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Trophic segregation inferred from stable isotopes between two sympatrically breeding tern species in the Mexican Caribbean

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Research Article

Keywords: $\delta^{13}C$, δ15 isotopic niche, resource partitioning, tropical seabirds, trophic ecology

Posted Date: September 10th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10757555/v1

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Additional Declarations: No competing interests reported.

Abstract

Resource partitioning facilitates coexistence among sympatric marine predators, yet its seasonal dynamics remain poorly understood in tropical ecosystems. The Sooty (*Onychoprion fuscatus*) and Bridled Terns (*O. anaethetus*) frequently breed sympatrically, but little is known about their trophic resource use across the annual cycle. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios were used to assess their trophic niche characteristics in the Mexican Caribbean during the pre-laying and non-breeding periods using chick down and adult feathers respectively. Samples were collected between April and May 2025 at 21.26° N, 86.75° W. Isotopic niches were characterized using Bayesian multivariate models and standard ellipse metrics, with species differences evaluated from posterior distributions and ellipse overlap. During the pre-laying period, both species showed similar $\delta^{13}C$ and $\delta^{15}N$ centroid positions, but Sooty Tern females occupied a significantly broader isotopic niche, primarily due to greater variation in $\delta^{13}C$. During the non-breeding period, no significant differences were detected in isotopic niche metrics, although overall niche overlap remained limited. Interspecific differences in the isotopic niches during the pre-laying period may reflect reproductive constraints on resource acquisition, whereas increased overlap during the non-breeding period suggests greater flexibility in habitat and resource use. The limited niche overlap observed between species suggests that trophic differentiation may contribute to their coexistence These findings highlight the importance of seasonal resource partitioning in tropical marine predator communities and provide new insights into sympatric seabird trophic ecology in the Caribbean.

Introduction

Seabirds are important marine predators and can serve as indicators of marine ecosystem conditions (Piatt et al. 2007; Parsons et al. 2008). Their trophic ecology provides valuable insights into marine food-web structure, prey availability, and ecosystem functioning, making seabirds effective sentinels of environmental change (Cairns 1988; Sydeman et al. 2015). Therefore, understanding how seabirds exploit marine resources is fundamental to predicting their responses to growing anthropogenic pressures, including overfishing, pollution, and climate change.

Research on seabird ecology has been biased toward temperate and polar species, while tropical seabirds remain comparatively understudied (Weimerskirch 2007). This represents an important knowledge gap because their direct trophic interactions with prey remain poorly documented (Cumming et al. 2024). Tropical marine environments are characterized by highly patchy and relatively unpredictable prey resources, which may impose significant constraints on seabird foraging and breeding (Weimerskirch 2007). These environmental conditions may promote unique foraging strategies and mechanisms of resource partitioning that remain poorly understood (Pontón-Cevallos et al. 2017; Soanes et al. 2021).

In this context, knowledge gaps are particularly pronounced in the Caribbean Sea, where information on the trophic ecology of breeding seabirds remains scarce despite the presence of important breeding

colonies (Bradley and Norton 2009). Most studies have focused on breeding biology, colony dynamics, reproductive success, habitat selection, and migration (Schreiber and Lee 2000; Bradley and Norton 2009), whereas comparatively few have examined diet composition, trophic niche, or resource partitioning using modern ecological approaches such as stable isotope analysis (Cumming et al., 2014). Consequently, the ecological mechanisms underlying the sympatric coexistence of Caribbean seabirds that exploit similar marine resources remain poorly understood, particularly outside the breeding season (Barrett et al. 2007; Cumming et al. 2024).

In addition to environmental variability, the ecology of colonial seabirds is strongly shaped by density-dependent competition for food. Ashmole (1963)proposed that breeding colonies deplete prey resources in waters around nesting sites, creating gradients of prey availability that increase with colony size, a concept widely known as Ashmole's halo. Subsequent empirical evidence from a tropical seabird colony on Ascension Island provided direct support for this mechanism, showing reduced prey densities near the colony and increasing prey availability with distance from the breeding site (Weber et al. 2021). Under this hypothesis, seabirds breeding in larger colonies are expected to face stronger intraspecific competition and to travel farther from the colony to locate prey (Ashmole, 1963; Lewis et al., 2001). Numerous studies have since documented the effects of colony size on seabird foraging behavior, demonstrating longer foraging trips, expanded foraging ranges, and greater individual variation in resource use (Lewis et al., 2001; Wakefield et al., 2013). These density-dependent processes may ultimately influence trophic niche width and resource partitioning among sympatric species, yet their role in tropical seabirds remains largely unexplored.

The Sooty Tern (*Onychoprion fuscatus*) and the Bridled Tern (*O. anaethetus*) are among the most widespread tropical seabirds, breeding colonially on offshore islands and cays throughout the tropical and subtropical regions of the Atlantic, Indian, and Pacific oceans (Haney et al. 2020; Schreiber et al. 2020). Although they often nest sympatrically and share broadly similar life histories, they differ in several aspects of their ecology, including colony size, nesting habitat, and foraging behavior (Garcia-Quintas, Barbraud, et al., 2024; Garcia-Quintas, Bustamante, et al., 2024; Harrison, 1985; Schreiber, 2020). Both species feed primarily on small pelagic fish and squid, but Sooty Terns are highly oceanic and commonly exploit prey concentrated near the surface by predatory fish such as tuna, whereas Bridled Terns tend to forage closer to continental or island shelves and frequently exploit localized prey concentrations, including those associated with floating Sargassum (Soanes et al. 2021; Reynolds et al. 2021). During the breeding season, they become central-place foragers, and their foraging is constrained by the need to provision offspring and return regularly to the colony (Corman et al. 2016; Garcia-Quintas et al. 2024b, a), making the breeding season particularly suitable for investigating trophic niche dynamics and potential mechanisms of resource partitioning.

