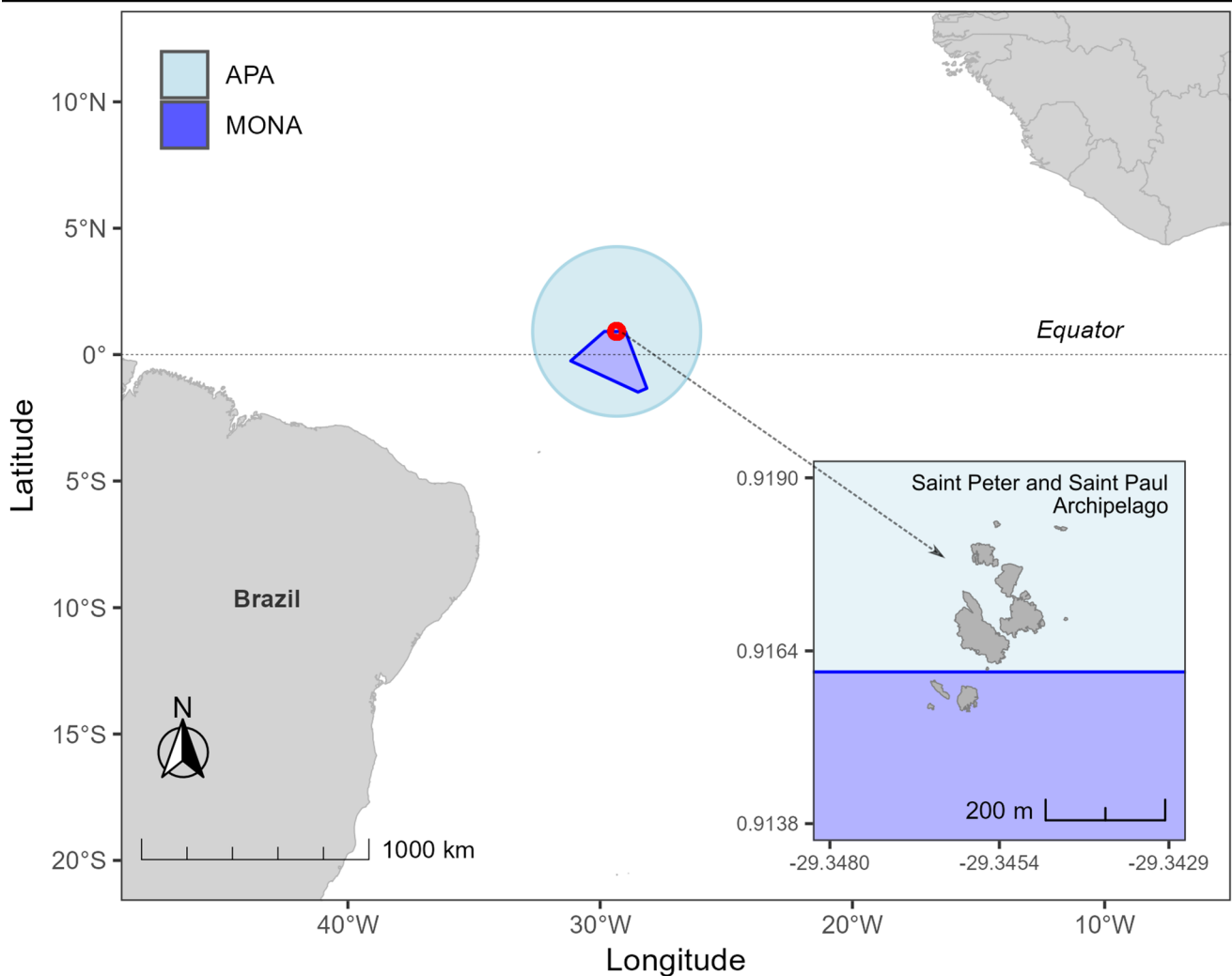
Given this context of extreme colonial constraints, recent environmental changes, and conservation management needs, we conducted a multi-year study (2014–2015 and 2023–2024) combining GPS tracking, stable isotope analysis, and dietary assessment to examine spatiotemporal variation in brown booby foraging strategies at SPSP. We tested specific hypotheses about how seabirds respond to shifting environmental conditions under extreme colonial constraints: H1: foraging effort would change over the study period in response to alterations in pelagic predator abundance following fishing restrictions. Two opposing mechanisms could operate: (a) increased competition for prey resources as predator populations recover, requiring longer foraging trips, or (b) enhanced prey aggregation through predator facilitation, potentially reducing foraging effort. H2: reduced foraging effort during austral summer, when margined flying fish spawning increases prey accessibility near the colony, compared to austral winter when alternative prey dominates, manifested as shorter trip durations, reduced distances, and elevated trophic positions reflecting increased consumption of flying fish. H3: high daily variability in foraging directions, reflecting the ephemeral nature of predator-facilitated prey aggregations and the movements of mobile pelagic predators. H4: given the extreme colonial constraints at SPSP, we predicted persistence of behavioral convergence between sexes despite pronounced reversed sexual dimorphism, contrasting with patterns observed in less constrained populations. Similarly, we predicted minimal differences across breeding stages due to continuous nest defense requirements overriding typical parental role division.

By examining these nested temporal scales and integrating multiple data sources, this study provides insights into how colonial seabirds balance intrinsic life-history constraints with dynamic environmental conditions, while demonstrating the value of multi-year monitoring for adaptive management of large-scale marine protected areas.

## Materials and methods

### Study area

Data were collected in the Saint Peter and Saint Paul Archipelago (SPSP; 0°55'10" N, 29°20'33" W), located approximately 1,000 km off the northeastern coast of Brazil in oceanic waters reaching depths of around 4,000 m (Fig. 1). The archipelago encompasses a total terrestrial area of 17,500 m<sup>2</sup>, with its highest elevation at 18 m above sea level (Vaske et al. 2006). SPSP consists of ten islands or rocks



**Fig. 1** Saint Peter and Saint Paul Archipelago. Background colors Very Large Marine Protected Areas: APA (Environmental Protection Area) in light blue and MONA (Natural Monument) in blue

and is influenced by the South Equatorial and Subsurface Equatorial Currents, which generate a vortex system that enhances local nutrient retention (Araujo and Cintra 2009). This oceanographic configuration sustains elevated local productivity and a rich assemblage of epipelagic predators, providing the foraging context for the brown booby colony studied here (Melo et al. 2012; Nunes et al. 2018).

### Fieldwork and sampling

Fieldwork occurred in four campaigns: May and June 2014, July 2015, August 2023, and February 2024 in the largest Belmonte Island. Only birds in the nest were captured, and the nest content were categorized as “empty” (adults defending nest areas without eggs), “egg”, or classified according

to chick age: N1 (0–2 weeks), N2 (3–6 weeks), N3 (7–14 weeks), and N4 (>15 weeks). Only breeding adults were captured and non-breeding prospectors and immature birds were excluded from the dataset.

Birds were captured manually or with hand nets, and each individual was equipped with a GPS logger: Gipsy models in 2014 ( $n=19$ ) and 2015 ( $n=97$ ), Axy-Trek Marine in 2023 ( $n=52$ ) and 2023 ( $n=52$ ) (Technosmart, Italy), and Igot-U 120 in 2024 ( $n=39$ ) (Mobile Action, Taiwan). Devices were attached to the four central rectrices using Tesa® 4651 adhesive tape. The total mass of the device, including attachment material, was approximately 25 g. This represents a maximum of 2.3% of the body mass for the lightest individuals sampled (minimum 1105 g), remaining well below the standard 3% benchmark (Phillips et al. 2003). Gipsy loggers

in 2014 and 2015 recorded at 1 and 5 s intervals, respectively; Axy-Trek Marine loggers in 2023 and 2024 recorded at 30 s intervals; Igot-U 120 loggers 2023 recorded at 30 s intervals. Tagged individuals were marked with metal bands from CEMAVE (*Centro Nacional de Pesquisa e Conservação de Aves Silvestres*) and released at the nest site. After two to six days, birds were recaptured for device retrieval.

During the recapture of tracked birds in 2023 and 2024, blood samples (0.3 mL) were collected from the metatarsal vein using sterile syringes and stored in microtubes and frozen at  $-20^{\circ}\text{C}$  for stable isotope analysis. Additionally, prey items were obtained from regurgitates collected opportunistically during bird handling in both occasions (capture and recapture). Regurgitated samples were stored in plastic bags and frozen at  $-20^{\circ}\text{C}$ .

### Tracking analysis

Tracking data was processed with a series of filters to remove erroneous locations. A speed-based filtering method was applied to remove erroneous GPS locations using speed filter (McConnell et al. 1992) implemented in the *trip* package in R (Sumner et al. 2009; Sumner 2011). A maximum speed threshold of 80 km/h was established, similar to that used in Mendez et al. (2016) and Poli et al. (2017).

