Ecological Research

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RESEARCH ARTICLE OPEN ACCESS

Intercolony and Intra-Annual Variations in Isotopic Niche of Red-Footed Boobies *Sula sula* in the Tropical Indian Ocean

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Received: 1 September 2025 | **Revised:** 6 January 2026 | **Accepted:** 18 February 2026

Keywords: diet | seabird | Seychelles | stable isotope analysis | trophic ecology

ABSTRACT

Foraging seabirds experience diverse environmental conditions, resulting in variation in their foraging ecology across different populations. Documenting this variability is important for understanding how seabirds adapt to environmental change. We examined the trophic ecology of red-footed boobies (*Sula sula*) at three relatively remote colonies in the tropical Indian Ocean: Aldabra Atoll, Farquhar Atoll and Diego Garcia. We compared red-footed booby diet and isotopic niches based on regurgitates and stable isotope compositions ($\delta^{15}N$ and $\delta^{13}C$) of whole blood and body feathers, representing breeding and non-breeding periods, respectively. At Diego Garcia, breeding red-footed boobies consumed only flying fish, whereas at Farquhar and Aldabra they had a more diverse diet. Breeding red-footed boobies at Diego Garcia had lower $\delta^{15}N$ and $\delta^{13}C$ values and a broader isotopic niche width along the $\delta^{13}C$ axis than those at Aldabra and Farquhar. Considering the resident behavior of red-footed boobies, we further explored intra-annual variation in isotopic niches within each colony. All colonies showed minimal isotopic niche overlap between breeding and non-breeding periods, which represent the northwest and southeast monsoon seasons, and had higher $\delta^{15}N$ and $\delta^{13}C$ values and larger isotopic niche widths during the southeast monsoon. Red-footed booby isotopic niches were segregated from those of other seabirds, such as lesser frigatebirds (*Fregata ariel*) at Aldabra and brown noddies (*Anous stolidus*) at Farquhar. Our study shows trophic niche plasticity in red-footed boobies in the tropical Indian Ocean. We provide ecological baselines to support monitoring of the impacts of environmental change on the diets and isotopic niches of red-footed boobies across the rapidly changing tropical Indian Ocean.

1 | Introduction

Seabirds are high trophic level predators in marine ecosystems and are good indicators of environmental conditions, reflecting the availability, variability, and distribution of lower trophic levels (Hazen et al. 2019). This makes widely distributed seabirds particularly useful sentinels, as they often display foraging plasticity in response to environmental variability. Conspecifics from separate colonies experience different habitats and prey communities (Jacoby et al. 2023; Marcuk et al. 2024). These differences are further compounded by the dynamic nature of marine environments, where prey availability fluctuates over multiple spatiotemporal scales (Weimerskirch 2007; Gaglio et al. 2018). During the breeding season, seabirds are restricted to foraging near their colonies to incubate eggs and feed their chicks and are thus more reliant on local conditions. Additionally, colony-specific factors, such as population density and seabird community composition, can generate intra- and inter-specific competition, respectively, therefore promoting resource partitioning as a mechanism for coexistence (Austin et al. 2021; Garcia-Quintas et al. 2024). Collectively, these factors shape how foraging characteristics vary across locations and seasons among populations. Understanding this variation is important for informing and predicting how seabird populations will respond to changing marine environments caused by climate change, overfishing, and other human-related disturbances (Gagne et al. 2018; Ramos et al. 2020).

Although biotelemetry has greatly enhanced our understanding of population-level variation in seabird foraging strategies (Paiva et al. 2010; Gilmour et al. 2018), it offers limited insight into diet and trophic ecology. To address this limitation, sampling of food items through regurgitated prey, complemented with intrinsic markers such as stable isotopes, can be used. The stable isotope composition of seabird tissues reflects that of their prey, allowing inferences about trophic niche (Barrett et al. 2007). Specifically, stable isotope ratios of carbon ($\delta^{13}C$) reveal the sources of carbon at the base of the food webs on which seabirds depend, therefore reflecting the habitat from which prey species were acquired, while stable isotope ratios of nitrogen ($\delta^{15}N$) increase with each trophic level, providing information about the trophic position of prey consumed (Newsome et al. 2007). When considered together, $\delta^{13}C$ and $\delta^{15}N$ values define a population's isotopic niche based on the spread of individual isotope values in Cartesian space (Newsome et al. 2007). Furthermore, animal tissues are synthesized and replaced at different rates, and their stable isotope signatures reflect assimilated diet at the time of tissue synthesis (Inger and Bearhop 2008). In seabirds, analyzing multiple tissues such as blood and feathers enables assessment of isotopic niche at different time periods (Barrett et al. 2007).

Red-footed boobies (*Sula sula*) are widely distributed across tropical and subtropical regions of the Atlantic, Pacific, and Indian Oceans. They are well suited for monitoring tropical oceans because they are non-migratory (Votier et al. 2024) and are sensitive to oceanographic conditions (Gilmour et al. 2018). Red-footed boobies are generalist and opportunistic foragers (Donahue et al. 2021), capturing prey either in flight or through short, shallow plunge dives and surface dives (Weimerskirch et al. 2005). Additionally, red-footed boobies forage in unpredictable prey patches, often concentrating where zooplankton biomass is high, which potentially signals greater prey availability (Jaquemet et al. 2014). Like many tropical seabirds, they also feed in multi-species feeding flocks and associate with subsurface predators that make prey available at the surface (Jaquemet et al. 2005; Spear et al. 2007). Variations in foraging strategies among red-footed booby colonies are well documented, showing the species' behavioral plasticity in optimizing resource acquisition in oligotrophic tropical oceans (Mendez et al. 2017; Gilmour et al. 2018). In contrast, population-level variation in trophic ecology remains less well understood.

Red-footed booby populations in the Indian Ocean have undergone substantial changes over the past two centuries. After experiencing major declines during the 20th century, primarily due to exploitation, habitat destruction, and the introduction of invasive species (Feare 1978), many red-footed booby populations have shown signs of recovery in the 21st century. Conservation efforts, including species protection and predator eradication, have contributed to the growth of extant colonies (Saunier et al. 2024; Risi et al. 2025), and observations of individuals roosting and breeding on new islands are increasing (Skerrett 2021). The Indian Ocean is characterized by diverse oceanographic features, such as mesoscale eddies, seamounts, and shelf edges, as well as seasonal monsoon dynamics, which influence the distribution and availability of prey resources for seabirds (Catry et al. 2013; Jaquemet et al. 2014; Trevail, Nicoll, et al. 2023). The diet of red-footed boobies in the Indian Ocean has been studied at only a few colonies (Diamond 1974; Weimerskirch et al. 2006; Kappes et al. 2011), and their trophic niche has been examined at a single site (Cherel et al. 2008). An assessment of geographic and seasonal variations in red-footed booby trophic ecology is needed to understand the persistence of their growing populations, especially as the tropical Indian Ocean is experiencing some of the most rapid oceanographic changes globally due to climate change (Roxy et al. 2016) and continuing intense fishing pressure threatens seabird populations (Danckwerts et al. 2014).

