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Plasticity and overlap of trophic niches in tropical breeding Laridae

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ABSTRACT: Trophic ecology of seabirds in tropical regions remains poorly understood despite the large number of multispecies breeding colonies supported by these ecosystems. Here, we used the isotopic niche ($\delta^{15}N$ and $\delta^{13}C$) of 5 Laridae species at 2 breeding areas in Cuba to analyze the plasticity and interspecific overlap of trophic niche determined from chick down and feather samples. The down samples reflected the female trophic regime before laying, while the feather samples incorporated the trophic regime of the chicks provided by the parents during rearing. Two main species groups were identified by their isotopic niche characteristics: species with small and quite stable isotopic niches (trophic specialists) and species with large and highly variable isotopic niches (trophic generalists). Laughing gull *Leucophaeus atricilla*, royal tern *Thalasseus maximus*, and sandwich tern *T. sandvicensis* were the generalists and showed significant isotopic niche differences between breeding areas and phases. Bridled tern *Onychoprion anaethetus* and roseate tern *Sterna dougallii* were trophic specialists, but only the former exhibited significant variations in isotopic niche breadth between breeding phases. Overall, trophic (inferred from isotopic) niche overlap was relatively low, suggesting that these tropical seabirds reduce competition through niche partitioning. We concluded that trophic niche plasticity and segregation appear to constitute an important adaptive strategy to ensure the breeding success of sympatrically breeding Laridae in north-central Cuba.

KEY WORDS: Niche overlap · Stable isotope analysis · Multispecies colonies · Breeding stages · Gulls · Terns

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1. INTRODUCTION

Studies on diet and feeding strategies of seabirds are key to understanding their ecology, changes in behavior, diets, and trophic position (Barrett et al. 2007). Most seabird populations display large seasonal changes in foraging behavior and diet patterns. The main contrast in foraging strategies occurs between the non-breeding and breeding periods when seabirds switch from a 'spatially free' (Ashmole 1963, Labbé et al. 2013, Lisnizer & Yorio 2019) to a 'central-place' (Ashmole 1963, Gatto et al. 2019, Lorentsen et al. 2019) foraging strategy. The latter limits the spatial extent that breeding seabirds can explore because of the need to return regularly to colonies to rear chicks (Paredes et al. 2015, Lamb et al. 2017). This induces changes in the diet compared to the non-breeding season (Barrett et al. 2007, Jaquemet et al. 2008). Also, the diet of adults may differ from that of chicks during the breeding season (Barrett et al. 2007, Jaeger et al.

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2017). Such differences in foraging and feeding behaviors can lead to patterns of intra- and interspecific segregation of trophic niches (Surman & Wooller 2003, Bolton et al. 2019, Gatto et al. 2019), thus reducing the competition level for trophic resources (Oppel et al. 2015, Ramos et al. 2020).

Stable isotope analysis is a widely used biochemical method for studying the trophic ecology of seabirds (e.g. Hobson 1990, Cherel et al. 2000, Barrett et al. 2007, Ausems et al. 2020). This technique is based on the natural variation in the proportions of stable isotopes of several chemical elements, where the proportions of heavier isotopes undergo changes relative to lighter isotopes as a function of differences in metabolic reaction rates (Inger & Bearhop 2008, Dunlop 2011). The δ^{15}N values allow to infer the trophic position and variety in the diet of the organisms due to the gradual and predictable increase along trophic transfers (Barrett et al. 2007, Ramos et al. 2020). The δ^{13}C values reflect the foraging areas and carbon sources used by species (Barrett et al. 2007, Cherel & Hobson 2007), as this compound varies naturally among primary producers with different photosynthetic pathways in the coastal—ocean gradient (Ramos et al. 2020).

Although a complete view of the trophic ecology of species would require an isotopic basis for the ecosystem, quantifying the isotopic signatures of predators alone allows basic descriptions, comparisons, and inferences on their trophic niches (e.g. Catry et al. 2008, Ausems et al. 2020). Newsome et al. (2007) conceptualized the isotopic niche wherein the stable isotope values are analogous to environmental variables associated with the ecologic niche. The isotopic niche summarizes the n-biochemical dimensions in a reduced number of axes (e.g. δ^{15}N and δ^{13}C), thus constituting a proxy of the trophic niche (Grecian et al. 2015), although the two are not exactly the same (Jackson et al. 2011).