To identify complete foraging trips, a 2 km colony buffer was established around SPSP ( $0^{\circ}55'\text{N}$ ,  $29^{\circ}21'\text{W}$ ) using the *tripSplit()* function from the *track2KBA* package (Beal et al. 2021). Trips were then defined as movements that departed from and returned to this buffer. Additionally, trips shorter than 15 min or with fewer than 5 GPS locations were excluded, as they were unlikely to represent foraging behavior or provide sufficient data for analysis. To standardize the temporal resolution of tracking data, a linear regularization was applied to all trips using the *redistraj()* function from the *adehabitatLT* package (Calenge 2006; Calenge et al. 2023), standardizing them to a 30 s interval. For complete trips, basic foraging metrics were calculated per trip, including total distance traveled (D), maximum distance from the colony (Dmax), trip duration (T), and sinuosity (calculated as  $D^2/D_{\text{max}}^{-1}$ ). Sinuosity serves as an indicator of path tortuosity, with higher values indicating more tortuous, potentially foraging-intensive movement, and values closer to 1 indicating more direct flight paths.

To assess differences in foraging metrics between sexes and seasons, we fitted generalized linear mixed models (GLMMs). For total distance traveled, maximum distance from colony, and trip duration, we used gamma distribution with log-link function to accommodate continuous positive

data with right skewness. Sinuosity was modeled using Gaussian distribution with identity link. For each foraging metric (total distance traveled, maximum distance from colony, trip duration, and sinuosity) we included bird identity as random effect to account for pseudo-replication arising from repeated measurements from the same individual. Models were constructed using the *glmmTMB* package in R (Brooks et al. 2017). Model fit was evaluated using the *DHARMA* package (Hartig 2022), which generates scaled residuals through simulation-based methods ( $n=1,000$  simulations). For each model, we inspected quantile-quantile plots and residual-versus-fitted plots and applied formal tests for overdispersion and zero-inflation. Dispersion tests were non-significant for all models ( $p>0.90$ ), and residual-versus-fitted plots showed no systematic patterns, indicating adequate model fit. Kolmogorov-Smirnov tests indicated significant deviations from uniformity in all models; however, this is expected with large sample sizes where the test detects trivially small deviations that do not affect inferential validity (Hartig 2022).

For intersexual comparisons, we used the full dataset with sex as a fixed effect and bird identity as a random effect. This analysis tests whether males and females differ in foraging behavior across the entire study period. Given the unbalanced sampling design in our full dataset for season (winter: trips across three years, i.e., 2014, 2015, 2023; summer: trips from 2024), we conducted a restricted analysis comparing only consecutive years (austral winter 2023 and austral summer 2024). To account for multiple testing across four response variables (trip duration, total distance, maximum distance, and sinuosity), we applied False Discovery Rate (FDR) correction using the Benjamini-Hochberg method (Benjamini and Hochberg 1995). This approach controls the expected proportion of false discoveries among all significant results while maintaining greater statistical power than family-wise error rate corrections such as Bonferroni. FDR correction was applied separately for sex comparisons and seasonal comparisons. All reported  $p$ -values are FDR-corrected unless otherwise stated.

To classify behavioral states during foraging trips, step length and turning angle were calculated from the regularized GPS data. These variables were computed using the *prepData()* function from the *moveHMM* package (Michelot et al. 2016) in R. Hidden Markov Models (HMMs) were then fitted to these variables using the *fitHMM()* function, assuming a gamma distribution for step length and a Von Mises distribution for turning angle. Models with two and three states were tested, and the best-fitting model was selected based on the lowest Akaike Information Criterion

(AIC) value and residual distribution diagnostics. The state with the lowest step length and the highest variation in turning angle was classified as the foraging behavior. To assess whether time allocation across behavioral states differed between sexes and seasons, we calculated the proportion of GPS locations assigned to each HMM state per trip. Finally, time allocation proportions were compared using GLMMs with Gaussian distribution, sex or season as fixed effect, and bird ID as random effect, similar to foraging metrics comparisons.

Population-level foraging areas were estimated using kernel density estimation. We first selected GPS locations identified as “foraging” behavioral states by Hidden Markov Models. Kernel densities were computed using the `akde()` function from the *ctmm* package (Calabrese et al. 2016; Fleming and Calabrese 2023), which accounts for autocorrelation inherent in tracking data. We calculated 95% utilization distributions (UD), representing total foraging areas, and 50% UD, representing core foraging areas, for each sampling period (austral winter 2014, 2015, 2023; austral summer 2024) and for each sex.

Spatial overlap between foraging areas by sex (within each sampling period) and season (austral winter 2023 vs. austral summer 2024) was calculated using the geometric intersection of 95% kernel density polygons. Overlap area was estimated as the geometric intersection of polygons, and overlap percentage was computed using the Udovitch index:  $2 \times (\text{overlap area}) / (\text{area}_1 + \text{area}_2)$ . This index ranges from 0% (no overlap) to 100% (complete overlap) and provides a conservative symmetrical measure that accounts for differences in area size (Fieberg and Kochanny 2005).

To assess temporal variation in foraging locations, we calculated daily centroids of foraging activity for each sampling period. For each day with GPS data, daily centroids were calculated as the mean latitude and longitude (X and Y coordinates) of all locations classified as “foraging” by HMMs. To ensure adequate representation and minimize bias from individual variation, we included only days with foraging records from at least three different individuals. Centroids were ordered chronologically within each sampling year and connected sequentially to visualize temporal progression and directional shifts in population-level foraging areas. Individual plots were generated for each year with optimized spatial scales to better display year-specific patterns.

All statistical analyses were conducted in R version 4.5.2 (R Core Team 2024) within the RStudio environment. In addition to packages mentioned above, we used: *tidyverse* (Wickham et al. 2019) for data manipulation, *ggplot2* (Wickham 2016) for visualization, and *sf* (Pebesma 2018) for spatial operations.

## Stable isotope analysis

Blood samples were lyophilized, homogenized, and ground to a fine powder. Lipid extraction was not performed, given the typically low lipid content in avian whole blood (Bearhop et al. 2002). Subsamples of approximately 0.7 mg were encapsulated in tin capsules for carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope analysis (SIA). Analyses were conducted using an isotope ratio mass spectrometer EA Flash 2000 Delta V Advantage coupled to an TC/EA, ThermoFisher Scientific™ (Bremen, Germany) at the *Centro Integrado de Análises* of the *Universidade Federal do Rio Grande* (CIA-FURG, Brazil). Stable isotope ratios were determined by Eq. 1 (Bond and Hobson 2012):

$$\delta X (\text{‰}) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \quad (1)$$

where R represents the ratio  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  of the sample and the analytical standard, and X is  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . Isotopic values are expressed in delta ( $\delta$ ) notation as parts per thousand (‰), as in Bond and Hobson (2012), relative to international standards: Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$  and atmospheric  $\text{N}_2$  for  $\delta^{15}\text{N}$ . Analytical precision was assessed by repeated measurements of internal standards (glutamic acid, acetanilide and caffeine), which results in an accuracy of  $\pm 0.13\text{‰}$  for  $\delta^{13}\text{C}$  and  $\pm 0.08\text{‰}$  for  $\delta^{15}\text{N}$ .

Univariate differences on isotopic values between years and between sexes within years were evaluated using the Mann-Whitney *U* test. Isotopic niche widths of males and females per year were estimated using a Bayesian framework that computes Bayesian Standard Ellipse Areas corrected for small sample size (SEAc), implemented in the *SIBER* package (Jackson et al. 2011). The isotopic niche overlap areas between years and between sexes within years were estimated using `maxLikOverlap()` (Jackson and Parnell 2023) and the overall proportion of shared niche space were calculated using Eq. 2:

$$\text{Overlap area proportion} = \left( \frac{\text{overlapped area}}{\text{ellipse area female} + \text{ellipse area males} - \text{overlapped area}} \right) * 100 \quad (2)$$

where values vary from 0% (no overlap) to 100% (complete overlap).

### Regurgitate analysis

Prey items were identified to the lowest taxonomic level and measured for total length, furcal length, caudal peduncle height, and distance between anal and caudal fins. Prey body mass was estimated using a Bayesian approach based on body shape and size relationships (Froese et al. 2013). Dietary composition was assessed by calculating the frequency of occurrence (%FO), defined as the proportion of samples in which a given prey item was present, and the numerical percentage (%N), representing the number of individuals of each prey type relative to the total prey count. To evaluate the dietary importance of each prey type in each season, the Prey-Specific Index of Relative Importance (%PSIRI) was calculated following Brown et al. (2012). The %PSIRI was computed using the Eq. (3):

$$\%PSIRI_i = \frac{\%FO_i * (\%PN_i + \%PM_i)}{2} \quad (3)$$

where PSIRI% = Prey-Specific Index of Relative Importance of food item *i*, FO% = frequency of occurrence of prey *i* in the samples, PN% = prey-specific numerical contribution of prey *i*; PM% = prey-specific contribution in reconstituted mass of prey *i*. Analyses were conducted both at the

species and family levels. Analysis of intersexual variation could not be performed due to the limited number of regurgitation samples obtained for each sex.

## Results

### Biologging data

A total of 706 foraging trips from 207 individual brown boobies were analyzed across four sampling periods: austral winter 2014 (27 trips from 19 individuals), austral winter 2015 (187 trips from 97 individuals), austral winter 2023 (252 trips from 52 individuals), and austral summer 2024 (240 trips from 39 individuals) (Table 1).