In this study, we use diet and stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) of blood and feathers to examine the trophic ecology of three red-footed booby colonies in the tropical Indian Ocean. We predict that variations in local marine conditions, such as oceanographic parameters and prey availability, will result in (1) differences in dietary composition among colonies during the breeding period and (2) intercolony differences in isotopic niches during both breeding and non-breeding periods. Additionally, we expect (3) intra-annual differences in isotopic niches between breeding and non-breeding periods. Given that red-footed boobies are resident at all these sites (Votier et al. 2024), such variation would likely reflect oceanographic changes associated with seasonal monsoon dynamics (Catry et al. 2008). Finally, (4) we predict that isotopic niches of red-footed boobies would segregate from those of other seabird species because of interspecific resource partitioning (Cherel et al. 2008; Young, McCauley, et al. 2010).

2 | Methods

2.1 | Study Sites

We studied red-footed boobies at Aldabra Atoll (9°24′ S, 46°20′ E) and Farquhar Atoll (10°11′ S, 51°06′ E) in the Seychelles archipelago, and at Diego Garcia (5°50′ S, 72°00′ E) in the Chagos archipelago (Figure 1). These remote, low-lying atolls are breeding grounds for some of the largest seabird populations in the tropical Indian Ocean and are classified as Important Bird and Biodiversity Areas (Rocamora and Skerrett 2001; Carr et al. 2021). Climate and oceanographic conditions at these atolls are shaped by two seasons (Schott and McCreary 2001). From May to October, southeasterly trade winds bring slightly cooler temperatures and lower rainfall. During this season, phytoplankton blooms occur near continental landmasses in the Bay of Bengal, the Arabian Sea, and East Africa, with low levels of productivity extending into the central Indian Ocean

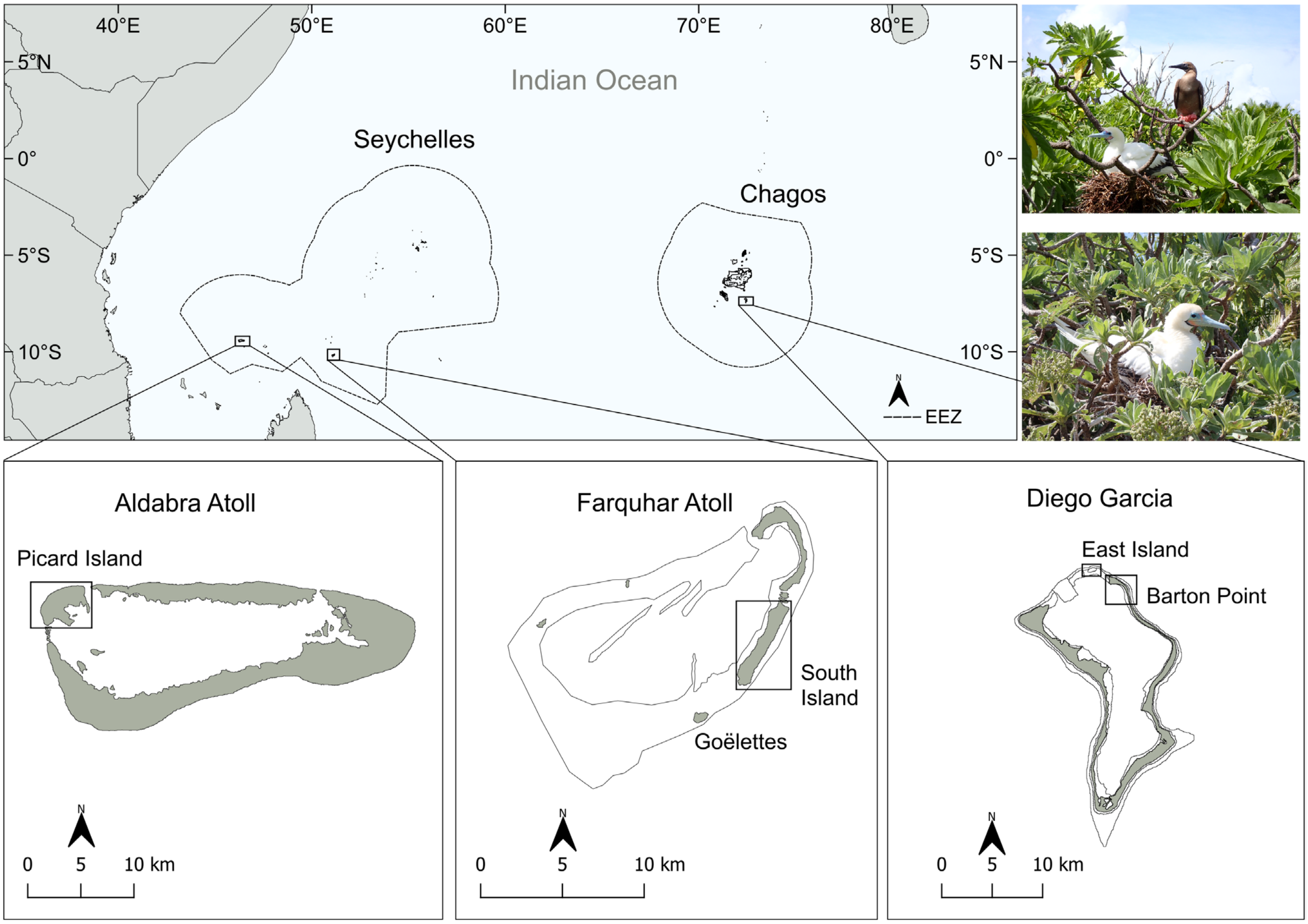

FIGURE 1 | Locations of the studied red-footed booby colonies in the tropical Indian Ocean, including Aldabra Atoll and Farquhar Atoll (Seychelles archipelago) and Diego Garcia (Chagos archipelago). Gray lines around Farquhar and Diego Garcia islands show the atoll rim. Photos show nesting red-footed boobies on Farquhar Atoll (source: J. Appoo).

(Lévy et al. 2007). In contrast, from November to April, winds blow from the northwest, resulting in slightly warmer and oligotrophic conditions (Lévy et al. 2007) and higher rainfall. Accordingly, these seasons are referred to as southeast and northwest monsoons.

Red-footed boobies are the only sulid species that nest on Aldabra, Farquhar, and Diego Garcia, and they are among the largest seabird populations on these atolls (Table 1). They are arboreal nesters, occupying mangrove trees at Aldabra and coastal trees and shrubs at Diego Garcia and Farquhar. On these atolls, red-footed boobies breed asynchronously, with two breeding peaks per year that coincide with the two monsoon seasons (Carr et al. 2021; Risi et al. 2025). In the Indian Ocean, red-footed boobies restrict their foraging to daytime hours (Weimerskirch et al. 2005; Trevail, Wood, et al. 2023), and their diet consists primarily of flying fish (Exocoetidae) and squid (Ommastrephidae) (Diamond 1974; Cherel et al. 2008; Kappes et al. 2011).