Understanding the trophic ecology of these species is increasingly important because seabirds worldwide are experiencing population declines linked to fisheries interactions, habitat degradation, invasive species, pollution, and climate-driven changes in marine food webs (Dias et al. 2019). Identifying the trophic resources and foraging strategies of sympatrically breeding seabirds provides

essential information for understanding their ecological requirements and for developing effective conservation strategies, particularly in tropical regions where baseline ecological information remains limited.

Carbon isotope ratios ($\delta^{13}C$) provide information primarily on foraging habitat and carbon sources, whereas nitrogen isotope ratios ($\delta^{15}N$) are commonly used to infer relative trophic position (Cherel et al. 2007). Specifically, we compared isotopic niche position, breadth, orientation, and overlap between species during the pre-laying and non-breeding periods to determine whether they exhibit trophic differences despite their ecological similarities. Stable isotope analysis of feathers offers a valuable opportunity to investigate trophic ecology across temporal windows. Feathers provide an isotopic record of the period during which they were grown, allowing inference of dietary and foraging information for non-breeding periods when adult birds are otherwise difficult to sample (Bridge et al., 2007; Cherel et al., 2000). By contrast, chick down reflects the isotopic composition from the maternal nutrients allocated to the egg during the pre-laying period (Ausems et al., 2020). In this study, we used stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from adult feathers and chick down to understand the trophic ecology of sympatrically breeding Sooty and Bridled Terns in the Mexican Caribbean during two periods of their annual cycle. We hypothesized that sympatric Sooty and Bridled Terns would exhibit partial trophic niche segregation despite broadly similar trophic positions. We predicted that this segregation would be expressed primarily through differences in isotopic niche breadth and $\delta^{13}C$ values, reflecting variation in foraging habitat use, whereas $\delta^{15}N$ values would show comparatively limited differentiation. We further predicted that both species would exhibit relatively narrow isotopic niches during the pre-laying period, reflecting restricted resource use associated with reproductive preparation. Additionally, based on Ashmole's halo hypothesis, we expected the species with the substantially larger breeding population at the study colony to have a broader isotopic niche than the other species, potentially reflecting greater density-dependent competition and variation in resource use.

Materials and Methods

Study area

This study was conducted during the 2025 breeding season (April to August) on Isla Mujeres, Quintana Roo, Mexico (Fig. 1). Approximately 2,500 Sooty Tern nests and 25 Bridled Tern nests were monitored. The breeding colony is located on the northern tip of the island, within and around the grounds of the Mia Reef Isla Mujeres Hotel, where Sooty and Bridled Terns nest annually. This colony is the largest known breeding aggregation of both species in the Mexican Caribbean (Fundación MIA Sustentable, fundacionmiasustentable.org). The only other confirmed breeding site in the region is approximately 30 km north, on Isla Contoy, where fewer than 10 Bridled Tern nests are typically recorded each year (pers. comm).

The two species exhibited distinct nesting patterns within the colony. Sooty Terns nested predominantly in vegetated areas around the hotel, whereas Bridled Terns nested in rocky crevices and beneath

stairways and elevated structures along the open-air corridors. Since 2020, the Mia Reef Isla Mujeres Foundation has implemented a conservation program to protect breeding terns through habitat management, nest protection, and public awareness. These actions have been linked to a marked increase in breeding pairs and fledglings, making this colony one of the most important breeding sites for tropical terns in the Mexican Caribbean (Fundación MIA Sustentable 2025, fundacionmiasustentable.org).

Sampling

Incubating adults were captured manually during the first 10 days of incubation (from April 19th to May 3rd), in order to collect their feathers. At this stage, adult body feathers had not yet been replaced during the current breeding season. Therefore, the sampled feathers provided trophic information on adults from the previous non-breeding period (Cherel et al., 2000). From each adult, the second primary feather (P2) of the left wing and the eighth secondary feather (S8) of the right wing were collected (17 Sooty and 5 Bridled Terns). Because no significant differences in $\delta^{13}C$ or $\delta^{15}N$ values were detected between the two feather types (Table S1), P2 was selected for subsequent analyses. Down feathers were collected from chicks' necks between 10 and 15 days after hatching (from May 24th to June 2nd, 18 Sooty and 5 Bridled chicks). The isotopic composition of chick down integrates maternal nutrients allocated to the egg during follicle development and egg formation, thus representing the trophic information of pre-laying adult females (Ausems et al., 2020). All feather samples were stored and labeled individually in paper envelopes until laboratory analysis.