Regarding the metrics of foraging behavior, brown boobies at SPSP exhibited relatively short foraging trips with mean duration of  $1.5 \pm 1.1$  h, total distance of  $35 \pm 22.2$  km, and maximum distance from colony of  $13 \pm 7.9$  km. Sinuosity averaged  $1.36 \pm 0.36$  (Table 1). Likewise, the three-state HMM model (AIC = −55,040) substantially outperformed the two-state model (AIC = −19,054), with states classified as traveling (high speed, directed movement), area-restricted searching (intermediate speed and turning angles), and active foraging (low speed, tortuous paths). Birds allocated approximately 36.3% of foraging time to traveling, 51.4% to searching, and 12.3% to active foraging.

**Table 1** Sample sizes (A), general foraging patterns (B) and behavioral classification (C) of brown boobies (*Sula leucogaster*) in the Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean

| A) Sample sizes ( <i>n</i> ) by sampling period       |        |                      |                |                         |                       |                     |
|-------------------------------------------------------|--------|----------------------|----------------|-------------------------|-----------------------|---------------------|
| Year                                                  | Season | <i>n</i> individuals | <i>n</i> trips | <i>n</i> blood samples  | <i>n</i> regurgitates | Breeding stages     |
| 2014                                                  | Winter | 19                   | 27             | -                       | -                     | -                   |
| 2015                                                  | Winter | 97                   | 187            | -                       | -                     | E:28, I:57, N1–4:75 |
| 2023                                                  | Winter | 52                   | 252            | 19                      | 40                    | E:0, I:48, N1–4:192 |
| 2024                                                  | Summer | 39                   | 240            | 39                      | 9                     | E:0, I:67, N1–4:163 |
| Total                                                 |        | 207                  | 706            | 58                      | 49                    |                     |
| B) General foraging trip metrics (all trips combined) |        |                      |                |                         |                       |                     |
| Metric                                                |        | Mean ± SD            |                | Range                   |                       | Median (IQR)        |
| Total distance (km)                                   |        | 35.0 ± 22.2          |                | 4.4–128.5               |                       | 28.9                |
| Maximum distance (km)                                 |        | 13.0 ± 7.9           |                | 2.5–48.0                |                       | 16.7                |
| Trip duration (h)                                     |        | 1.5 ± 1.1            |                | 0.3–9.3                 |                       | 1.2                 |
| Sinuosity                                             |        | 1.4 ± 0.4            |                | 0.8–3.3                 |                       | 1.3                 |
| State parameters (3-state model)                      |        |                      |                |                         |                       |                     |
| Behavioral state                                      |        | Step length (m/s)    |                | Angular variance (rad.) |                       | Time allocation (%) |
| Travelling                                            |        | 11.4 ± 2.6           |                | 0.16 ± 0.15             |                       | 31.5                |
| Searching                                             |        | 4.4 ± 2.66           |                | 1.00 ± 0.88             |                       | 52.0                |
| Foraging                                              |        | 0.52 ± 0.32          |                | 0.52 ± 0.88             |                       | 16.5                |
| C) Hidden Markov Model selection and state parameters |        |                      |                |                         |                       |                     |
| Model                                                 | States | AIC                  |                | ΔAIC                    |                       | Selected            |
| HMM-2                                                 | 2      | −19,054              |                | 36,014                  |                       | No                  |
| HMM-3                                                 | 3      | −55,040              |                | 0                       |                       | Yes                 |

E=Empty nest, I=Incubating egg, N1–4=Chick age classes (see Methods)

**Table 2** Foraging trip metrics (D=total distance traveled, Dmax=maximum distance from the colony, T=trip duration in hours, Sin=sinuosity) (mean±SD) of brown boobies (*Sula leucogaster*) by sex (A), season and year (B) in the Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean

| A) By sex      |       |          |           |           |           |         |
|----------------|-------|----------|-----------|-----------|-----------|---------|
|                | Year  | <i>n</i> | D (km)    | Dmax (km) | Sin       | T (h)   |
| Female         | 2015  | 95       | 23±10     | 8.8±3.8   | 1.32±0.2  | 1±0.9   |
|                | 2023  | 133      | 46±24.6   | 18.5±8.8  | 1.22±0.2  | 1.8±1.1 |
|                | 2024  | 144      | 34±22.9   | 10.9±6    | 1.5±0.5   | 1.5±1.2 |
|                | Total | 372      | 33.4±22.4 | 12±7.2    | 1.38±0.4  | 1.4±1.1 |
| Male           | 2015  | 65       | 23.8±10.5 | 8.7±3.8   | 1.39±0.3  | 1.2±1.3 |
|                | 2023  | 107      | 45.8±22.6 | 18.6±8.5  | 1.23±0.19 | 1.7±0.9 |
|                | 2024  | 86       | 32±20.8   | 10.7±5.7  | 1.46±0.4  | 1.5±1.1 |
|                | Total | 258      | 33.9±21.8 | 12.4±7.7  | 1.37±0.3  | 1.5±1.1 |
| B) By season   |       |          |           |           |           |         |
|                | Year  | <i>n</i> | D (km)    | Dmax (km) | Sin       | T (h)   |
| Austral winter | 2014  | 27       | 23.6±13.8 | 8.8±5.6   | 1.39±0.3  | 0.9±0.4 |
|                | 2015  | 187      | 23.2±10.6 | 8.8±3.9   | 1.34±0.3  | 1.1±1   |
|                | 2023  | 252      | 46.4±23.7 | 18.8±8.7  | 1.22±0.2  | 1.7±1   |
| Austral summer | 2024  | 240      | 33.9±22.6 | 10.9±5.9  | 1.51±0.5  | 1.5±1.1 |

Blood samples were not collected during 2014, so we did not determinate sex for this year

Locations classified as active foraging were used for subsequent spatial analyses using autocorrelation kernel density estimation.

Regarding sexes, females ( $n=372$  trips) and males ( $n=258$  trips) showed nearly identical values in total distance ( $33.4\pm22.4$  vs.  $33.9\pm21.8$  km), maximum distance from the colony ( $12.0\pm7.2$  vs.  $12.4\pm7.7$  km), trip duration ( $1.4\pm1.1$  vs.  $1.5\pm1.1$  h), and sinuosity ( $1.38\pm0.4$  vs.  $1.37\pm0.3$ ). Both sexes tracked the same interannual variation in foraging effort, with shorter trips in 2015, longer trips in 2023, and intermediate values in 2024 (Table 2; Fig. 2). No significant differences between sexes were detected for any metric (GLMM, all  $p$ -values FDR>0.05) (Table 3). Consistent with this behavioral similarity, foraging area sizes were also similar between sexes (males:  $522.1\pm204.9$  km<sup>2</sup>; females:  $694.4\pm855.2$  km<sup>2</sup>). Spatial overlap between sexes was high, with Udovitch indices ranging from 55.1% to 82.2% across years (mean:  $69.4\pm13.6\%$ ) (Table 4, Fig. S1). Similarly, time allocation across behavioral states did not differ significantly between sexes (Table S3, Fig. 3). Males and females allocated similar proportions of foraging time to traveling, active foraging, and area-restricted searching. All  $p$ -values remained non-significant after FDR correction (Table 4).