Our study was conducted on red-footed boobies nesting on East Island and Barton Point (Diego Garcia) in February 2022, South Island (Farquhar) in March 2022, and Picard Island (Aldabra) in February 2023 (Figure 1). Sampling at all sites was conducted during the northwest monsoon. Individuals from East Island and Barton Point are considered part of a single population, since the two sites are less than 2 km apart and their foraging areas overlap (Trevail, Wood, et al. 2023). During the sampling period, a separate group of individuals from the same colonies at Diego Garcia and Farquhar was equipped with biologging devices to investigate their at-sea distribution and foraging behavior. These devices revealed that breeding red-footed boobies at Diego Garcia foraged, on average, within 160 km of the colony (Trevail, Wood, et al. 2023), while individuals at Farquhar foraged, on average, within 81 km of the colony (Nicoll et al. 2025; Table 1). Additionally, they took short (mean ± SD: 4 ± 13 min) and shallow (0.7 ± 0.6 m) plunge or surface dives (Dunn et al. 2024). Remotely sensed data indicated that during their respective sampling periods, breeding red-footed boobies foraged in slightly cooler waters around Aldabra (24°C) and in warmer waters near Diego Garcia and Farquhar (28°C–29°C), with chlorophyll-*a* concentrations < 0.2 $mg.m^{-3}$ across all sites (Table 1).

2.2 | Field Sampling

To investigate the trophic ecology of red-footed boobies, we sampled adults on nests, either incubating or rearing chicks, by hand or using a net or pole. From each individual, we collected up to 0.5 mL of blood from the brachial vein using a 29G needle and syringe. Blood is a metabolically active tissue, and the isotopic

TABLE 1 | Colony size of red-footed boobies at Aldabra, Farquhar, and Diego Garcia, with foraging ranges and foraging conditions during the sampling period.

	Colony size (breeding pairs)	Sampling period	Mean maximum foraging distance (min–max) (km)	Mean monthly sea water temperature at 0.5 m depth (± SD) (°C)	Mean monthly surface chlorophyll-*a* concentration (± SD) ($mg.m^{-3}$)	Reference for colony size and/or tracking study
Aldabra	45,817	February 2023	NA	24.95 ± 0.32	0.09 ± 0.05	Risi et al. 2025
Farquhar	9112	March 2022	160.1 (1.4–422.8)	28.69 ± 0.21	0.08 ± 0.07	Nicoll et al. 2025
Diego Garcia	10,382	February 2022	81.1 (10.3–279.8)	29.24 ± 0.07	0.14 ± 0.04	Trevail, Wood, et al. 2023

Note: Oceanographic variables were obtained from Copernicus Marine Service for the month preceding the sampling period, aligning with the isotopic integration timeframe of whole blood (see Section 2), and within a 200 km radius of each colony location. Sea water temperature (dataset ID: GLOBAL_MULTIYEAR_PHY_001_030) was retrieved at a depth of 0.5 m with a spatial resolution of 0.083°, while surface chlorophyll-*a* concentration (dataset ID: OCEANCOLOUR_GLO_BGC_L4_MY_009_104) was extracted with a spatial resolution of 0.04°.

ratios of seabird whole blood reflect the diet assimilated during the 3–4 weeks before collection (Bearhop et al. 2002). Therefore, whole blood isotopic ratios of birds sampled on nests reflect the birds' diet during the pre-laying or incubation period. We also collected five breast feathers from each individual. Breast feathers were chosen because they have minimal impact on flight ability. Feather keratin is metabolically inert after synthesis and the isotopic ratios of feathers reflect the diet assimilated during molting, which can occur over several weeks to months (Inger and Bearhop 2008). In red-footed boobies, the molt of body and flight feathers is protracted, beginning while adults are still feeding chicks and continuing into the non-breeding period (Diamond 1974; Nelson 1969). However, we observed no signs of active molt during handling, such as missing primary feathers or evidence of feather growth or wear, confirming that birds were not molting. Consequently, isotopic signatures of breast feathers likely reflect the diet during non-breeding periods.

We collected blood samples from 64 red-footed boobies (Aldabra $n=26$, Diego Garcia $n=12$, Farquhar $n=26$). Feather samples were obtained from these same individuals and four additional birds, resulting in 68 feather samples (Aldabra $n=26$, Diego Garcia $n=14$, Farquhar $n=28$). Blood samples were stored in vials and frozen upon return to the laboratory, while feathers were stored at room temperature in Ziplock bags. To compare the isotopic niche of red-footed boobies with other seabird species, we also collected up to 25 blood and breast feather samples from other large seabird populations breeding at the same time and location. These included lesser frigatebirds, *Fregata ariel*, on Aldabra (6600 breeding pairs; Šúr et al. 2013) and brown noddies *Anous stolidus* on Farquhar (19,139 breeding pairs on nearby Goëlettes Island; Duhec et al. 2017). Lesser frigatebirds forage by capturing prey in flight through surface dipping and snatching, or by engaging in kleptoparasitism of other seabirds. Their diet mainly consists of flying fish, halfbeaks (Hemiramphidae), and squid (Diamond 1973; Spear et al. 2007). Brown noddies also employ surface dipping to catch their prey (Villard et al. 2015). They feed on a variety of pelagic juvenile fish, such as goatfish (Mullidae), jackfish (Carangidae), anchovy (Engraulidae), and flying fish, and also consume squid (Catry et al. 2009).

We collected regurgitates from red-footed boobies opportunistically during handling to examine diet composition. Samples were kept cool in the field and sorted upon return to the laboratory. The degree of digestion varied among samples, limiting the identification of small fish prey. As a result, we focused on the occurrence of the main prey types. Given that flying fish and squid are the primary prey of red-footed boobies, we categorized regurgitate contents into three groups: flying fish, squid, and other fish families. This classification was based on the presence of hard remains, such as fish bones or squid beaks and internal shells. Fieldwork protocol and ethical approval were provided by the relevant authorities in Chagos (BIOT) and Seychelles (Seychelles Bureau of Standards, permit number A0157).

2.3 | Laboratory Analysis

Whole blood was dried at 50°C for up to 48 h, and then powdered using a ball mill. The low lipid content of avian whole blood negates the need for lipid extraction (Bearhop et al. 2000). Feathers were cleaned of surface contaminants for 2 min using a 2:1 chloroform: methanol solution in an ultrasonic bath, and then washed in two successive methanol rinses. Feathers were dried at 50°C for 48 h, and then cut into very small fragments. For each blood and feather sample, 1 mg of homogenized material was packed into tin cups for stable isotope analyses. Similarly, small sections of white muscle tissue were cut from prey items, dried, ground, and weighed into capsules for stable isotope analyses. Samples were combusted using a Vario MICRO Cube Elemental Analyzer, and δ^{15}N and δ^{13}C were measured using an Isoprime 100 Isotope Ratio Mass Spectrometer with international standards IAEA 600, IAEA-CH6, and USGS 41 at the stable isotope facility at Lancaster University (Lancaster, UK). Isotope ratios are expressed in parts per thousand (‰), relative to atmospheric N_2 (air) for ^{15}N and Vienna Pee Dee Belemnite for ^{13}C. Accuracy, based on internal laboratory standards, was within 0.2‰ standard deviation and selected samples were run in triplicate to further ensure accuracy of readings.