Isotope Analyses

Isotope analyses of feathers were conducted at the Stable Isotopes Laboratory (LAIE) of the Chemistry Faculty at the National Autonomous University of Mexico in Yucatan. Feathers were cleaned to remove surface contamination by sequentially rinsing them with deionized water, ethanol, and deionized water again. They were then oven-dried at a temperature not exceeding 60°C for 24 h and allowed to cool at room temperature. The clean, dry feathers were cut into small fragments with scissors, and approximately 1 mg of each sample was weighed into tin capsules for subsequent isotopic analysis. The samples were combusted using a Costech ECS 4010 Elemental Analyzer equipped with a Zero Blank autosampler, coupled via continuous flow to a Thermo Scientific Delta V Plus Isotope Ratio Mass Spectrometer. Isotopic compositions were expressed in delta notation (δ), according to the following equation:

$$\delta X\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X represents $\delta^{13}C$ or $\delta^{15}N$ isotope, and R represents the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotope ratio. The internationally accepted reference scales were Vienna Pee Dee Belemnite (VPDB) for carbon

and atmospheric nitrogen (AIR) for nitrogen. External lipids removal from feathers and down through the cleaning treatment was successful since the C:N ratios were all < 3.5 (Table S2).

Data analysis

The isotopic niche ($\delta^{13}C$ and $\delta^{15}N$) of each species was modeled for pre-laying adult females (based on down) and non-breeding adults (based on feathers), using the Stable Isotope Bayesian Ellipses approach (Jackson et al., 2011). This method enables quantification of the isotopic δ-space from data, facilitating the computation of standard ellipses using a Bayesian approach. The ellipses represent the isotopic niches and are derived from the variance-covariance matrix of the data. We generated the standard ellipses corrected for small sample sizes solely for illustrative purposes, while 500 replicates of Bayesian standard ellipses were simulated to characterize the isotopic niches. To construct the Bayesian standard ellipses, we fitted a Bayesian multivariate normal distribution to the dataset using the "rjags" package (Plummer, 2023). This procedure uses Markov chain Monte Carlo models based on iterated Gibbs sampling (Jackson et al., 2011). The following ‘parameters’ were utilized in the Bayesian standard ellipses simulation: 2,500 iterations, 1,000 burn-in, 10 thin, and 2 chains; and the 'priors' were: R = 1 * diag(2), k = 2, and tau.mu = 0.001.

We computed six metrics from the Bayesian standard ellipses as proxies for characterizing different features of the trophic niche: (1) centroid-$\delta^{13}C$ and (2) centroid-$\delta^{15}N$ (‰) — indicators of the mean tendency in foraging habitats and trophic level (based on consumed prey), respectively; (3) semi-axis-$\delta^{13}C$ and (4) semi-axis-$\delta^{15}N$ (‰), defined by the bivariate standard deviations of the data set — thus indicating the respective niche extents across the variety of foraging habitats and trophic levels occupied—; (5) orientation (ranging between 0° and 180° relative to the $\delta^{13}C$ axis), calculated from the variance-covariance matrix and providing insights into the relationship between both isotopes, and consequently between the foraging habitats and trophic positions; and (6) area ($‰^2$), which constitutes a proxy of the niche breadth. We compared the ellipse metrics between species by pre-laying adult females and non-breeding adults, calculating the probability that the posterior distribution —from the 500 replicates— of one ellipse metric is larger than the other: p = sum (metric [ellipse X] > metric [ellipse Y]) / 500 (Jackson & Parnell, 2023). We considered significance for 0.025 > p > 0.975, corresponding to an α = 0.05 for a 2-tailed test.

The pairwise overlap of standard ellipses for pre-laying females and non-breeding adults was calculated using the maximum-likelihood ‘maxLikOverlap’ function, with ellipses fitted to 95% of the data. The isotopic niche overlap between species was calculated as a proportion of the sum of the non-overlapping areas of the ellipses: 100 × (Ellipse overlapping areas / (Σ Ellipse areas - Ellipse overlapping areas)) by species, and 100 × (Ellipse overlapping area / Σ Ellipse areas) for each community (i.e., pre-laying adult females and non-breeding adults). Overlap ranges from 0% if the ellipses are completely separated to 100% if they align completely. All data analysis and graphical representation were conducted using R 4.4.2 (R Core Team, 2024).

Results

In general, the $\delta^{13}C$ and $\delta^{15}N$ isotopic values from both tissues exhibited low variability across both tern species (Table S2).

Pre-laying adult females

During the pre-laying period, the isotopic niche of Sooty Tern females was broader than that of Bridled Tern females (Fig. 2), and both niches differed significantly across three ellipse metrics (Fig. 3, Table S3). Specifically, the $\delta^{13}C$ semi-axis and area of Sooty Terns were larger than those of Bridled Terns and the orientation of the Bridled Tern ellipse was significantly different (*i.e.*, right-oriented) from that of the Sooty Terns (left-oriented). The remaining ellipse metrics did not differ between pre-laying females of the two species (Fig. 3, Table S3). Overall, isotopic niche overlap between pre-laying females of the two species was low (11.29%), although, independently, Bridled Terns showed higher overlap than Sooty Terns (Fig. 2).

Non-breeding adults

The isotopic niche of non-breeding adults of the Sooty Tern was also broader than that of non-breeding adults of the Bridled Tern (Fig. 2). However, there were no significant differences in the ellipse metrics between the two species (Fig. 4, Table S3). The overall isotopic niche overlap among non-breeding adults was slightly higher (17.21%) than that observed between pre-laying adult females. The non-breeding adults of the Bridled Tern exhibited greater niche overlap than those of the Sooty tern (Fig. 2).