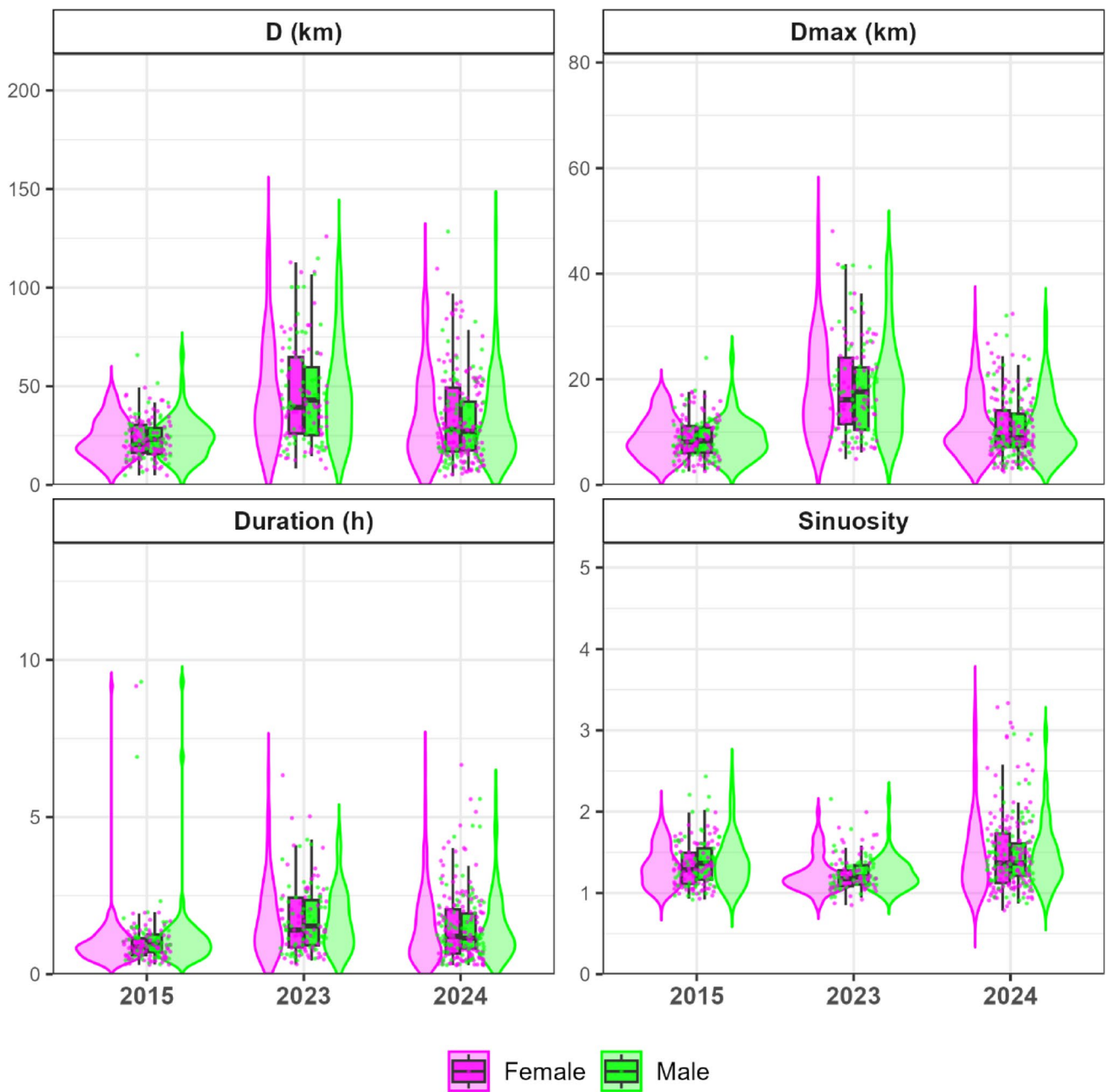
Regarding seasonal and interannual variation, foraging behavior was substantially different (Table 4). Among winter periods, total distance traveled was longest in 2023 ( $46.4\pm23.7$  km) compared to 2015 ( $23.2\pm10.6$  km) and 2014 ( $23.6\pm13.8$  km). Similarly, maximum distance from the colony was greatest in winter 2023 ( $18.8\pm8.7$  km) compared to winter 2015 ( $8.8\pm3.9$  km) and winter 2014 ( $8.8\pm5.6$  km). Trip duration also showed an increasing pattern from 2014 ( $0.9\pm0.4$  h) and 2015 ( $1.1\pm1.0$  h) to 2023

( $1.7\pm1.0$  h). In contrast, seasonal comparison between winter 2023 and summer 2024 revealed no significant differences in any foraging trip metric. Total distance (summer:  $33.9\pm22.6$  km), maximum distance (summer:  $10.9\pm5.9$  km), trip duration (summer:  $1.5\pm1.1$  h), and sinuosity (winter:  $1.22\pm0.2$ ; summer:  $1.51\pm0.5$ ) did not differ significantly between seasons (GLMM  $p>0.05$  for all metrics after FDR correction, Table 3).

Otherwise, time spent in different behavioral states differed significantly between seasons (Table S3, Fig. 3). In austral summer 2024, birds allocated significantly less time to traveling (GLMM:  $\beta = -0.19\pm0.02$ ,  $z = -11.70$ ,  $p<0.001$ ) and significantly more time to area-restricted searching ( $\beta=0.004\pm0.02$ ,  $z=+11.85$ ,  $p<0.001$ ) compared to winter 2023. Time allocated to active foraging did not differ significantly between seasons ( $\beta=0.18\pm0.01$ ,  $z=0.43$ ,  $p=0.667$ ). All significant  $p$ -values remained after FDR correction (Table 3).

Kernel density areas varied over years, reflecting the differences in foraging distances (Table 4; Fig. 4). The 95% utilization distribution increased from 453.3 km<sup>2</sup> (Confidence Interval CI: 317.4–613.0) in 2014 and 420.9 km<sup>2</sup> (CI: 274.5–598.2) in 2015 to 1,130 km<sup>2</sup> (CI: 15.1–4,515.4) in winter 2023. Summer 2024 showed an intermediate area of 554.6 km<sup>2</sup> (CI: 167.9–1,168.3), larger than the earlier winter periods but smaller than winter 2023. Spatial overlap between winter 2023 and summer 2024 was moderate (Udovitch index=46.6%), indicating partial segregation in foraging areas between seasons (Table 4).

In relation to daily activity, visualization of chronologically connected daily centroids revealed distinctive patterns of spatial displacement in foraging areas over time (Fig. 5). In 2014, centroids showed a displacement pattern



**Fig. 2** Foraging trip metrics of brown boobies (*Sula leucogaster*) in the Saint Peter and Saint Paul Archipelago across sampling years (2015, 2023, 2024), separated by sex. Violin plots with embedded box plots show the distribution of total distance traveled (D, km), maximum dis-

tance from colony (Dmax, km), trip duration (hours), and sinuosity values. Box plots display the median (central line), interquartile range (box), and  $1.5\times$  interquartile range (whiskers), with individual data points overlaid

primarily toward the southeast, with a relatively concentrated trajectory due to the limited number of sampling days. In 2015, the greatest spatial variability was observed, with centroids distributed widely from northwest to east of the archipelago, indicating extensive exploration of the foraging area. In 2023, centroids exhibited displacements predominantly toward the north and northeast, with some excursions toward the northwest, showing a more directional pattern. In 2024, despite a general trend toward the

northeast, centroids showed considerable daily variability, including displacements toward areas closer to the colony. Given that sampling duration differed among years, these patterns should be interpreted as qualitative descriptors of foraging directionality rather than quantitative comparisons of displacement magnitude.

Finally, foraging metrics showed no significant differences among chick developmental stages N1–N4 (Table 5, Fig. S3). However, nests containing eggs or those that were

**Table 3** Generalized Linear Mixed Model (GLMM) results for foraging metrics and time allocation by sex (A) and season (B) in brown boobies (*Sula leucogaster*) from the Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean

| A) Sex comparisons                                    |         |      |        |        |         |                 |
|-------------------------------------------------------|---------|------|--------|--------|---------|-----------------|
| Response variable                                     | $\beta$ | SE   | $z/t$  | $p$    | $p$ FDR | $n$ trips (F/M) |
| <b>Foraging trips metrics</b>                         |         |      |        |        |         | <b>372/258</b>  |
| Total distance                                        | 0.08    | 0.12 | 0.67   | 0.50   | 0.59    |                 |
| Maximum distance                                      | 0.06    | 0.12 | 0.54   | 0.59   | 0.59    |                 |
| Trip duration                                         | 0.10    | 0.13 | 0.83   | 0.41   | 0.59    |                 |
| Sinuosity                                             | 0.02    | 0.03 | 0.54   | 0.59   | 0.59    |                 |
| <b>Time allocation</b>                                |         |      |        |        |         |                 |
| % Travelling                                          | 0.00    | 0.02 | 0.08   | 0.93   | 0.93    |                 |
| % Searching                                           | 0.01    | 0.02 | 0.58   | 0.56   | 0.84    |                 |
| % Foraging                                            | -0.02   | 0.01 | -1.43  | 0.13   | 0.46    |                 |
| B) Seasonal comparisons (Winter 2023 vs. Summer 2024) |         |      |        |        |         |                 |
| Response variable                                     | $\beta$ | SE   | $z/t$  | $p$    | $p$ FDR | $n$ trips (W/S) |
| <b>Foraging trips metrics</b>                         |         |      |        |        |         | <b>237/240</b>  |
| Total distance                                        | 0.09    | 0.13 | 0.73   | 0.46   | 0.79    |                 |
| Maximum distance                                      | 0.06    | 0.12 | 0.54   | 0.59   | 0.79    |                 |
| Trip duration                                         | 0.15    | 0.13 | 1.13   | 0.26   | 0.79    |                 |
| Sinuosity                                             | 0.01    | 0.03 | 0.21   | 0.83   | 0.83    |                 |
| <b>Time allocation</b>                                |         |      |        |        |         |                 |
| % Travelling                                          | -0.19   | 0.02 | -11.70 | >0.001 | >0.001  |                 |
| % Searching                                           | 0.004   | 0.02 | 11.85  | >0.001 | >0.001  |                 |
| % Foraging                                            | 0.18    | 0.01 | 0.43   | 0.67   | 0.67    |                 |

**Table 4** Spatial overlap and foraging area sizes of brown boobies (*Sula leucogaster*) by sex (A) and season (B) in the Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean

| A) Intersexual overlap |                                |                                  |                            |              |
|------------------------|--------------------------------|----------------------------------|----------------------------|--------------|
| Year                   | Male 95% UD (km <sup>2</sup> ) | Female 95% UD (km <sup>2</sup> ) | Overlap (km <sup>2</sup> ) | Udovitch (%) |
| 2015                   | 360.5 (190–584)                | 338.3 (196.0–518.0)              | 287.1                      | 82.2         |
| 2023                   | 752.3 (92–2090)                | 1938.7 (920.0–1,379.0)           | 741.7                      | 55.1         |
| 2024                   | 453.1 (145–933)                | 616.1 (158.0–1,378.0)            | 379.7                      | 71.0         |
| Mean                   | 522.1 ± 204.9                  | 694.4 ± 855.2                    | 469.5 ± 240.2              | 69.4 ± 13.6  |
| B) Seasonal overlap    |                                |                                  |                            |              |
| Comparison             | 95% UD (km <sup>2</sup> )      | Overlap (km <sup>2</sup> )       | Udovitch (%)               |              |
| Austral winter 2023    | 1,130.0 (15.1–4,515.4)         | -                                | -                          |              |
| Austral summer 2024    | 554.6 (167.9–1,168.3)          | -                                | -                          |              |
| Winter – Summer        | -                              | 392.3                            | 46.6                       |              |

In parenthesis CI=Confidence Interval

empty exhibited a trend toward lower foraging effort compared to nests with chicks, though these differences did not reach statistical significance.