We verified potential lipid-related bias of δ^{13}C values using the C:N threshold of 3.5 recommended for aquatic organisms by Post et al. (2007), above which high lipid content can lead to lower δ^{13}C values. All prey samples, except one, fell below this threshold, indicating that lipid extraction was unnecessary (Skinner et al. 2016). Although whole blood generally has low lipid content (Cherel et al. 2005), a few samples exceeded the threshold and required correction (C:N range = 3.1–3.7). For these samples ($n = 1$ prey, $n = 8$ blood), we estimated lipid-extracted δ^{13}C values using Post et al. (2007) normalization equation: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N$. These normalized δ^{13}C values were used in all subsequent analyses.

2.4 | Data Analysis

2.4.1 | Prey Items and Isotopic Ratios

To examine the diet of breeding individuals, we quantified food load and diet composition of red-footed boobies from 44 regurgitate samples (Aldabra $n = 21$, Diego Garcia $n = 9$, Farquhar $n = 14$). We calculated numerical abundance as the proportion of each prey type relative to the total number of prey items and compared between colonies using Fisher's exact test. We also calculated the relative frequency of occurrence for each prey type as the percentage of birds with that prey type present in their regurgitate.

Prey isotopic data included flying fish, squid, and other fish families from Aldabra, and only flying fish from Diego Garcia and Farquhar. We compared δ^{15}N and δ^{13}C values of flying fish separately among atolls. Shapiro–Wilk and Levene's tests confirmed normality and homogeneity of variances, so we applied one-way ANOVAs for each isotope. Significant results were followed by post hoc comparisons using the *emmeans* package with Bonferroni correction (Lenth et al. 2023). Isotopic discrimination factors between blood and prey muscle tissue have not been established for sulids. To compute isospace of red-footed booby blood and regurgitated prey muscle tissue, we applied mean diet-blood discrimination factors and their standard deviations derived from comparable seabird species in the literature. We used discrimination factors of 1.96‰ ± 0.79‰ for δ^{15}N and 0.32‰ ± 0.86‰ for δ^{13}C based on the mean values from eight studies of seabirds and lipid-extracted marine prey muscle (see Appendix S6 in Austin et al. 2021).

2.4.2 | Red-Footed Booby Isotopic Ratios and Niche

Due to tissue-dependent metabolic routing and enrichment factors, whole blood has lower δ^{15}N and δ^{13}C values than feathers (Podlesak and McWilliams 2006; Quillfeldt et al. 2008). To account for this, we standardized whole blood isotopic ratios using linear regression equations from Cherel et al. (2014): $\delta^{15}N_{feather} = 1.014\ (\pm 0.056)\ \delta^{15}N_{blood} + 0.447\ (\pm 0.414)$ and $\delta^{13}C_{feather} = 0.972\ (\pm 0.020)\ \delta^{13}C_{blood} + 0.962\ (\pm 0.414)$. We then used generalized linear mixed models (GLMMs) to test red-footed booby δ^{15}N and δ^{13}C values separately, with colony (three levels), period (two levels), and their interaction as fixed effects, and bird ID as a random effect to account for repeated measurements. Post hoc comparisons were used to identify intercolony differences within each period, and intra-annual differences within each colony. To examine interspecific differences between red-footed boobies and other seabird species on Aldabra and Farquhar, we used GLMMs for each atoll, testing δ^{15}N and δ^{13}C separately with species (two levels), period (two levels), and their interaction as fixed effects, and bird ID as a random effect. Post hoc comparisons assessed interspecific differences within each period. All GLMMs were fitted using the *lme4* package (Bates et al. 2015), and post hoc pairwise tests with Bonferroni correction were conducted using the *emmeans* package (Lenth et al. 2023). We performed diagnostics on model residuals to verify normality, homogeneity of variance, and independence.

We examined intercolony, intra-annual, and interspecific isotopic niche variations using the *SIBER* package (Jackson et al. 2011). We estimated isotopic niche width as a measure of trophic diversity and resource use within a group using the standard ellipse area, encompassing 40% of the data and corrected for small sample size (SEA_C). To account for uncertainty in the data, we also estimated the Bayesian standard ellipse areas (SEA_B) using Monte Carlo simulation with 10^4 iterations. We then determined the probability that SEA_B posterior distributions were smaller (or larger) among groups. We quantified isotopic niche overlap to assess similarity in resource use between breeding and non-breeding red-footed boobies, as well as between red-footed boobies and other seabirds. Niche overlap was based on 95% ellipses and calculated as (area of overlapping region)/([area of ellipse 1] + [area of ellipse 2] − [area of overlapping region]). All statistical analyses were performed in R version 4.4.2 (R Core Team 2024), and $\alpha < 0.05$ was used as the threshold for statistical significance.

3 | Results

3.1 | Prey Types and Isotopic Ratios

The 44 regurgitate samples collected from the three colonies contained 167 individual prey items. Red-footed boobies from Aldabra had 5.4 ± 3.3 (mean ± SD) prey items per sample, compared with 1.4 ± 0.7 at Diego Garcia and 2.9 ± 1.4 at Farquhar (Table 2). Red-footed booby regurgitates differed among the

TABLE 2 | Number of regurgitate samples and individual prey items recorded at Aldabra, Farquhar and Diego Garcia from breeding red-footed boobies.

	Aldabra	Farquhar	Diego Garcia
No. of samples	21	14	9
No. of prey items	113	41	13
Mean no. of prey items/sample (± SD)	5.4 ± 3.3	2.9 ± 1.4	1.4 ± 0.7
Mean no. of fish/ sample (± SD)	3.4 ± 2.3	2.8 ± 1.3	1.4 ± 0.7
Mean no. of squid/ sample (± SD)	2.0 ± 1.8	0.1 ± 0.5	0

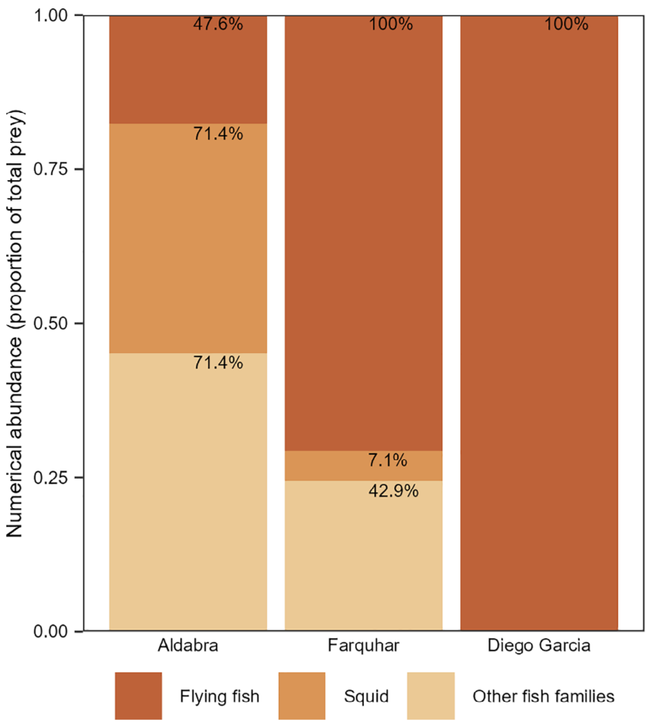

FIGURE 2 | Numerical abundance of different prey types in regurgitate samples (expressed as the proportion of each prey type out of total prey sampled) from breeding red-footed boobies at Aldabra, Farquhar and Diego Garcia. Values on bars correspond to the frequency of occurrence (percentage of birds with a prey type present in their regurgitate).