Discussion

Despite their widespread distribution across tropical oceans (Haney et al. 2020; Schreiber et al. 2020), relatively little is known about the trophic ecology of Sooty and Bridled Terns in the Caribbean (Garcia-Quintas et al., 2024a; Cumming et al., 2024). Our results provide the first isotopic evidence that both species are trophic specialists during the breeding and non-breeding seasons in the Mexican Caribbean. Nevertheless, differences in isotopic niche metrics indicate some degree of trophic differentiation between the species, despite their similarly narrow niche widths. Such differentiation may reduce interspecific competition and facilitate coexistence among these sympatric seabirds.

Both the Sooty and Bridled Terns exhibited narrow isotopic niche widths (SEAc < 1‰), indicating limited variation in their feeding and foraging niches during the early breeding season and a high degree of trophic specialization. This finding aligns with recent studies describing both species as dietary specialists that rely on a relatively restricted range of prey and foraging habitats while breeding (Garcia-Quintas et al., 2024a, b). Such specialization may increase vulnerability if preferred prey become less available, particularly during the pre-laying period, when females must acquire the nutrients required for egg formation and reproduction. The restricted isotopic niches observed in both species may therefore reflect the use of a relatively limited set of prey resources capable of meeting the energetic and

nutritional requirements of egg production. Although trophic specialization may enhance foraging efficiency under stable environmental conditions, it also reduces dietary flexibility, potentially increasing susceptibility to environmental perturbations that alter prey availability or the quality of foraging habitats (Zango et al. 2019). In tropical marine ecosystems, prey resources are typically patchy and exhibit greater spatial and temporal variability than at higher latitudes, posing additional challenges for breeding seabirds that rely on consistent prey delivery to provision their chicks (Weimerskirch 2007; Soanes et al. 2021). Consequently, dependence on a limited suite of prey resources could increase sensitivity to changes in prey availability, with potential consequences for reproductive success and population resilience (Soanes et al. 2021, Dias et al. 2019).

The pre-laying period is one of the most energetically demanding stages of the annual cycle because females must acquire nutrients necessary for egg formation (Hobson 2006; Bond and Diamond 2010). Species-specific strategies for meeting these energetic and nutritional demands may explain the differences in niche width observed between Sooty and Bridled Terns (Garcia-Quintas, Barbraud, et al., 2024; Jaeger et al., 2017). These studies report that the pre-laying phase is a period of particular vulnerability for Sooty and Bridled Tern females, due to their dependence on a relatively restricted set of prey resources to meet the nutritional requirements of egg formation. The restricted isotopic niche observed in Bridled Terns in the present study is consistent with this hypothesis and suggests that reductions in prey availability or accessibility during this stage could disproportionately affect reproductive performance if preferred resources become less available or accessible. In contrast, the broader niche of Sooty Terns may indicate access to a wider range of habitats and the ability to obtain the resources required during egg formation. Contrary to Bridled Terns (with a right-oriented niche), female Sooty Terns exhibited a left-oriented trophic niche, indicating that individuals foraging close to the coast (high $\delta^{13}C$ values) consumed prey at lower trophic positions (low $\delta^{15}N$ values) than those foraging farther away. The opposite pattern occurred among pre-laying females of the Bridled Tern. These differences in niche orientation suggest that the relationship between foraging habitat use and trophic position differed between species during the pre-laying period, potentially contributing to trophic niche differentiation (Fig. 2).

An additional feature of the studied colony in Isla Mujeres is the apparently short interval between colony arrival and egg laying. Individuals were first observed at the colony on 2 April, and eggs were present by 9 April 2025, suggesting an interval of approximately one week between arrival and laying. This pattern contrasts with the more pronounced pre-laying exodus reported for Sooty Terns at Bird Island, Seychelles, where individuals spent approximately one month foraging in a distant area between colony arrival and egg laying (Jaeger et al., 2017). Although the available observations cannot rule out movements before colony arrival, they provide no evidence of a prolonged pre-laying exodus at Isla Mujeres. Such differences in breeding phenology may influence the mechanisms underlying pre-laying resource acquisition. A pre-laying exodus has been interpreted as a strategy that provides females with uninterrupted foraging opportunities to accumulate reserves required for egg production (Jaeger et al., 2017). In a colony where arrival is followed rapidly by egg laying, females may instead acquire the nutrients required for reproduction before reaching the colony or during a relatively short period

immediately preceding laying. Consequently, the narrow isotopic niches observed in both species may reflect not only restricted resource use but also temporal constraints associated with rapid preparation for reproduction.

There were no differences in $\delta^{13}C$ or $\delta^{15}N$ centroids between Sooty and Bridled Terns during the pre-laying period, suggesting that both species exploit comparable foraging habitats and occupy similar trophic positions (Bearhop et al. 2004; Newsome et al. 2007; Layman et al. 2012). However, pre-laying Sooty Tern females exhibited a significantly broader isotopic niche area than female Bridled Terns. According to (Bearhop et al. 2004), broader isotopic niches may result from greater dietary diversity, increased habitat use, or individual specialization within a population. In this study, the larger niche breadth observed in Sooty Terns appeared to be primarily associated with their larger $\delta^{13}C$ semi-axis relative to Bridled Terns. This suggests that Sooty Tern females may exploit a wider range of foraging areas than Bridled Terns during the pre-laying period, given the role of $\delta^{13}C$ in inferring the foraging habitats of seabirds (Cherel and Hobson 2007; Jaeger et al. 2010).