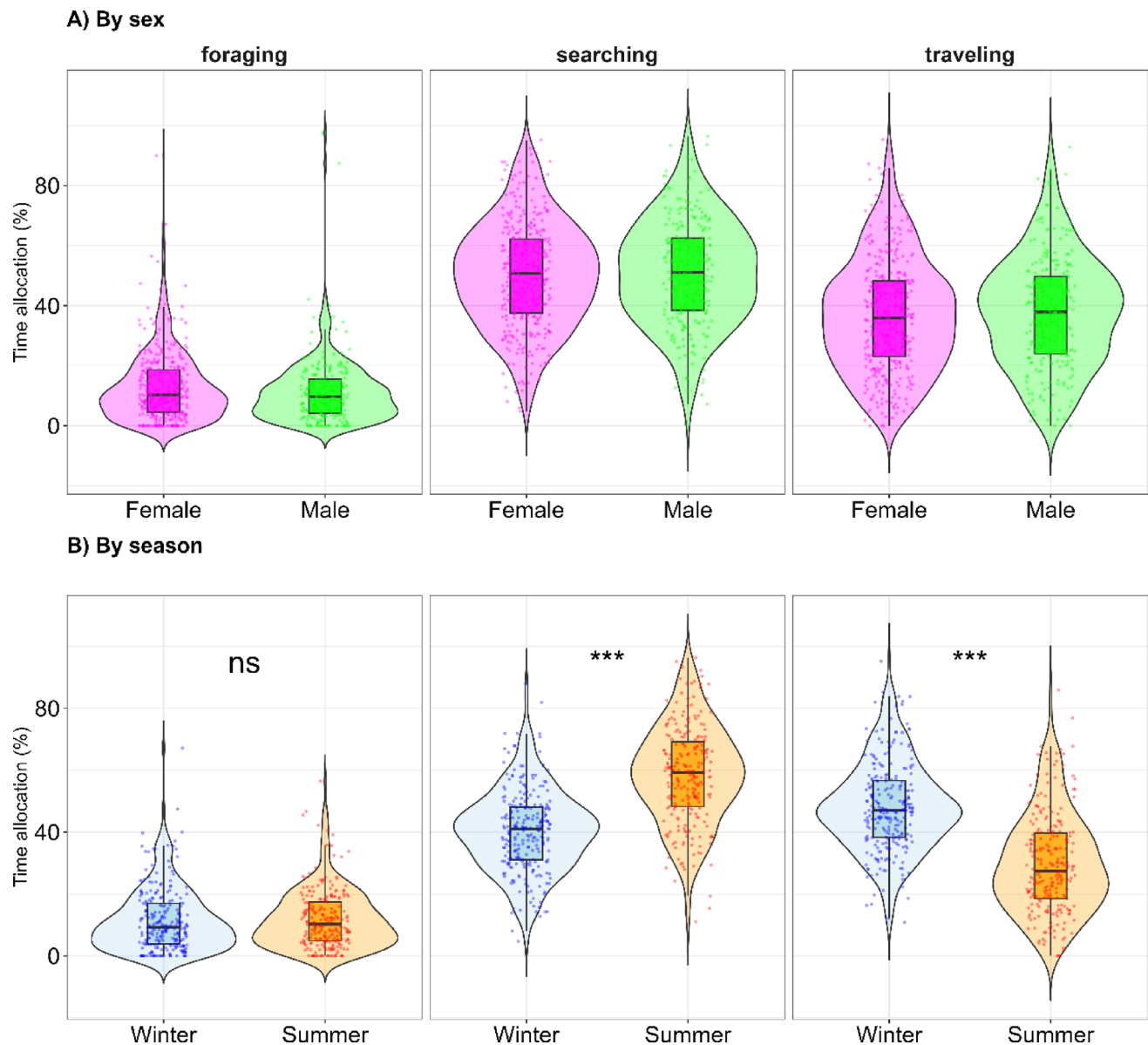
### Stable isotope analysis

A total of 58 blood samples were collected for stable isotope analysis (19 in winter 2023, 39 in summer 2024) (Table 1). Analysis revealed overall mean  $\delta^{13}\text{C}$  values of  $-17.74 \pm 0.25\text{‰}$  and  $\delta^{15}\text{N}$  values of  $10.0 \pm 0.59\text{‰}$  across all samples, consistent with foraging in pelagic surface waters at a secondary consumer trophic level.

Regarding sexes, stable isotope analysis revealed significant sexual differences in  $\delta^{15}\text{N}$  values in both seasons

(austral winter 2023:  $U=78.5$ ,  $p<0.01$ ; austral summer 2024:  $U=312.0$ ,  $p<0.01$ ), with females exhibiting higher values than males in both periods (Table 6; Fig. 6). In contrast,  $\delta^{13}\text{C}$  values did not differ significantly between sexes in either season (winter 2023:  $U=56.0$ ,  $p=0.40$ ; summer 2024:  $U=213.5$ ,  $p=0.50$ ). Isotopic niche overlap between males and females ranged from 42 to 47% of total ellipse areas across sampling periods (Table 6; Fig. 6).

Concerning season and interannual variation, both sexes combined showed significantly higher  $\delta^{15}\text{N}$  values in austral summer 2024 ( $10.40 \pm 0.17\text{‰}$ ) than in austral winter 2023 ( $9.21 \pm 0.22\text{‰}$ ) ( $U=0$ ,  $p<0.001$ , Table 6), indicating an elevated trophic position during the summer breeding period. Similarly,  $\delta^{13}\text{C}$  values were significantly lower in



**Fig. 3** Time allocation across behavioral states by sex and season in brown boobies (*Sula leucogaster*) from the Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean. Upper panels: by sex (females pink, males green). Lower panels: by season (winter 2023 blue; summer 2024 orange,  $n=240$ ). Behavioral states classified using Hidden

Markov Models (Table 1). Sex: no significant differences ( $p>0.05$ , Table 5A). Season: significant differences in traveling (winter>summer,  $p<0.001$ ) and searching (summer>winter,  $p<0.001$ ); foraging similar ( $p=0.667$ , Table 5B)

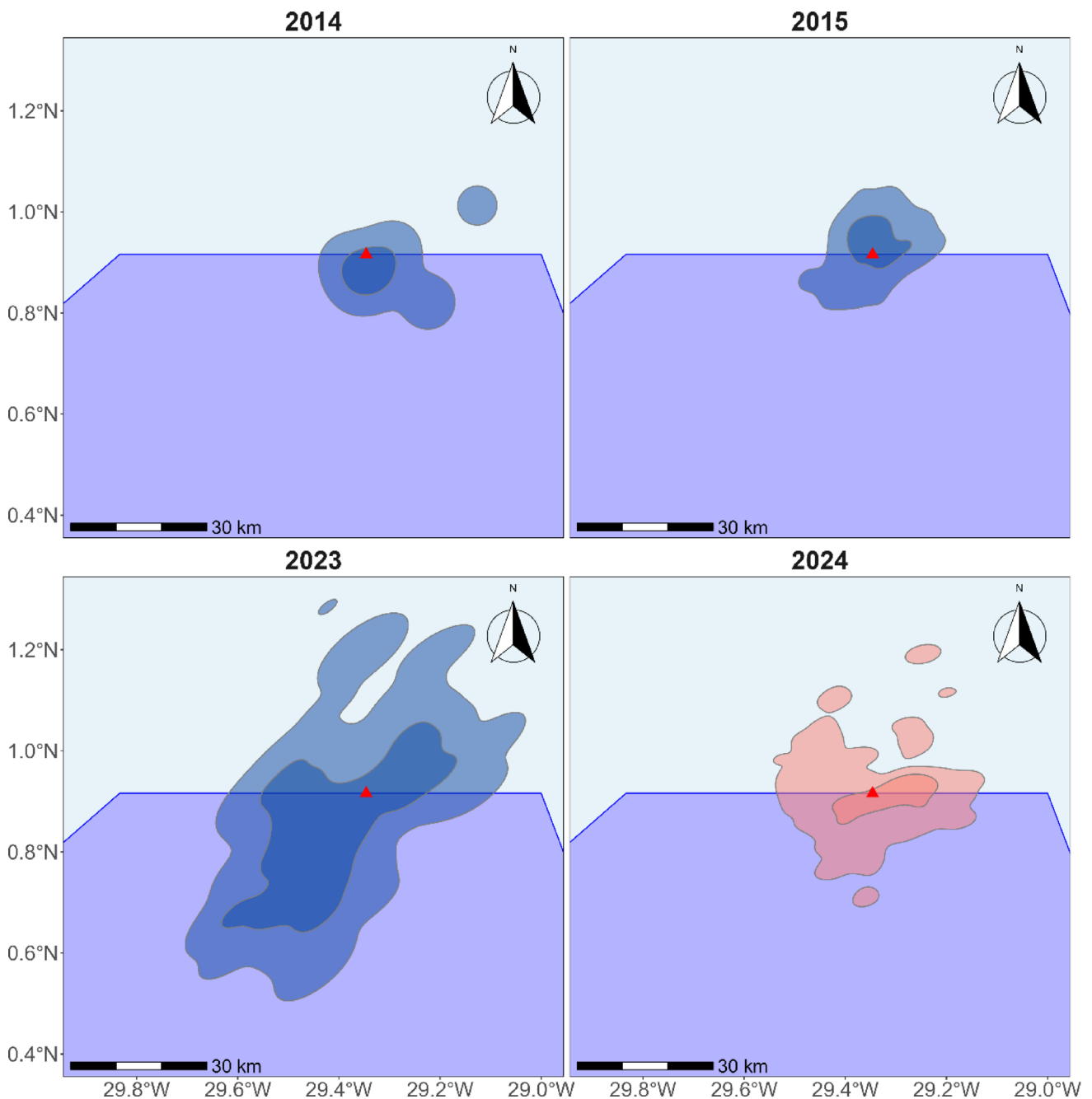
summer ( $-17.82 \pm 0.26\%$ ) than in winter ( $-17.57 \pm 0.14\%$ ) ( $U=596$ ,  $p<0.01$ , Table 6). Isotopic niche ellipses from the two periods showed no overlap (Fig. 6).