three colonies in the numerical abundance of prey types ($p < 0.0001$). Flying fish was the only prey item for red-footed boobies at Diego Garcia, with a 100% frequency of occurrence (by number), whereas squid and other fish families were more common at Farquhar and Aldabra (Figure 2). About 71% of birds from Aldabra and 50% of birds from Farquhar had two or more prey types in their regurgitates. Flying fish isotopic values differed among atolls, with higher δ^{15}N values at Diego Garcia compared to Aldabra ($n = 23$, $p = 0.02$) and higher δ^{13}C values at Diego Garcia compared with both Aldabra ($p = 0.01$) and Farquhar ($p = 0.02$). Prey isotopic values corrected for trophic-fractionation overlapped with red-footed booby blood isotopic values at Aldabra and Farquhar, but not at Diego Garcia (Figure S1).

3.2 | Red-Footed Booby Isotopic Ratios and Niche

3.2.1 | Intercolony Differences

Red-footed booby isotopic ratios differed among atolls (δ^{15}N: $F_{2,61} = 14.26$, $p < 0.0001$; δ^{13}C: $F_{2,61} = 8.25$, $p = 0.0007$; Table S1). During the breeding season, birds from Diego Garcia showed lower blood δ^{15}N and δ^{13}C values than those from Aldabra and Farquhar (Figure 3a; Table S2). The isotopic niche width of breeding birds was larger at Diego Garcia, mainly along the δ^{13}C axis (SEA_B mode, 95% credible intervals: 0.10‰, 0.06‰–0.19‰^{2}) than Aldabra (0.07‰, 0.05‰–0.10‰^{2}, probability = 0.93) and Farquhar (0.05‰, 0.04‰–0.08‰^{2}, probability = 0.98; Figure 4a). Feather isotopic ratios also differed among red-footed booby colonies, due to higher δ^{15}N values for birds at Farquhar than those at Aldabra and Diego Garcia (Figure 3b, Table S2). Non-breeding red-footed boobies at Aldabra had a smaller isotopic niche width (0.10‰, 0.07‰–0.15‰^{2}) than at Diego Garcia (0.16‰, 0.09‰–0.29‰^{2}, probability = 0.94) and Farquhar (0.16‰, 0.11‰–0.24‰^{2}, probability = 0.96; Figure 4b).

3.2.2 | Intra-Annual Differences

All three colonies displayed lower δ^{15}N and δ^{13}C values during the breeding period than during the non-breeding period (δ^{15}N: $F_{1,61} = 249.6$, $p < 0.0001$; δ^{13}C: $F_{1,61} = 748.8$, $p < 0.0001$; Figure S2; Tables S1 and S3). The isotopic niche widths of red-footed boobies at all three colonies were larger during the non-breeding than the breeding period (Aldabra: probability = 0.93; Diego Garcia: probability = 0.83; Farquhar: probability = 0.99; Figure 4), and isotopic niches between the two periods had minimal overlap (< 2%; Figure S2).

3.2.3 | Interspecific Differences

At Aldabra, breeding red-footed boobies exhibited lower δ^{15}N values than lesser frigatebirds ($n = 50$, $p < 0.0001$; Table 3; Figure S3a). In the non-breeding period, red-footed boobies also showed lower δ^{15}N values ($p < 0.0001$) but higher δ^{13}C values ($p < 0.001$) than lesser frigatebirds (Figure S3b). Isotopic niche widths were similar for the two species during the breeding period (probability = 0.69) but were smaller for red-footed boobies during the non-breeding period (probability = 0.99; Figure S4a; Table S4). Niche overlap between the two species increased from 3% during the breeding period to 12% in the non-breeding period.

At Farquhar, breeding red-footed boobies showed higher δ^{15}N ($n = 51$, $p = 0.007$) and δ^{13}C values ($p < 0.0001$) than brown noddies (Table 3; Figure S3c). In contrast, during the non-breeding period, red-footed boobies exhibited lower δ^{15}N values ($p < 0.0001$) but higher δ^{13}C values ($p < 0.001$) compared to brown noddies (Figure S3d). Isotopic niche widths were slightly larger for brown noddies during breeding

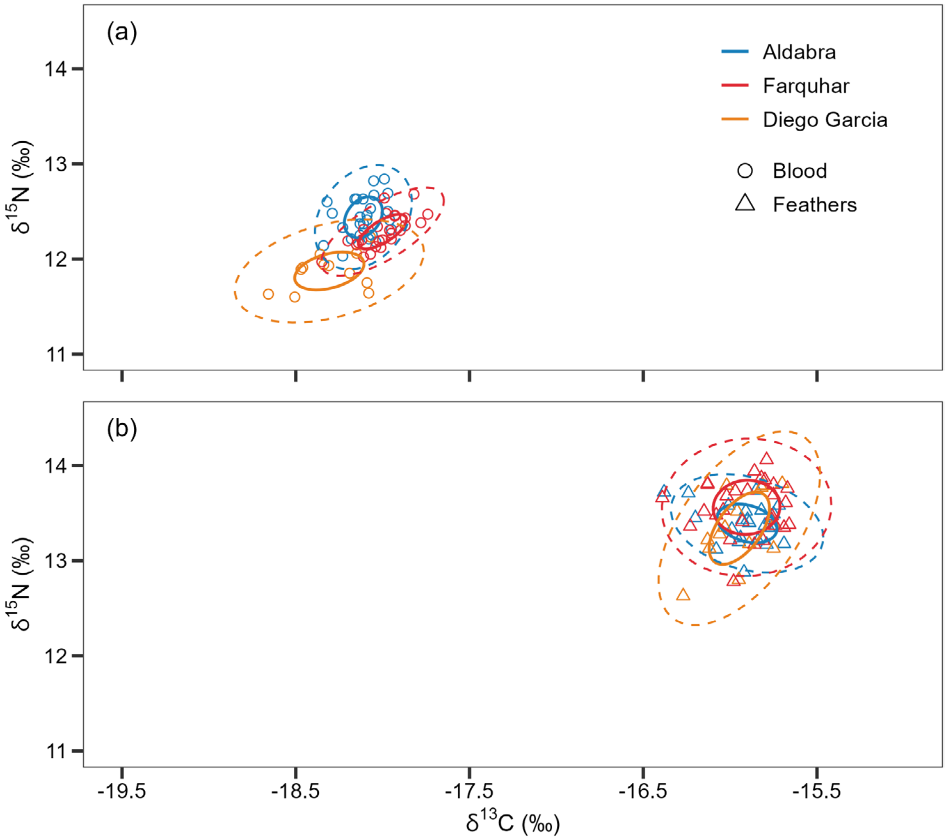

FIGURE 3 | Isotopic niche of red-footed boobies at Aldabra, Farquhar and Diego Garcia during the (a) breeding (whole blood) and (b) non-breeding (body feathers) periods. Full and dashed lines represent standard ellipses at 40% (SEA_C) and 95%, respectively.