Most studies on the trophic ecology of breeding seabirds have focused on polar and temperate regions, which highlights the lack of work on tropical ecosystems (Weimerskirch 2007). The lower productivity and seasonal variability of tropical marine environments compared to higher latitudes (highly variable, patchy, and unpredictable food resources) lead to specific foraging and diet patterns in tropical seabirds (Jaquemet et al. 2008, Oppel et al. 2015). However, despite these characteristics, tropical seas and oceans host a large diversity of breeding seabirds (e.g. the Caribbean, Bradley & Norton 2009). Stable isotope approaches can help to clarify traits of the trophic relations between tropical breeding seabirds, which are expected to be more complex than those of their counterparts in cold-water assemblages (Surman & Wooller 2003).

The West Indies are among the lesser studied tropical regions with regard to the trophic ecology of seabirds (e.g. Soanes et al. 2015, Madden & Eggermont 2020). However, this area hosts large breeding colonies with a total of 22 breeding species (Bradley & Norton 2009). Specifically, Cuba stands out with 14 species and more than 7100 breeding pairs (Jiménez et al. 2009). The cays of the north-central part of this country constitute one of the most important breeding centers, with the family Laridae (gulls and terns; Winkler et al. 2020) best represented and exhibiting different species-specific trophic behaviors (Table 1). Nevertheless, the basic trophic ecology patterns that allow sympatric reproduction of these species in Cuba are still unknown.

In this context, we aimed to assess (1) the trophic niche plasticity of Laridae species and (2) the trophic niche overlap within breeding communities and by pairs of species at 2 breeding locations in north-central Cuba. Both questions are analyzed considering that isotopic niche (δ^{15}N and δ^{13}C values) acts as a proxy for the trophic niche. Two periods of the breeding season were considered: pre-laying (adult females' niches) and rearing (chick niches) to infer the trophic niche patterns that allow several species to successfully breed in the same areas. Five Laridae species were considered, whereby laughing gull, royal tern, and sandwich tern were expected to be trophic generalists, while bridled and roseate terns were expected to be specialists considering the known differences in foraging behavior and diet characteristics of these species elsewhere (Table 1). Thus, we expected an interspecific isotopic niche segregation based on the contrasted foraging distances (inshore, offshore) and trophic positions during the breeding season. We also hypothesized that generalist species should display large and overlapping isotopic niches (because of the broad spectrum of trophic resources used), while the opposite was expected to occur for specialists.

2. MATERIALS AND METHODS

2.1. Study areas

Tissue samples from Laridae were collected in 3 cays (Felipe de Barlovento, Felipe de Sotavento, and Paredón de Lado) of the Sabana-Camagüey archipelago in the central-northern region of Cuba (Fig. 1). These low-lying cays are small in size (<0.1 km^2) and

Table 1. Trophic characteristics of 5 Laridae species during breeding

Species	Trophic pattern	Habitats and foraging strategy	Prey consuming	Interactions with sympatric breeding Laridae	References
Laughing gull	– Generalist – Opportunist	– Open seawater – Coasts – Estuaries – Open grassland – Agriculture – Urbanized coasts – Forages through the pick-up technique during the day and at night	Marine: – Fishes – Crabs – Shrimps – Bivalves Terrestrial: – Earthworms – Snails – Insects – Fruits – Plant materials Anthropogenic: – Bread – Chicken – Vegetables – Garbage	– Predator of eggs and chicks of terns	Dosch (2003) Raynor et al. (2012) Washburn et al. (2013) Garcia-Quintas et al. (2023)
Bridled tern	– Specialist	– Floating *Sargassum* spp. – Macro-algae reefs – Oligotrophic waters (near-offshore) with low salinity and productivity – Forages through the 'contact-dipping' strategy	– Small fishes – Marine invertebrates – Insects (sometimes)	–	Kohno & Kishimoto (1991) Dunlop & Surman (2012) Moser & Lee (2012) Labbé et al. (2013)
Roseate tern	– Specialist	– Inshore waters – Forages mainly by snatching food from the sea surface or by plunge-diving up to 1 m in depth, in association with predatory fish that facilitate the capture	– Low-diversity – Usually very small fish	–	Shealer (1996) Surman & Wooller (2003) Robertson et al. (2014)
Royal and sandwich terns	– Generalist	– From riverine estuaries to open ocean but nearshore – Mainly diurnal surface foragers	– Fishes – Invertebrates – Demersal prey – Fishing discards	– Trophic niche segregation among both species supported by the different proportions and sizes of prey consumed or by the different use of their foraging areas	Shealer (1996) McGinnis & Emslie (2001) Perrow et al. (2011) Liechty et al. (2016) Gatto et al. (2019)