### Regurgitate analysis

A total of 49 regurgitate samples were obtained from boobies for diet analysis (40 in winter 2023, 9 in summer 2024) (Table 1). Diet analysis identified flying fishes (Exocoetidae) as the dominant prey family, occurring in above 80% of the regurgitates (Table S1). The tropical two-winged flying

fish (*Exocoetus volitans*) and the bigwing halfbeak (*Oxyprorhampus micropterus*) were the most frequently consumed species in both seasons (Table S1).

Regurgitate samples from 2023 to 2024 revealed seasonal differences in prey composition (Table 7). Flying fishes (Exocoetidae) dominated the diet in both seasons (%PSIRI winter 2023: 72.0%; summer 2024: 77.9%), but species importance differed markedly. In austral winter 2023 *E. volitans* was the primary prey (57.7% PSIRI), followed by *O. micropterus* (27.1%), while in austral summer 2024, *E. volitans* remained as main prey, followed by



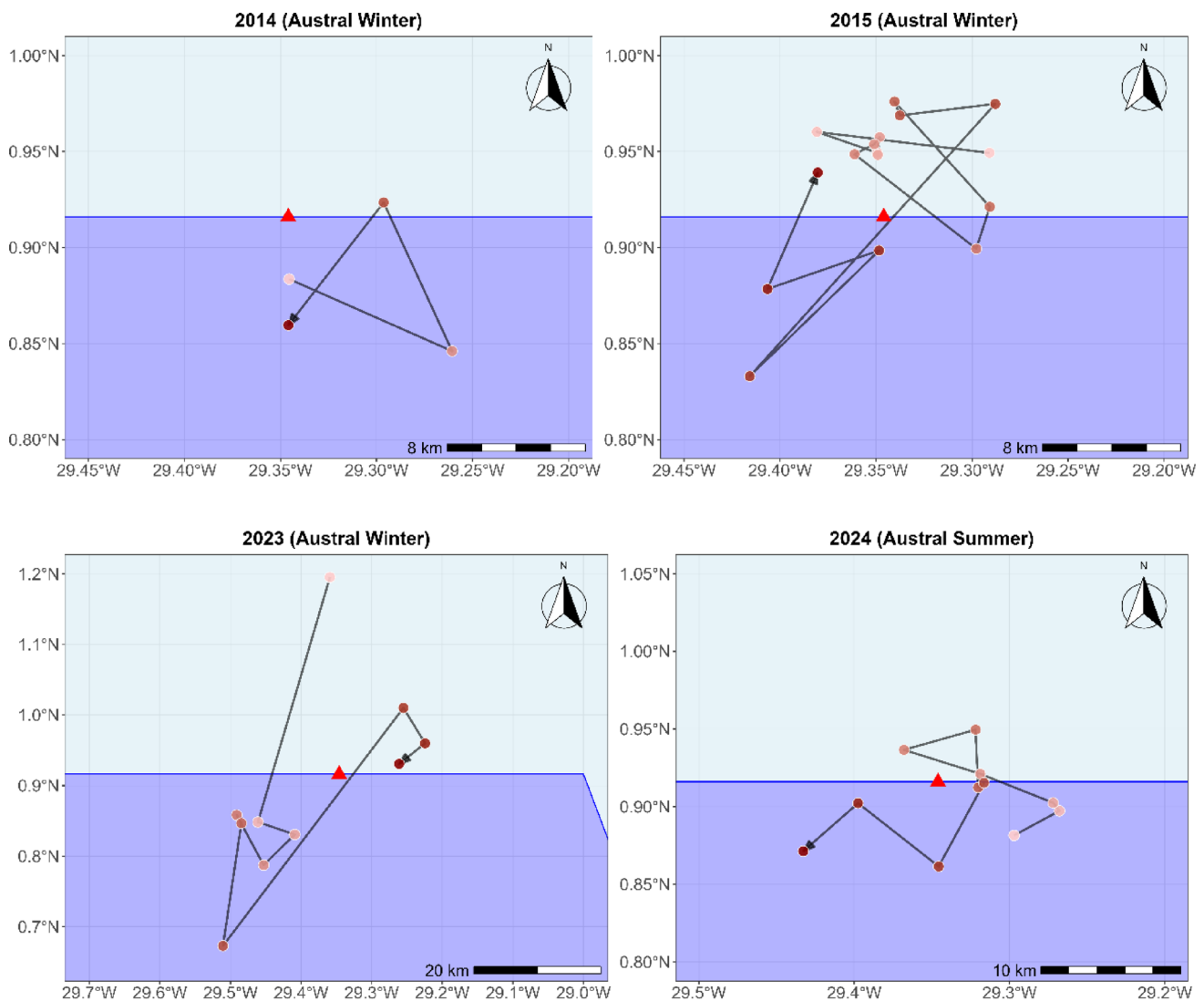
**Fig. 4** Seasonal foraging areas (95% and 50% kernel utilization distributions) of brown boobies (*Sula leucogaster*) in the Saint Peter and Saint Paul Archipelago across years. Blue areas represent austral winter (2014, 2015 and 2023); red areas represent austral summer (2024).

*Cheilopogon cyanopterus* (22.2% PSIRI) (Table 7). Squid (Ommastrephidae) importance increased from 1.9% in winter to 4.4% in summer (Table 7).

Red triangle indicates the colony location. Background colors represent protected areas: APA (Environmental Protection Area) in light blue and MONA (Natural Monument) in blue

## Discussion

Our multi-year study on the foraging ecology of brown boobies at SPSP reveals marked spatiotemporal plasticity in foraging behavior while demonstrating persistent behavioral sexual convergence despite pronounced sexual dimorphism. Five key findings emerged: (1) substantial



**Fig. 5** Daily centroids of foraging locations classified as "foraging" by Hidden Markov Models for brown boobies (*Sula leucogaster*) by year in the Saint Peter and Saint Paul Archipelago. Each point represents the daily centroid of foraging activity, with colors corresponding to the chronological sequence of sampling days within each year. Black lines

connect consecutive daily centroids to illustrate temporal progression of foraging area displacement and black arrow the last point. Red triangle indicates the colony location. Background colors represent protected areas: APA (Environmental Protection Area) in light blue and MONA (Natural Monument) in blue

**Table 5** Foraging trip metrics (D=total distance traveled, Dmax=maximum distance from the colony, T=trip duration in hours) (mean±SD) of brown boobies (*Sula leucogaster*) by nest content in the Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean

| Nest contents | n   | D (km)    | Dmax (km) | Sin      | T (h)   |
|---------------|-----|-----------|-----------|----------|---------|
| Empty         | 28  | 21.6±8.9  | 8.8±3.5   | 1.23±0.2 | 1.1±1.6 |
| Egg           | 148 | 30.1±21.0 | 10.9±6.7  | 1.38±0.3 | 1.3±1.1 |
| N1            | 53  | 35.9±20.3 | 12.5±7.1  | 1.45±0.4 | 1.7±1.4 |
| N2            | 111 | 37.7±23.0 | 12.9±7.0  | 1.46±0.5 | 1.6±1.1 |
| N3            | 103 | 34.9±23.0 | 12.6±8.1  | 1.38±0.4 | 1.4±0.9 |
| N4            | 83  | 35.5±24.3 | 13.8±8.9  | 1.28±0.3 | 1.5±1.2 |