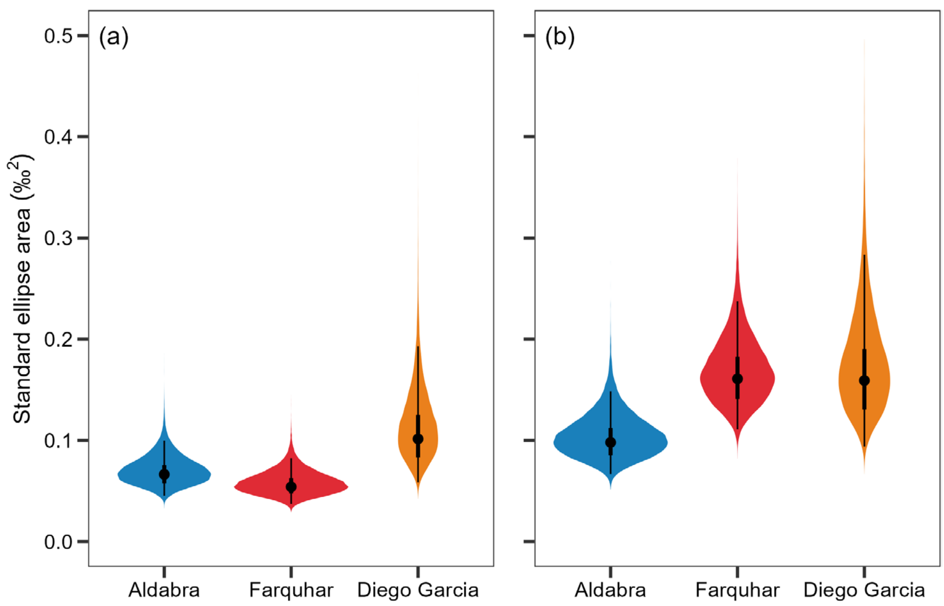

FIGURE 4 | Bayesian standard ellipse areas (SEA_B) of red-footed boobies at Aldabra, Farquhar and Diego Garcia during the (a) breeding and (b) non-breeding periods. Points are posterior modes, and thick and thin lines are 50% and 95% credible intervals, respectively.

(probability = 0.72) and non-breeding periods (probability = 0.82; Figure S4b; Table S4). Furthermore, niche overlap was 18.6% and 23% during the breeding and non-breeding periods, respectively.

4 | Discussion

Seabirds encounter diverse foraging conditions, which can generate population-level variation in foraging ecology. We compared

TABLE 3 | Stable isotope values ($\delta^{15}N$ and $\delta^{13}C$) and C:N ratios of whole blood and body feathers sampled from adult seabirds at Aldabra, Farquhar, and Diego Garcia.

		Whole blood (Mean ± SD)				Feathers (Mean ± SD)			
	Species	***n***	**$\delta^{15}N$ (‰)**	**$\delta^{13}C$ (‰)**	**C:N**	***n***	**$\delta^{15}N$ (‰)**	**$\delta^{13}C$ (‰)**	**C:N**
Aldabra	Red-footed booby	26	12.4 ± 0.2	−18.1 ± 0.1	3.4 ± 0.1	26	13.4 ± 0.2	−15.9 ± 0.2	3.1 ± 0.02
	Lesser frigatebird	24	13.3 ± 0.2	−18.1 ± 0.1	3.4 ± 0.02	24	14.1 ± 0.3	−16.4 ± 0.3	3.1 ± 0.03
Farquhar	Red-footed booby	26	12.3 ± 0.2	−18.0 ± 0.1	3.4 ± 0.1	28	13.6 ± 0.3	−15.9 ± 0.2	3.2 ± 0.03
	Brown noddy	25	12.1 ± 0.1	−18.4 ± 0.1	3.4 ± 0.1	25	13.9 ± 0.3	−16.2 ± 0.2	3.2 ± 0.03
Diego Garcia	Red-footed booby	12	11.9 ± 0.2	−18.4 ± 0.2	3.5 ± 0.1	14	13.3 ± 0.4	−15.9 ± 0.2	3.2 ± 0.03

Note: Whole blood isotopic values are unstandardized measurements, except $\delta^{13}C$ values were normalized for samples with C:N > 3.5.

the diet of red-footed booby and isotopic compositions of blood and feathers at three Indian Ocean atolls lying between 5° and 10° S. We identified differences in dietary composition among breeding colonies, along with intercolony variation in isotopic values and niche widths during the breeding and non-breeding periods. We observed intra-annual shifts, with increases in isotopic values and niche widths during the non-breeding period at all three colonies. The isotopic niche of red-footed boobies was segregated from those of other seabird species, although some overlap occurred mainly during the non-breeding period. Our results show the trophic niche plasticity of red-footed boobies throughout the study area and provide baseline data to support long-term monitoring of marine food webs across the rapidly changing tropical Indian Ocean.

4.1 | Diet

As predicted, the dietary composition of breeding red-footed boobies differed among the three sites. These differences likely reflect prey availability around the colonies (Marcuk et al. 2024). According to Spalding's marine ecoregions, which classify areas based on fish distributions and oceanographic and geomorphological factors, Aldabra and Farquhar belong to a different marine ecoregion from Diego Garcia (Spalding et al. 2007). However, in our study, dietary variation could also be due to differences in breeding stage. At Diego Garcia, all sampled birds were rearing chicks and were therefore likely providing smaller or softer prey to their chicks. This could also explain the reduced prey numbers and lower prey diversity in regurgitates at Diego Garcia compared with birds from Aldabra and Farquhar, which were mostly incubating. Additionally, red-footed booby isotopic values at Diego Garcia did not overlap with the isotopic composition of regurgitated prey, indicating that some prey items were missing from the regurgitate samples. This highlights the usefulness of stable isotopes as a useful complementary tool in dietary investigations, as they integrate information on assimilated prey (Inger and Bearhop 2008).