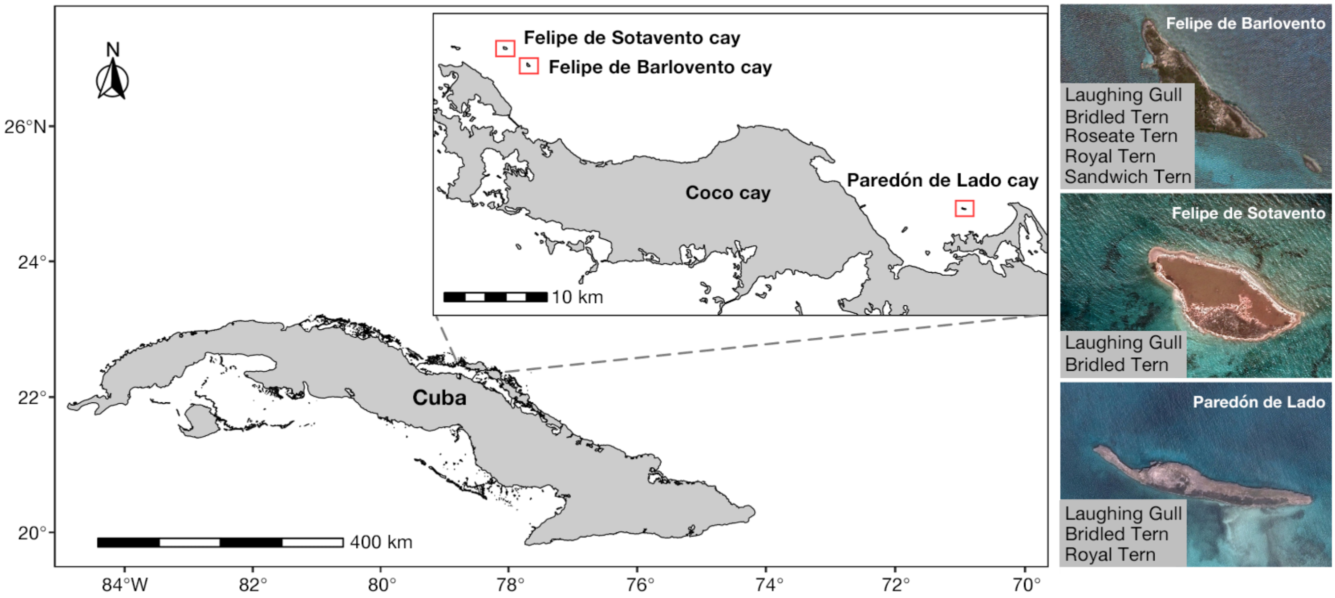

Fig. 1. Sampling areas in Cuba (cays enclosed by red squares) and breeding Laridae species during the 2021 breeding season

have sandy and rocky substrata with sparse vegetation (details in Garcia-Quintas et al. 2023). The entire area is one of Cuba's most important seabird breeding grounds, in terms of the number of species and breeding pairs. Felipe de Barlovento hosts the largest number of breeding Laridae species (6 in total, Jiménez et al. 2009).