Nest contents include: N1 (0–2 weeks), N2 (3–6 weeks), N3 (7–14 weeks), and N4 (>15 weeks)

interannual variation in foraging effort, with expanded ranges during austral winter 2023 coinciding with documented recovery of large pelagic predators; (2) persistent intersexual convergence in spatial and movement strategies across all temporal scales, suggesting that extreme colonial constraints override sexual dimorphism effects even under changing environmental conditions; (3) subtle trophic segregation revealed by  $\delta^{15}\text{N}$  differences between sexes, indicating that physiological niche differentiation persists despite behavioral similarity; (4) high daily variability in foraging directions indicating opportunistic responses to ephemeral prey distributions; and (5) minimal influence of breeding stage on foraging behavior, reinforcing the dominant role of environmental over intrinsic factors in shaping

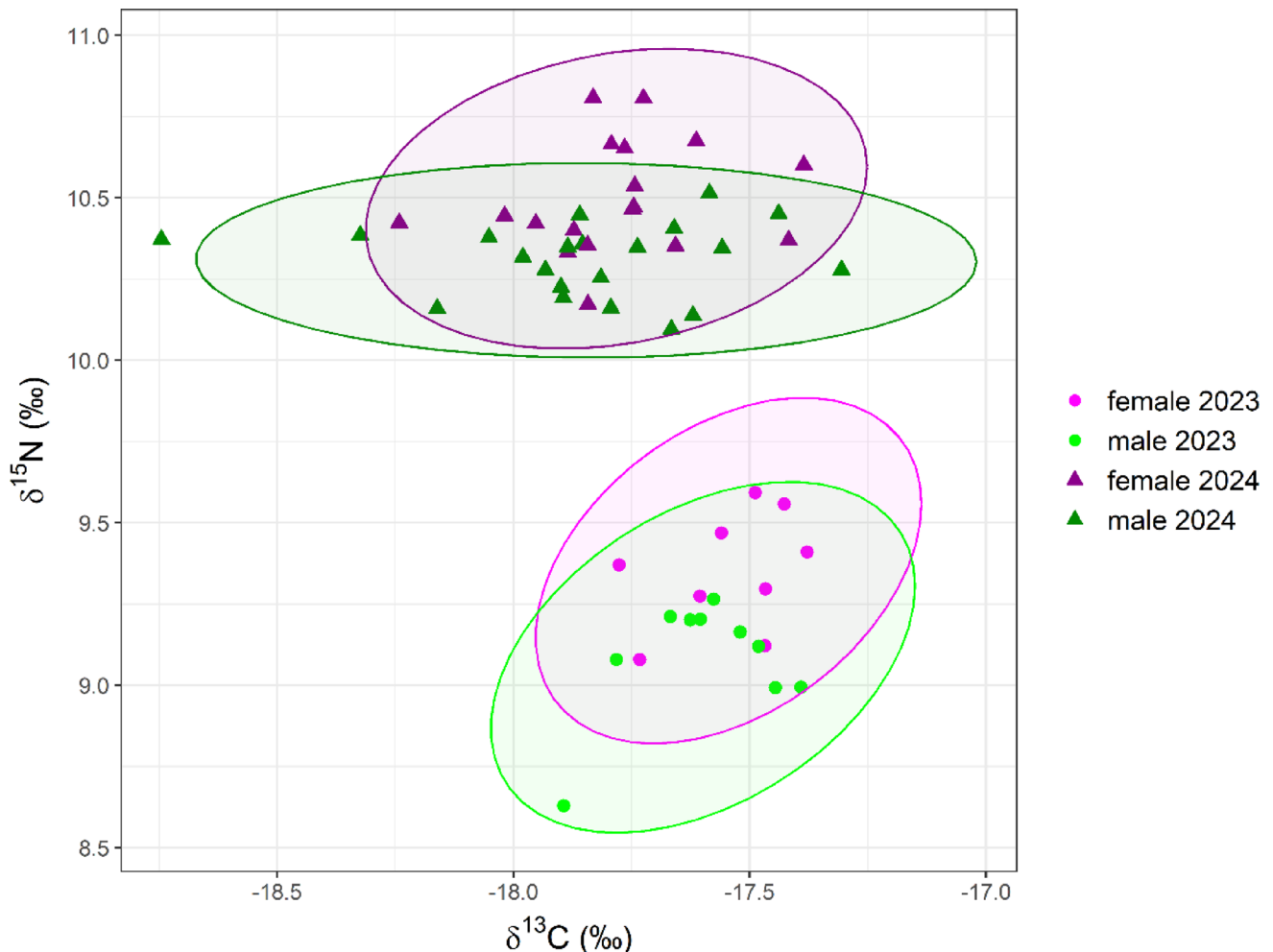
**Table 6** Sample size ( $n$ ), and mean stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , ‰  $\pm$  SD) from whole blood of brown boobies (*Sula leucogaster*) from Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean grouped by season and sex, Standard Ellipse areas corrected for small sample sizes (SEAc) and the respective overall overlap proportion between sexes in each year

| Year/Taxon                 | $n$ | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | SEAc |
|----------------------------|-----|---------------------------|---------------------------|------|
| <b>Austral winter 2023</b> |     |                           |                           |      |
| Female                     | 9   | $-17.54 \pm 0.14$         | $9.35 \pm 0.18$           | 0.48 |
| Male                       | 10  | $-17.60 \pm 0.15$         | $9.09 \pm 0.19$           | 0.55 |
| Total                      | 19  | $-17.57 \pm 0.14$         | $9.21 \pm 0.22$           |      |
| Overlap area proportion    |     |                           |                           | 47%  |
| <b>Austral summer 2024</b> |     |                           |                           |      |
| Female                     | 18  | $-17.78 \pm 0.2$          | $10.50 \pm 0.17$          | 0.67 |
| Male                       | 21  | $-17.85 \pm 0.31$         | $10.31 \pm 0.11$          | 0.70 |
| Total                      | 39  | $-17.82 \pm 0.26$         | $10.40 \pm 0.17$          |      |
| Overlap area proportion    |     |                           |                           | 42%  |

Samples were collected in the Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean, during the austral winter 2023 and austral summer of 2024

foraging decisions at this population. Together, these findings highlight how extreme colonial constraints interact with environmental variability to shape foraging strategies in a tropical seabird breeding under high nest density in an oligotrophic oceanic environment.

Foraging effort increased substantially in austral winter 2023 compared to earlier years (2014–2015), with birds nearly doubling travel distances ( $\sim 23$  to  $\sim 46$  km) and maximum ranges ( $\sim 9$  to  $\sim 19$  km). Diet remained dominated by flying fish in comparison to Nunes et al. (2018), suggesting that preferred prey did not change but became less accessible near the colony. Multiple non-exclusive mechanisms could explain this pattern: changes in predator communities affecting prey aggregation and accessibility (Au and Pitman 1986; Queiroz et al. 2021; Afonso et al. 2022; Alexandre 2024), fisheries pressure reducing flying fish availability near the colony (G.T. Nunes, pers. obs.), and broader oceanographic changes affecting prey distribution (Grémillet and Boulinier 2009). The interaction of these factors precludes



**Fig. 6** Standard ellipse areas of stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) from blood samples of male and female brown boobies (*Sula leucogaster*) during austral winter 2023 and austral summer 2024 in the Saint

Peter and Saint Paul Archipelago, tropical Atlantic Ocean. Ellipses encompass 95% of the data

**Table 7** Prey composition in regurgitated material from breeding brown boobies (*Sula leucogaster*) in austral winter 2023 and austral summer 2024 in the Saint Peter and Saint Paul Archipelago, tropical Atlantic Ocean

| Prey                             | %PSIRI         |                |
|----------------------------------|----------------|----------------|
|                                  | Austral winter | Austral summer |
| Carangidae                       | 5.36           | -              |
| <i>Caranx crysos</i>             | 0.9            | -              |
| <i>Elegatis bipinnulata</i>      | 3.9            | -              |
| Ommastrephidae                   | 1.67           | 3.44           |
| Unidentified squids              | 1.9            | 4.4            |
| Exocoetidae                      | 72.02          | 77.93          |
| <i>Cheilopogon melanurus</i>     | 2.6            | -              |
| <i>Cheilopogon cyanopterus</i>   | 3.9            | 22.2           |
| <i>Exocoetus volitans</i>        | 57.7           | 30.1           |
| <i>Prognichthys gibbifrons</i>   | 0.9            | -              |
| <i>Cheilopogon</i> sp.           | -              | 21.7           |
| Hemiramphidae                    | 20.11          | 18.63          |
| <i>Oxyporhamphus micropterus</i> | 27.1           | 10.4           |
| <i>Euleptorhamphus velox</i>     | -              | 11.1           |
| Scombridae                       | 0.84           | -              |
| <i>Thunnus albacares</i>         | 1.1            | -              |

Analyses were made by family and species level. Therefore, the sum of the importance of families is 100%, and the same occurs with the the sum of the importance at the species level. %PSIRI = Prey-Specific Relative Importance Index

attribution of the observed range expansion to any single driver.