Nevertheless, regurgitate samples showed that flying fish were the most common prey consumed by red-footed boobies at Diego Garcia and Farquhar. The dominance of flying fish in the red-footed booby diet aligns with findings from other colonies across the species' range, including in the Indian Ocean (Europa Island, Cherel et al. 2008), the Atlantic Ocean (Cayman Islands, Austin et al. 2021), and the Pacific Ocean (Palmyra Atoll, Young, Shaffer, et al. 2010; Clarion Island Lerma et al. 2024). In contrast, the red-footed booby diet at Aldabra contained a higher proportion and frequency of squid and other fish families. Squid have previously been identified as a key component of the red-footed booby diet at Aldabra (Diamond 1974) and have also been reported as dominant prey at other sites, such as Tromelin Island in the Indian Ocean (Kappes et al. 2011) and O'ahu, Hawai'i, in the Pacific Ocean (Donahue et al. 2021). The high proportions of these two prey groups at Aldabra may also be linked to the colony's larger size to reduce intraspecific competition for food (Trevail, Wood, et al. 2023). It could also be related to the higher number of regurgitates sampled compared with the other two sites, which could lead to a better representation of diet composition. Overall, our findings demonstrate the dietary plasticity of red-footed boobies. Moving forward, dietary studies would benefit from the use of genetic methods (Donahue et al. 2021) to document the diversity and abundance of prey consumed by red-footed boobies throughout the study area.

4.2 | Intercolony Differences

Isotopic ratios and niche widths of red-footed boobies differed among colonies, in line with our predictions. During the breeding period, red-footed boobies at Aldabra and Farquhar showed higher $\delta^{15}N$ and $\delta^{13}C$ values than those at Diego Garcia. The isotopic signatures of birds at Aldabra and Farquhar overlapped with those of their regurgitated prey, suggesting differences linked to diet composition and prey isotopic values. However, flying fish isotopic ratios were higher at Diego Garcia, and this mismatch with red-footed booby signatures may be associated with chick-rearing activity, which limits food consumption by adults that instead feed on themselves (i.e., on lipid reserves). Seabirds often provision their chicks with higher quality prey, which can lead to the lower adult $\delta^{15}N$ values observed at Diego Garcia (Cherel et al. 2008; Young, McCauley, et al. 2010). Moreover, adult seabirds may forage in different areas for self-feeding than for chick provisioning (Connan et al. 2018). In addition to integrating information on prey species' habitat and trophic level, the isotopic signatures of marine consumers are also linked to isotopic baselines (i.e., isoscapes) within their foraging areas (Moreno et al. 2011), which may explain the intercolony isotopic differences observed. Studies on other marine predators indicate latitudinal variations in $\delta^{15}N$ baselines in this region (Lorrain et al. 2015; Dhurmeea et al. 2020). Furthermore, during the sampled breeding period, the isotopic niche width was broader at Diego Garcia mainly along the δ^{13}C axis than Aldabra and Farquhar. In tropical oceans, δ^{13}C isoscapes are homogeneous (Magozzi et al. 2017), which can limit the ability to distinguish habitats at the foraging scale of red-footed boobies. Nevertheless, the wider δ^{13}C range at Diego Garcia may reflect the greater habitat heterogeneity within the foraging range of red-footed boobies, such as submerged banks and deep oceanic waters (Trevail, Wood, et al. 2023). In contrast, Aldabra and Farquhar are atolls surrounded by more uniform oceanic waters.

During the non-breeding period, red-footed boobies at Farquhar had higher δ^{15}N values than those at Aldabra and Diego Garcia. However, these differences were small, and when combined with the absence of δ^{13}C variation, this suggests the occurrence of more homogeneous marine isotopic gradients or isotopically similar prey among colonies during the non-breeding period. Additionally, isotopic niche widths of birds at Diego Garcia and Farquhar were similar, suggesting comparable resource use. The use of additional methods, such as compound-specific nitrogen isotope analyses of amino acids, would distinguish between trophic level and baseline influences on consumer isotopic ratios (Quillfeldt and Masello 2020). Despite this limitation, the combined differences in diet, isotopic ratios, and niche widths observed among colonies suggest trophic niche plasticity in red-footed booby populations in the tropical Indian Ocean, aligning with their known foraging behavioral plasticity (Trevail, Wood, et al. 2023; Nicoll et al. 2025).

4.3 | Intra-Annual Differences

The tropical Indian Ocean exhibits strong contrasts in oceanographic conditions between monsoon seasons, especially north of 10° S. The northwest monsoon is characterized by warmer, oligotrophic waters, whereas the southeast monsoon brings cooler waters and phytoplankton blooms (Lévy et al. 2007). These seasonal shifts are likely to promote intra-annual differences in isotopic niches, since red-footed boobies depend on terrestrial breeding sites throughout the year (Votier et al. 2024). In our study, the breeding and non-breeding periods coincided with the northwest and southeast monsoons, respectively. We observed intra-annual differences in isotopic ratios and niche widths at all colonies, consistent with our predictions. Red-footed booby isotopic niches showed little or no overlap between breeding and non-breeding periods, and isotopic ratios shifted toward higher δ^{15}N and δ^{13}C values during the non-breeding period (southeast monsoon). This seasonal shift may be driven by changes in prey composition and availability (Jafari et al. 2021; Ramírez et al. 2021). Warmer waters promote the spawning, growth, and abundance of flying fishes (Oxenford et al. 1994; Lewallen et al. 2018) and squid (Donahue et al. 2021). Indeed, lower proportions of squid have been recorded in the diet of breeding red-footed boobies at Aldabra during the cooler southeast monsoon (Diamond 1974). Moreover, aggregations of subsurface predators, such as tuna and billfish, increase during the southeast monsoon (Danckwerts et al. 2014), which drive prey to the surface and improves foraging opportunities for seabirds. These prey dynamics may also explain the broader isotopic niche widths during the non-breeding period (southeast monsoon) than the breeding period (northwest monsoon) at all three colonies, suggesting greater diet diversity during the southeast monsoon, when surface waters are overall more productive.

Seabirds breeding at Aride Island (4° S, Seychelles), such as white-tailed tropicbird *Phaeton lepturus*, lesser noddy *Anous tenuirostris*, and white tern *Gygis alba*, also exhibited higher δ^{15}N and δ^{13}C values during the southeast monsoon (Catry et al. 2008), suggesting an enrichment in baseline isotopic signatures during this season. At Clarion Island (Pacific Ocean), intra-annual variation in environmental conditions is less pronounced, and red-footed boobies did not show shifts in δ^{13}C values between breeding and non-breeding periods (Lerma et al. 2024). Shifts in δ^{13}C values observed in our study may also reflect changes in foraging areas between breeding and non-breeding periods, potentially driven by intraspecific competition. At all three colonies, red-footed boobies breed during both seasons, and tracking studies show that breeding individuals use the same foraging areas during the northwest and southeast monsoons (Trevail, Wood, et al. 2023). Being less constrained by their colonies, non-breeding individuals can therefore exploit alternative foraging areas to reduce competition, even if they return to the colony to roost. Further studies using approaches that integrate biotelemetry with tissue isotopes are needed to delineate and clarify spatiotemporal variations in marine isotopic gradients in this region (Ceia et al. 2018).