The relatively short interval between colony arrival and egg laying may also help explain the isotopic patterns observed between species. The broader $\delta^{13}C$ niche of Sooty Terns suggests greater variation in the foraging habitats or carbon sources contributing to maternal nutrient acquisition, whereas the narrower $\delta^{13}C$ niche of Bridled Terns may indicate more spatially constrained resource use during the pre-laying period. Stable carbon isotope ratios can provide information on marine foraging habitats because $\delta^{13}C$ varies geographically and can distinguish among different foraging areas or habitat types (Cherel & Hobson, 2007). However, because movements before colony arrival were not tracked, these interpretations remain tentative. Differences in $\delta^{13}C$ niche breadth could alternatively reflect variation in foraging areas used before birds reached the colony, rather than movements occurring during the short interval between arrival and laying.

Given the low overlap between niches, trophic interactions between pre-laying females of Sooty and Bridled Terns were limited. This pattern likely reflects trophic segregation among species to reduce or avoid competition just before reproduction. Coexistence between pre-laying females of these species does not appear to be driven by differences in trophic level but rather by other dimensions of resource partitioning, including the extent of the foraging habitat, trophic niche breadth, and individual-specific trophic differences. Habitat partitioning among sympatric seabird species is common and may facilitate coexistence by reducing interspecific competition (Petalas et al. 2021, 2024). Such behavioral flexibility may be particularly advantageous in tropical marine ecosystems, where prey distribution is often patchy and highly variable (Ballance et al. 1997). The higher niche overlap of female Bridled Terns relative to female Sooty Terns may not necessarily translate into strong interspecific trophic competition, given the substantial non-overlapping portion of the Sooty Tern niche. Thus, the two species may experience limited trophic competition during the pre-laying period.

No differences in ellipse metrics, and hence in isotopic niches, were detected among non-breeding adults of the Sooty and Bridled Terns, suggesting broadly similar isotopic niche characteristics. Although

the two species occupied similar trophic niches during the non-breeding period, overall overlap between isotopic ellipses was low, indicating trophic niche segregation. This pattern suggests that the species may use isotopically distinct resources despite similar niche breadths. Niche theory predicts that sympatric species can coexist when they partition resources along one or more ecological dimensions, thereby reducing interspecific competition (Petalas et al. 2021, 2024; Ceia et al. 2023).

The isotopic niches of non-breeding adults showed similar characteristics between Sooty and Bridled Terns, with no significant differences in ellipse metrics and limited overlap between their isotopic ellipses. This pattern indicates that some degree of interspecific trophic differentiation persisted outside the reproductive period, despite the absence of significant differences in niche characteristics. However, comparisons between the pre-laying and non-breeding periods should be interpreted cautiously because the pre-laying analysis included only females, whereas the non-breeding sample included both females and males. Therefore, the observed differences in niche overlap and breadth between periods cannot be attributed solely to seasonal changes in trophic ecology. Instead, the non-breeding results provide evidence that the two species continued to occupy partially differentiated isotopic niches outside the pre-laying period, while the extent to which this differentiation changes seasonally remains unresolved. This pattern is consistent with niche theory, which predicts that sympatric species can coexist by partitioning resources along one or more ecological dimensions, thereby reducing interspecific competition (Ceia et al., 2023; Petalas et al., 2021, 2024).

In the present study, trophic segregation appears to arise from differences in habitat use or resource diversity rather than from differences in trophic level. Similar mechanisms have been documented in other seabird communities (Lewis et al. 2001; Navarro et al. 2009; Wakefield et al. 2013). Although both species behaved as trophic specialists, one potential mechanism that could contribute to this pattern is density-dependent competition. Ashmole (1963) proposed that large seabird colonies can deplete prey resources around breeding sites, creating an “Ashmole’s halo” in which prey availability increases with distance from the colony. Under this mechanism, individuals breeding in larger colonies are expected to experience stronger intraspecific competition and may compensate by traveling farther from the colony or exploiting a greater diversity of foraging habitats and prey resources (Ashmole, 1963; Lewis et al., 2001; Wakefield et al., 2013). Empirical evidence from tropical seabird colonies has also shown reduced prey availability near large breeding aggregations, supporting the potential relevance of density-dependent competition in shaping foraging behavior (Weber et al., 2021). At Isla Mujeres, the breeding population of Sooty Terns was approximately 100 times larger than that of Bridled Terns, potentially exposing Sooty Terns to greater intraspecific competition for local prey resources. Such density-dependent effects could contribute to the greater variation in $\delta^{13}C$ observed in Sooty Tern females, if individuals from the larger colony exploited a wider range of foraging habitats or carbon sources. However, this interpretation remains tentative because the present study did not quantify colony-level prey depletion, prey availability, foraging ranges, or individual movements. Thus, the broader isotopic niche of Sooty Terns is compatible with the predictions of Ashmole’s hypothesis, but additional tracking and prey-availability data would be required to determine whether density-dependent competition contributes to the observed difference in niche breadth.