Despite substantial interannual variation in foraging effort, behavioral sexual segregation was generally limited across temporal scales and environmental conditions. This pattern is particularly striking given the pronounced reversed sexual dimorphism in brown boobies at SPSP (Nunes et al. 2017), and contrasts with GPS-based studies showing spatial segregation in brown boobies from other colonies (Miller et al. 2018a; Almeida et al. 2021; Correia et al. 2021) and other sexually dimorphic seabirds where environmental stress typically enhances niche segregation (Phillips et al. 2011; Reyes-González et al. 2021). Spatial overlap between sexes varied interannually, with reduced overlap during the high-effort year 2023 when females expanded their foraging areas. Despite this variation, foraging trip metrics showed no significant differences between sexes, and time allocation across behavioral states was also statistically indistinguishable.

Two complementary hypotheses may explain this pattern. First, the extreme colonial constraints hypothesis posits that exceptionally high nest density forces adults to prioritize territory defense over foraging optimization, creating strong selection for conservative strategies regardless of sex-specific demands (Weimerskirch et al. 2009b; Castillo-Guerrero and Mellink 2011; Nunes et al. 2018). Second, the facilitated foraging hypothesis suggests that predator-facilitated prey aggregations near the colony (Au

and Pitman 1986; Mancini and Bugoni 2014) allow both sexes to meet energetic requirements efficiently without spatial partitioning. Foraging ranges at SPSP (~9–19 km) are considerably shorter than those reported for other colonies in Australia (13–77 km; Miller et al. 2018a) and the Gulf of Guinea (6–203 km; Correia et al. 2021), supporting this interpretation. These constraints are environment-dependent: during periods of reduced prey accessibility, larger females may explore more distant areas while smaller males remain closer to the colony, producing reduced spatial overlap without affecting trip metrics or time allocation.

Seasonal analysis revealed shifts in foraging behavior and diet composition between austral winter and summer. Despite descriptive differences in foraging distances, trip metrics did not differ significantly between seasons, reflecting high individual variability and overlapping ranges. However, time allocation across behavioral states differed markedly: summer birds allocated significantly less time to traveling (29.7% vs. 48.1%) and more time to area-restricted searching (58.4% vs. 40.3%) compared to winter, while active foraging remained similar (~12%). This behavioral shift indicates that birds adjusted their search strategies rather than overall foraging effort in response to seasonal prey availability. The discordance between trip metrics and time allocation highlights the multifaceted nature of foraging behavioral response: seasonal changes in prey availability primarily affect fine-scale foraging tactics rather than trip-level decisions, potentially because colonial constraints maintain pressure to minimize time away from nests regardless of season (Oppel et al. 2015).

High daily variability in foraging directions and centroid locations across all years further reinforces this interpretation of opportunistic foraging. Daily centroid positions shifted unpredictably between consecutive days with no consistent directional pattern, suggesting that birds respond to dynamic oceanographic conditions and ephemeral prey distributions rather than returning to predictable foraging grounds (Weimerskirch et al. 2009a; Wilkinson et al. 2020). This behavioral flexibility likely reflects the transient nature of predator-facilitated foraging opportunities, where subsurface predators such as tunas and dolphins enhance prey accessibility unpredictably across space and time (Au and Pitman 1986; Ballance and Pitman 1999; Cansse et al. 2020).

Contrary to predictions for colonial seabirds, where breeding stage typically influences foraging effort through trade-offs between parental investment and self-maintenance (Mendez et al. 2016; Phillips et al. 2017; Poli et al. 2017), breeding stage showed minimal influence on foraging behavior at SPSP. Birds with eggs or empty nests exhibited only marginally shorter foraging trips compared to those with chicks, and no significant differences were detected

among chick developmental stages. This muted response likely reflects the same extreme colonial constraints that suppress sexual segregation: the high risk of territory loss during extended absences maintains selection for conservative foraging strategies regardless of immediate reproductive demands (Angel et al. 2015). The minimal magnitude of breeding stage effects compared to pronounced interannual and seasonal variation reinforces the dominant role of environmental over intrinsic factors in shaping foraging decisions.

Our tracking data demonstrate that brown boobies utilize both the APA and MONA established around SPSP, with seasonal and interannual variation in foraging extent determining the effective degree of protection. The expanded ranges during austral winter 2023 resulted in increased use of APA waters where fishing is allowed, while the more concentrated summer foraging remained largely within MONA boundaries. This spatiotemporal variability highlights a fundamental challenge for marine spatial planning in dynamic pelagic ecosystems: static zoning approaches may provide incomplete protection when species exhibit substantial flexibility in space use driven by environmental conditions (Oppel et al. 2015; Carneiro et al. 2020), compounded by the existing design limitations and governance challenges already identified for these VLMPAs.

Subtle trophic segregation emerged despite limited behavioral differences. Females exhibited significantly higher  $\delta^{15}\text{N}$  values than males in both seasons, suggesting a slightly higher trophic position or consumption of larger prey individuals (Phillips et al. 2011; Miller et al. 2018a; Mancini et al. 2023). However, this isotopic difference did not translate into spatial segregation, i.e., both sexes foraged in overlapping areas targeting the same prey types, with no  $\delta^{13}\text{C}$  differences in values, confirming use of the same oceanographic habitats (Pontón-Cevallos et al. 2017). The  $\delta^{15}\text{N}$  divergence could additionally reflect segregation along axes not captured by our methods, such as differences in foraging depth or differential associations with subsurface predators that aggregate distinct prey assemblages (Lewis et al. 2005; Zavalaga et al. 2007). Resolving this would require future studies combining time-depth recorders with isotopic sampling. Taken together, the discordance between isotopic and behavioral patterns underscores how colonial and ecological constraints homogenize foraging strategies despite underlying physiological differences between sexes. Indeed, the unique combination of extreme nest density, year-round breeding, genetic differentiation, and larger body size at SPSP (Nunes et al. 2017, 2018) may have driven local adaptation favoring behavioral convergence while preserving subtle trophic differences.

Both sexes combined showed significantly higher  $\delta^{15}\text{N}$  values in summer than in winter, indicating an elevated

trophic position during the summer breeding period, alongside lower  $\delta^{13}\text{C}$  values, suggesting a subtle shift in foraging habitat between seasons. The absence of overlap between seasonal isotopic ellipses reinforces the magnitude of this trophic shift, consistent with the behavioral reallocation of time toward area-restricted searching observed in summer tracking data. These isotopic patterns were corroborated by pronounced seasonal shifts in diet composition. Two-winged flying fish dominated in both seasons, but species of secondary importance shifted from the bigwing halfbeak in winter to the margined flying fish in summer, coinciding with its spawning season from November to March (Lessa et al. 1999; Vaske et al. 2003). The combination of shorter foraging ranges, increased searching behavior, and exploitation of spawning flying fish suggests that summer represents a period of enhanced prey accessibility near the colony, creating a critical seasonal resource pulse in this oligotrophic oceanic environment (Ballance and Pitman 1999).

The pronounced interannual variation in foraging effort observed during our study period, coupled with documented changes in predator communities, underscores the value of seabird tracking as a cost-effective tool for monitoring spatiotemporal ecosystem dynamics across vast oceanic areas where direct sampling is logistically challenging (Lascelles et al. 2016). Because brown boobies closely track the surface distribution of flying fish, a key conduit of energy transfer in pelagic food webs, they can serve as ecological indicators of shifts in pelagic productivity and predator-prey dynamics (Grémillet and Boulinier 2009). This indicator role is particularly important for VLMPAs in isolated oceanic systems where conventional ecosystem monitoring is often limited or unfeasible. However, the unique characteristics of this population, e.g., genetic isolation, large body size, extreme breeding density, and apparent dependence on aquatic predator-facilitated foraging, may increase vulnerability to cumulative environmental changes, emphasizing the need for adaptive management approaches that integrate multi-year seabird tracking data to detect ecologically meaningful shifts and inform conservation strategies.

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**Author contributions** Fiorella Vilela: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, writing—review and editing. Júlia Jacoby: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, writing—review and editing. Maicon Pegoraro: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, writing—review and editing. Felipe Campos Nery: Conceptualization, Writing—original draft. Sophie Lanco: Conceptualization, Writing—review and editing. Leandro Bugoni: Conceptualization, Writing—review and editing. Guilherme Tavares Nunes: Conceptualization, Investigation, Resources, Supervision, Writing—original draft, writing—review and editing. All authors contributed to the article and approved the submitted version.

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**Data availability** All data used in this study, as well as the R programming code, are available under request for download at Github ([https://github.com/Fiorella2891/SPSP\\_Sleucogaster\\_foraging](https://github.com/Fiorella2891/SPSP_Sleucogaster_foraging)).

## Declarations

**Ethics approval** All procedures involving animals were approved by the Animal Ethics Committee of Universidade Federal do Rio Grande do Sul (UFRGS, Approval No. 37905) and authorized by the Brazilian biodiversity authorization system (SISBIO permit No. 64234).

**Competing interests** The authors declare that they have no competing interests.

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