This subtropical area has an average annual temperature of 26.3 ± 0.4°C, while its average monthly rainfall is 88.5 ± 18.1 mm. Easterlies (average annual wind speed: 14.5 ± 2.2 km h^{-1}) prevail year-round. From May to August (breeding season for Laridae species in Cuba, Garrido & Kirkconnell 2011), temperature values are 28.0 ± 1.0°C while precipitation averages 109.2 ± 83.1 mm for the entire period. Data were obtained from the Meteorological Station 78339 of the Coastal Ecosystem Research Center (Cayo Coco, Ciego de Ávila, Cuba).

2.2. Study species

Seven Laridae species bred in these cays during the 2021 breeding season; however, brown noddy *Anous stolidus* and sooty tern *Onychoprion fuscatus* were not considered in this study, as they had very low representation. Laughing gull *Leucophaeus atricilla* and bridled tern *O. anaethetus* nested on all 3 cays, royal tern *Thalasseus maximus* bred in Felipe de Barlovento and Paredón de Lado, and roseate tern *Sterna dougallii* and sandwich tern *T. sandvicensis* nested in Felipe de Barlovento (Fig. 1). The trophic profile of these species differs, showing great contrasts in their foraging strategies and the prey they consume (Table 1).

2.3. Tissue sampling and stable isotope analysis

During the 2021 breeding season (May to August), down (n = 123) and body feathers (n = 111) were collected from laughing gull, bridled tern, roseate tern, royal tern, and sandwich tern chicks in the studied cays according to colony composition (detailed sample sizes in Table S1 in the Supplement at www.int-res.com/articles/suppl/m742p131_supp.pdf). Both types of samples were pulled (small handful for down, 5 or 6 body feathers) from the chicks' back during the growth phase (a few days after hatching and before fledging) and stored in labeled plastic bags until analysis. The birds sampled were banded (ringed) for identification purposes, thus ensuring the collection of 1 tissue sample (down or feather) per individual (avoiding the risk of pseudoreplication). The down samples recorded the characteristics of the foraging areas and prey consumed by the mothers (adult females) during the pre-laying phase (a few days before egg laying), while the body feathers reflected the food provided by both parents to the chicks during their rearing (Klaassen et al. 2004, Ausems et al. 2020).

Down and body feathers were cleaned to remove surface contaminants using a 2:1 chloroform and methanol solution in an ultrasonic bath, followed by 2 methanol rinses. They were then oven dried for 24 h at 45°C and cut into small fragments with stainless steel scissors. Approximately 0.3 mg of down and body feather homogenates were encapsulated in tin cups. Their stable isotope values were subsequently determined by a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyzer (Thermo Scientific Flash 2000) at La Rochelle University, France. Stable isotope values are reported following the δ notation and expressed as ‰ according to the equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N, R is the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N, and R_{standard} is the ratio of international references Vienna PeeDee Belemnite for carbon and atmospheric N_2 (AIR) for nitrogen. Replicate measurements of internal laboratory standards (USGS-61 and USGS-62) indicated measurement errors <0.10 and <0.15‰ for δ^{13}C and δ^{15}N, respectively. C:N ratios were consistently below 3.5 (Table S1), indicating that lipids from preen oil were efficiently removed by the cleaning treatment.

2.4. Data analysis

As Felipe de Barlovento and Felipe de Sotavento cays are very close to each other (Fig. 1), they were pooled and thus 2 breeding areas were considered for the data analysis: the Felipes and Paredón de Lado (hereafter FBA and PBA, respectively). Furthermore, 2 breeding phases were considered: pre-laying and rearing, represented by chicks' down and feathers, respectively, considering the aforementioned tissue stable isotope significance (Fig. 2). Isotope values were expressed as mean ± SD.

The δ^{15}N and δ^{13}C isotopic niches of the species by breeding phase and breeding area were calculated using the Stable Isotope Bayesian Ellipses method (Jackson et al. 2011). This method quantifies the isotopic δ-space from data using Bayesian inference based on the metric of multivariate standard ellipses. The ellipses represent the core of the isotopic niches and are computed from the variance and covariance of the bivariate data matrix. This approach corrects for the effects of small sample sizes by generating standard ellipse areas (SEAc, representing the isotopic niche breadth) that facilitate comparisons between spaces and the overlap of core isotopic niches (Jackson et al. 2011). Centroids (δ^{13}C, δ^{15}N) were extracted from the ellipses (indicating mean isotopic niche position) and together with SEAc were the metrics used to characterize the isotopic niche by species in each breeding phase and breeding area.