Understanding how species adjust their foraging strategies during energetically demanding periods is particularly important for conservation, as breeding seabirds may be highly sensitive to environmental changes affecting prey availability and access to key foraging habitats (Croxall et al., 2012; Sydeman et al., 2015). Our results suggest that coexistence between sympatrically breeding Sooty and Bridled Terns is not primarily associated with differences in trophic position, but rather with seasonal variation in habitat use, niche breadth, and resource use, consistent with evidence that sympatric seabirds can partition resources along multiple ecological dimensions (Ceia et al., 2023; Petalas et al., 2021, 2024). The significant trophic differentiation between adult females Sooty and Bridled Terns observed during the pre-laying period may reflect the nutritional demands and temporal constraints associated with reproduction (Bond & Diamond, 2010; Hobson, 2006), whereas greater niche overlap during the non-breeding period suggests that these differences may relax outside the reproductive context, when there are no constraints on foraging movements (Weimerskirch, 2007; Corman et al., 2016b). More broadly, our findings suggest that trophic coexistence among tropical seabirds may be structured not simply by persistent differences in trophic position, but by flexible, seasonally dependent use of habitats and resources. The findings of this work highlight the importance of considering multiple dimensions of the trophic niche when evaluating coexistence among tropical seabirds. From a conservation perspective, identifying differences in habitat use and resource dependence may help anticipate species-specific responses to changes in marine productivity, fisheries, and other anthropogenic pressures, particularly during energetically demanding periods of the annual cycle. Future studies combining stable isotope analyses with GPS tracking and prey-availability surveys could directly assess differences in foraging areas, movement patterns, and resource availability, and test whether density-dependent competition associated with colony size contributes to the broader isotopic niche observed in Sooty Terns.

Declarations

Funding

“This work was supported by the James A. Kushlan Research and Conservation Fund granted by Birds Caribbean to Adriana Vallarino for the period 2025 - 2026.”

Competing Interests

“The authors have no relevant financial or non-financial interests to disclose.”

Author Contributions

“Adriana Vallarino performed the study conception and design. Material preparation, samples and data collection in the field were performed by Carlos Barranco, Salvatore Martini and Adriana Vallarino. Samples preparation for isotope analysis were performed by Carlos Barranco, Salvatore Martini, Korynthia López Aguiar and Fernanda Lases. Statistical analysis and interpretation were carried out by Antonio Quintas. Figures were performed by Antonio Quintas. The first draft of the manuscript was

written by Adriana Vallarino and Antonio Quintas and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript."

Data Availability

"The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request."

Ethics approval

"The collection of feather samples from wild seabirds was conducted under a scientific wildlife collection permit issued by SEMARNAT, Mexico (Permit No. SPARN/DGVS/01847/25 addendum SBRA/DGVS/06332/25). All sampling procedures followed the conditions established in the permit and applicable Mexican wildlife regulations. Moreover, ethical approval was granted by the Escuela Nacional de Estudios Superiores Unidad Merida UNAM by the Ethics Committee in Research and Teaching (013/INV/2025.)"

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Figures



Figure 1

Location of the breeding colonies of the Sooty (*Onychoprion fuscatus*) and Bridled (*O. anaethetus*) Terns (black circle) in Isla Mujeres, Mexico, during the 2025 breeding season. Source of the map: own elaboration