4.4 | Interspecific Differences

At Aldabra, red-footed boobies and lesser frigatebirds form single and mixed species breeding colonies in mangrove forests (Diamond 1973, 1974). During breeding, the two species did not differ in δ^{13}C values and showed similar isotopic niche widths, suggesting that they foraged in similar areas and on the same variety of prey, respectively. Lesser frigatebirds frequently engage in kleptoparasitism of red-footed boobies on Aldabra (Diamond 1973). In addition, at-sea observations show that red-footed boobies and lesser frigatebirds form foraging associations, aligning with our results (Jaquemet et al. 2005). Nevertheless, in line with our predictions, niche partitioning was evident because lesser frigatebirds displayed higher δ^{15}N values than red-footed boobies, and the two species had low niche overlap. Given the kleptoparasitic interactions between the two species, these differences might be attributed to species-specific fractionation patterns (Young, McCauley, et al. 2010). It could also suggest that when lesser frigatebirds forage for their own prey, they consume a greater proportion of higher trophic level organisms. This is plausible given their larger bills, which enable them to capture larger prey species at higher trophic levels than red-footed boobies (Mancini et al. 2014). Additionally, lesser frigatebirds do not undertake plunge dives and consequently capture different prey species. During the non-breeding period, lesser frigatebirds had a larger isotopic niche width than red-footed boobies. After breeding, lesser frigatebirds disperse widely over oceanic areas, allowing them to access a greater variety of habitats and prey, resulting in a wider isotopic niche (Cherel et al. 2008). Lesser frigatebirds also exhibited lower δ^{13}C values, indicating a pelagic foraging habitat (Cherel and Hobson 2007), further supporting their post-breeding migratory behavior. The isotopic niches of red-footed boobies and lesser frigatebirds overlapped slightly during the non-breeding period, suggesting that the two species share a subset of their prey diversity. The isotopic ratios of red-footed boobies and lesser frigatebirds, across both breeding and non-breeding periods, are consistent with those reported from Europa Island, located in the southwestern Indian Ocean (Cherel et al. 2008).

At Farquhar, brown noddies can nest simultaneously with red-footed boobies (Duhec et al. 2017). The isotopic niche widths of both species were generally similar and overlapped partially during both breeding and non-breeding periods, suggesting similarities in their prey diversity. Brown noddies feed on a broad range of pelagic juvenile fish, including flying fish, and can consume high proportions of squid (Catry et al. 2009; Villard et al. 2015). However, their isotopic signatures were segregated along both the $\delta^{15}N$ and $\delta^{13}C$ axes. During the breeding period, brown noddies displayed lower $\delta^{15}N$ values than red-footed boobies. This suggests they consumed a greater proportion of prey from lower trophic levels, which is consistent with their smaller size (Mancini et al. 2014). Because they forage by surface dipping, they also capture different prey species than red-footed boobies. In the non-breeding period, brown noddies are short or long distance migrants (Votier et al. 2024). Accordingly, they exhibited a more pelagic signal with lower $\delta^{13}C$ values than non-migratory red-footed boobies.

5 | Conclusion

Red-footed booby abundance and distribution have increased across the tropical Indian Ocean (Duhec et al. 2017; Carr et al. 2021; Risi et al. 2025), making the species a valuable indicator for monitoring marine conditions in this region. Long-term recovery of red-footed booby populations relies not only on land-based conservation efforts and research to understand their foraging patterns but also on fisheries management. To support this, our study fills an important knowledge gap in the trophic ecology of red-footed booby colonies in this region by documenting diet and quantifying geographic and seasonal variations in their isotopic niches. Our results show diet and trophic niche plasticity, potentially linked to local environmental conditions, breeding stage, and colony-specific factors. While seabird isotope ecology is a well-established tool in temperate and polar oceans for monitoring long-term environmental change and its impacts on seabird populations (Will and Kitaysky 2018; Ceia et al. 2023; Cherel et al. 2025), its application remains limited in tropical regions. Our study provides important baselines to facilitate similar monitoring efforts in the tropical Indian Ocean.

Author Contributions

Conceptualization: J.A., N.B., and S.J. Data curation and methodology: J.A., J.L., A.H. and C.W.J. Formal analysis, writing – original draft: J.A. Writing – review and editing: N.B., J.L., A.H., C.W.J., N.A.J.G., and S.J.

Acknowledgments

We thank the Seychelles Islands Foundation, Island Conservation Society, Island Development Company and the crew of the BPV Grampian Frontier (BIOT Reef1 2022 expedition) for providing island access and logistical and administrative support during the fieldwork in 2022 and 2023. Thank you to individuals who assisted with field sampling, including Ervin Ally on Aldabra, Annie Gendron on Farquhar, and Nia Stephens on Diego Garcia. This study received funding from the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science (N.A.J.G). J.A. was supported by a doctoral fellowship from the Région Réunion. Open access publication funding provided by COUPERIN CY26.

Funding

This work was supported by the Bertarelli Foundation through the Bertarelli Programme in Marine Science, and the Région Réunion Doctoral fellowship.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author, Jennifer Appoo, upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Results of GLMMs fitted to test differences in red-footed booby $\delta^{15}N$ and $\delta^{13}C$ values among colonies (Aldabra, Farquhar and Diego Garcia) and periods (breeding and non-breeding), with bird ID as random effect. Statistically significant results ($p < 0.05$) are marked in bold. df: Degree of freedom. **Table S2:** Results of post hoc contrast tests applied to GLMMs to test differences in isotopic ratios among red-footed booby colonies during each period. Statistically significant results ($p < 0.05$) are marked in bold. **Table S3:** Results of post hoc contrast tests applied to GLMMs to test differences in isotopic ratios between breeding and non-breeding periods for each colony. Statistically significant results ($p < 0.05$) are marked in bold. **Table S4:** Isotopic niche areas and overlap between red-footed boobies and other species, during the breeding and non-breeding periods. CI: credible intervals. **Figure S1:** Isospace plot showing mean ± SD of $\delta^{15}N$ and $\delta^{13}C$ values for red-footed booby whole blood (gray points), alongside mean ± SD values of regurgitated prey items from colonies on Aldabra, Farquhar and Diego Garcia. Small gray points represent an individual bird. Prey values were corrected using trophic discrimination factors of 1.96‰ ± 0.79‰ for $\delta^{15}N$ and 0.32‰ ± 0.86‰ for $\delta^{13}C$ (Austin et al. 2021). **Figure S2:** Isotopic niche of red-footed boobies at (a) Aldabra, (b) Farquhar and (c) Diego Garcia, based on standardized whole blood, and body feather values, representing the breeding and non-breeding periods, respectively. Full and dashed lines represent standard ellipses at 40% (SEA_C) and 95%, respectively. Points represent individual measurements. **Figure S3:** Isotopic niche of red-footed boobies and lesser frigatebirds at Aldabra during the (a) breeding (whole blood) and (b) non-breeding (body feathers) periods. Isotopic niche of red-footed boobies and brown noddies at Farquhar during the (c) breeding (whole blood) and (d) non-breeding periods (body feathers). Full and dashed lines represent standard ellipses at 40% (SEA_C) and 95%, respectively. Points represent individual measurements. **Figure S4:** Bayesian standard ellipse areas (SEA_B) of red-footed boobies and other seabirds at (a) Aldabra and (b) Farquhar, during the breeding and non-breeding periods. Points are posterior modes, and thick and thin lines are 50% and 95% credible intervals, respectively.