Variations in the species' isotopic niches were assessed by comparing the centroid position (predicted mean of δ^{13}C and δ^{15}N) and SEAc of ellipses between breeding areas and between breeding phases (Fig. 2). Isotopic niche differences between breeding phases and areas were addressed at the species level (not at the individual level) because the diet of breeding seabirds may vary between adults and chicks, sexes, and within breeding seasons (Barrett et al. 2007, Jaeger et al. 2017). Nevertheless, it is also important to consider that the trophic niche width of the chicks may be broader than that of the pre-laying mothers because they are fed by both parents, who may specialize in different prey.

We first fitted Bayesian multivariate normal distributions to each group (i.e. each species–breeding phase–breeding area combination) of the data set using the R package 'rjags' (Plummer 2023). This method is based on iterated Gibbs sampling using Markov chain Monte Carlo models (Jackson et al. 2011). 'Parms' parameters of the built model included 1500 iterations, 1000 burn-in, 10 thin, and 2 chains, while the 'priors' used were R = 1 × diag(2), k = 2, and tau.mu = 0.001 (further parameterization details in Jackson & Parnell 2023).

Each of the metrics was then calculated for 300 replicates of the fitted ellipses. To compare the intraspecific isotopic niche between breeding areas and phases (Fig. 2), we calculated the probability that the

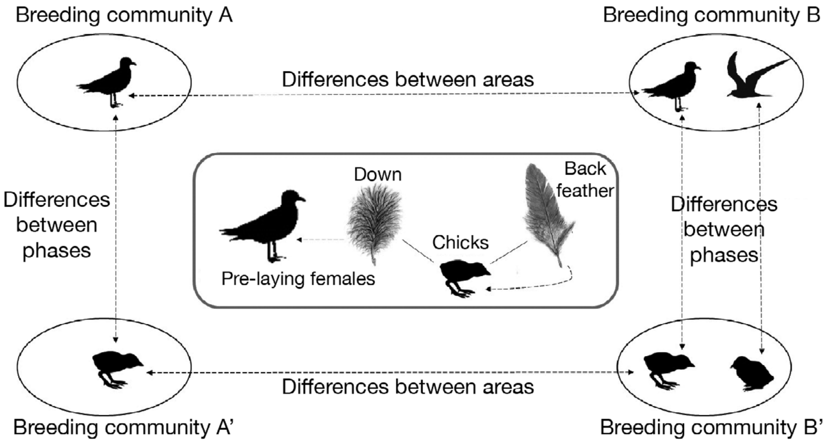

Fig. 2. Methodological approach to assess isotopic niche variation (and thus, trophic niche plasticity) of 5 breeding species of Laridae in Cuba (represented outside the central gray-bordered rectangle). Down and feather samples reflected the diets of pre-laying females and chicks, respectively (represented inside the central rectangle)

posterior distribution of one ellipse was greater than that of the other. In this way, we found the proportion of larger draws, which is a direct approximation of the probability that the posterior distribution of one ellipse (for each metric) is larger than the other: p = sum (metric [ellipse 1] > metric [ellipse 2]) / 300 (Jackson & Parnell 2023). Statistical significance was considered for $p < 0.025$ and $p > 0.975$, thus establishing an $\alpha = 0.05$ for a 2-tailed test.

The pairwise overlap of standard ellipses between pre-laying females and between chicks per breeding area was calculated by maximum likelihood using the 'maxLikOverlap' function with ellipses fitted to 95% of the data. The isotopic niche overlap for each breeding phase–area combination (e.g. pre-laying at FBA) was expressed as a proportion of the sum of the non-overlapping areas and computed as:

$$100 \times (\text{Ellipse overlapping area}_{\text{species } X \text{ and } Y} / (\Sigma \text{ Ellipse areas}_{\text{species } X \text{ and } Y} - \text{Ellipse overlapping area}_{\text{species } X \text{ and } Y})) \quad (1)$$

by each pair of species and:

$$100 \times (\text{Ellipse overlapping area}_{\text{all species}} / (\Sigma \text{ Ellipse areas}_{\text{all species}} - \text{Ellipse overlapping area}_{\text{all species}})) \quad (2)$$

by each breeding community.