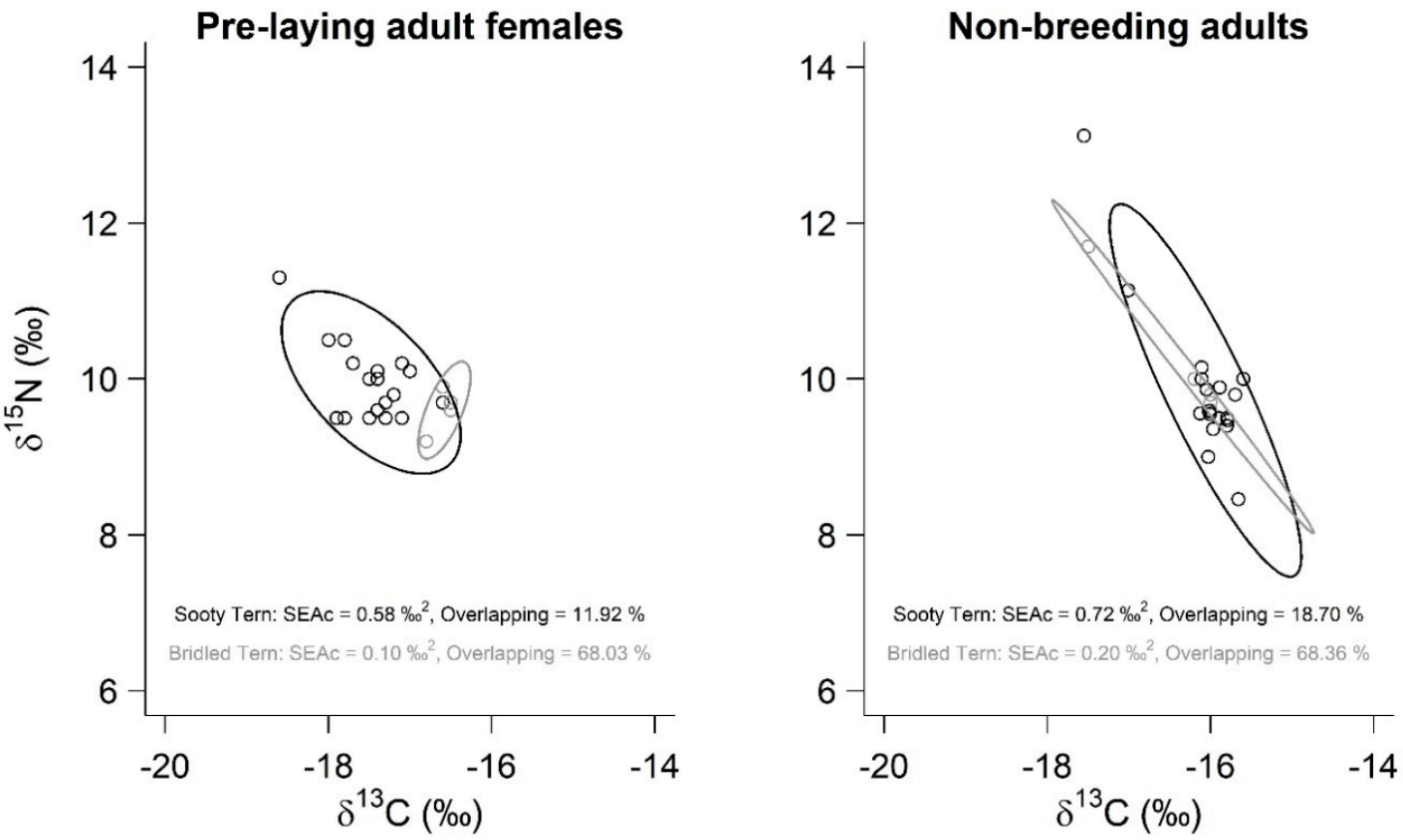


Figure 2

Bayesian standard ellipses representing the isotopic niches ($\delta^{13}C$ and $\delta^{15}N$) of pre-laying adult females (from chick down) and non-breeding adults (from adult feathers) of the Sooty (*Onychoprion fuscatus*) and Bridled (*O. anaethetus*) Terns breeding on Isla Mujeres, Mexico, in 2025. SEAc = standard ellipse areas corrected for small sample sizes.

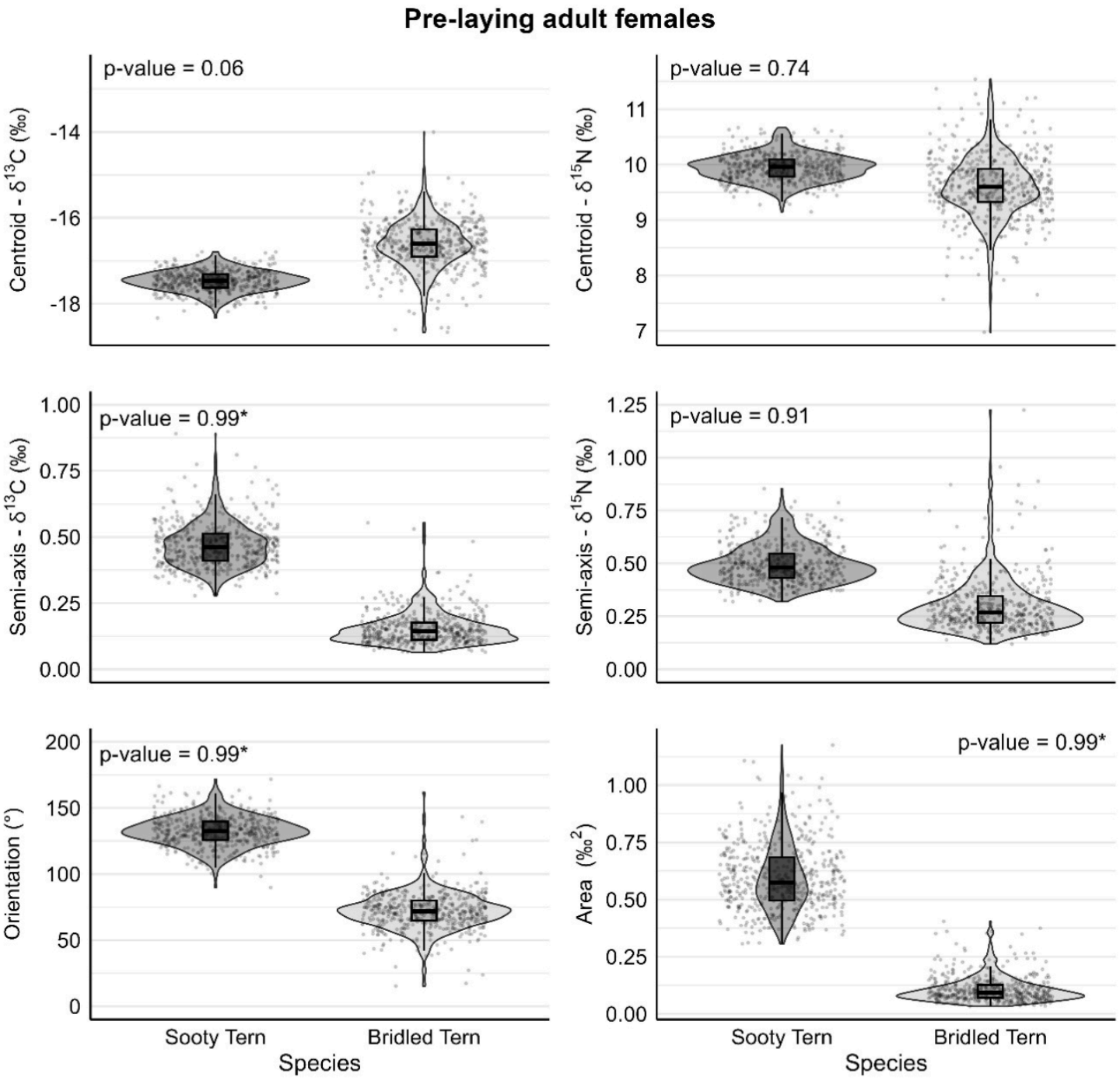


Figure 3

Comparison of six metrics for the Bayesian standard ellipses representing the isotopic niches ($\delta^{13}C$ and $\delta^{15}N$) of pre-laying adult females of the Sooty (*Onychoprion fuscatus*) and Bridled (*O. anaethetus*) Terns breeding on Isla Mujeres, Mexico, in 2025. * Significant differences.

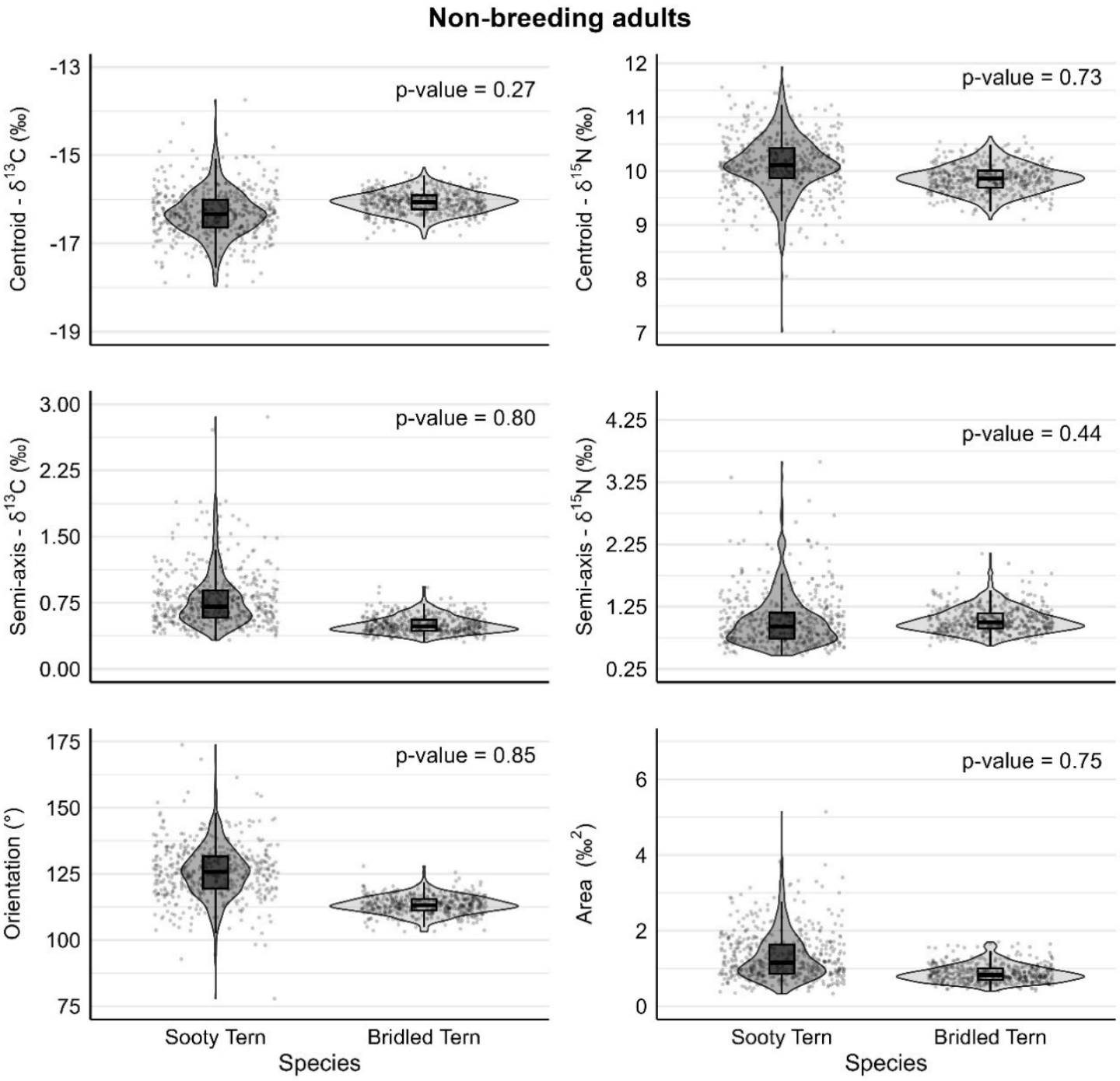


Figure 4

Comparison of six metrics for the Bayesian standard ellipses representing the isotopic niches ($\delta^{13}C$ and $\delta^{15}N$) of non-breeding adults of the Sooty (*Onychoprion fuscatus*) and Bridled (*O. anaethetus*) Terns breeding on Isla Mujeres, Mexico, in 2025.

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