This proportion ranges from 0% when the ellipses are completely separated, to 100% when the ellipses coincide completely. Overlapping <30, 30–60, and >60% were considered ecologically low, moderate, and high, respectively (Schwartz-Narbonne et al. 2019). All computing of ellipses was realized via the R package 'SIBER' (Jackson & Parnell 2023) in R 4.3.1 (R Core Team 2023).

3. RESULTS

3.1. Isotopic niche breadth

In general, isotope variability was low for both tissues and all species (Table S1). The Bayesian standard ellipses showed the existence of 2 Laridae groups: species with small and low-variable isotopic niches (bridled and roseate terns) and species with large and highly variable isotopic niches (laughing gull, royal and sandwich terns) (Fig. 3, Table 2).

3.2. Variations in isotopic niches

The $\delta^{13}C$ predicted mean of laughing gull in PBA was higher than in FBA for both breeding phases. Moreover, the SEAc of this species was significantly broader in the pre-laying phase than during the rearing phase in PBA (Figs. 3 & 4; Fig. S1, Table S2).

Royal tern rearing chicks exhibited broader SEAc in FBA than in PBA. Among breeding phases, this

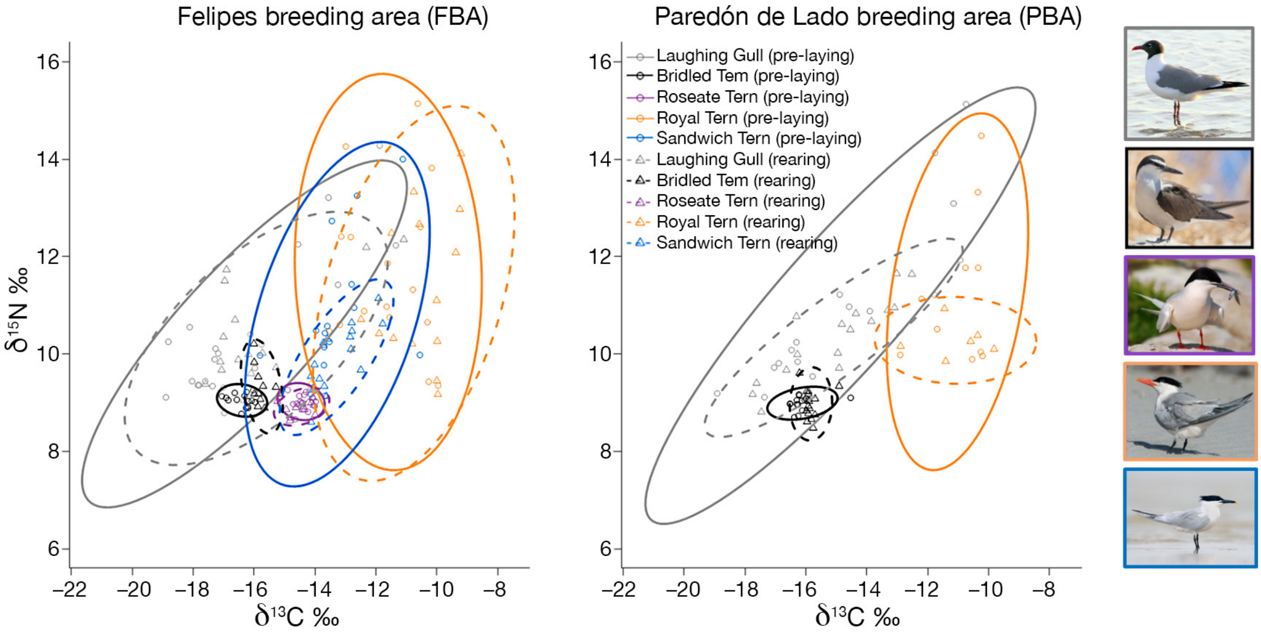

Fig. 3. Bayesian standard ellipses for corrected sample sizes representing the isotopic niches (‰^{2}, $\delta^{15}N$ and $\delta^{13}C$) of 5 Laridae species from 2 breeding areas in central-northern Cuba during 2 phases (pre-laying and rearing) of the 2021 breeding season

Table 2. Metrics of the Bayesian standard ellipses representing the isotopic niches ($\delta^{15}N$ and $\delta^{13}C$) of 5 Laridae species at 2 breeding areas in central-northern Cuba, during 2 phases of the 2021 breeding season. SEAc = Bayesian standard ellipse areas corrected for small sample sizes

Species	Breeding areas	Breeding phases	$\delta^{13}C$ predicted mean (‰)	$\delta^{15}N$ predicted mean (‰)	SEAc (‰^{2})
Laughing gull	Felipes	Pre-laying	−16.32	10.41	5.61
		Rearing	−15.94	10.32	4.98
	Paredón de Lado	Pre-laying	−14.87	10.99	6.84
		Rearing	−15.09	10.33	2.27
Bridled tern	Felipes	Pre-laying	−16.40	9.05	0.15
		Rearing	−15.75	9.33	0.36
	Paredón de Lado	Pre-laying	−16.11	8.99	0.21
		Rearing	−15.83	8.97	0.30
Roseate tern	Felipes	Pre-laying	−14.46	9.02	0.17
		Rearing	−14.44	8.92	0.19
Royal tern	Felipes	Pre-laying	−11.60	11.68	7.01
		Rearing	−10.76	11.24	6.53
	Paredón de Lado	Pre-laying	−11.02	11.28	4.66
		Rearing	−11.09	10.28	1.55
Sandwich tern	Felipes	Pre-laying	−13.27	10.82	5.35
		Rearing	−13.30	9.93	1.14

species exhibited higher $\delta^{13}C$ predicted mean values during rearing than in pre-laying in FBA. Furthermore, the SEAc of this species was broader during pre-laying than in rearing in PBA (Figs. 3 & 4; Fig. S1, Table S2).

The SEAc of bridled tern was broader during rearing than during pre-laying in FBA. Sandwich tern in FBA had significantly higher $\delta^{15}N$ predicted mean values and broader SEAc during pre-laying than rearing. The rest of the comparisons did not show significant differences (Figs. 3 & 4; Fig. S1, Table S2).

3.3. Isotopic niche overlap

Whole communities in the rearing phase in FBA (21.21%), and during the pre-laying (15.28%) and rearing phases in PBA (8.46%) exhibited low overlap. The overlap of the pre-laying community in FBA (31.76%) was moderate. Overlap by species pairs was predominantly low. Only royal and sandwich terns in the pre-laying phase in FBA showed moderate overlap (Table 3, Fig. 3).

Regardless of the breeding area, niche overlap between pairs of species and entire communities tended, in most cases, to decrease or relatively stabilize from the pre-laying to the rearing phases (Table 3, Fig. 3). Only the overlap between laughing gull—bridled tern, laughing gull—roseate tern, and bridled tern—roseate tern exhibited a slight increase. The overlap between roseate and sandwich terns exhibited a larger increase, although it remained within the low category (Table 3).

4. DISCUSSION

4.1. Trophic niche breadth

Breeding Laridae communities were clearly composed of 2 species groups with contrasting isotopic niche breadths, where species with larger isotopic niches (laughing gull, royal tern, and sandwich tern) corresponded to trophic generalists, while species with smaller isotopic niches (bridled and roseate terns) constituted trophic specialists. Trophic generalist species are expected to be more resilient to changes in food availability because they can use a broad range of available resources (Morera-Pujol et al. 2018). This may also imply the ingestion of 'junk food', e.g. when gulls (including laughing gull) occasionally consume foods from anthropogenic sources (Washburn et al. 2013, Morera-Pujol et al. 2018). Conversely, trophic specialization may not be as efficient in the face of food scarcity, which typically occurs in the low-productive tropical seas (Oppel et al. 2015). Given their trophic specialization, bridled and roseate terns should maintain their food choices and, consequently, the extent of their trophic niches at a relatively constant level, regardless of the specific circumstances (Morera-Pujol et al. 2018).

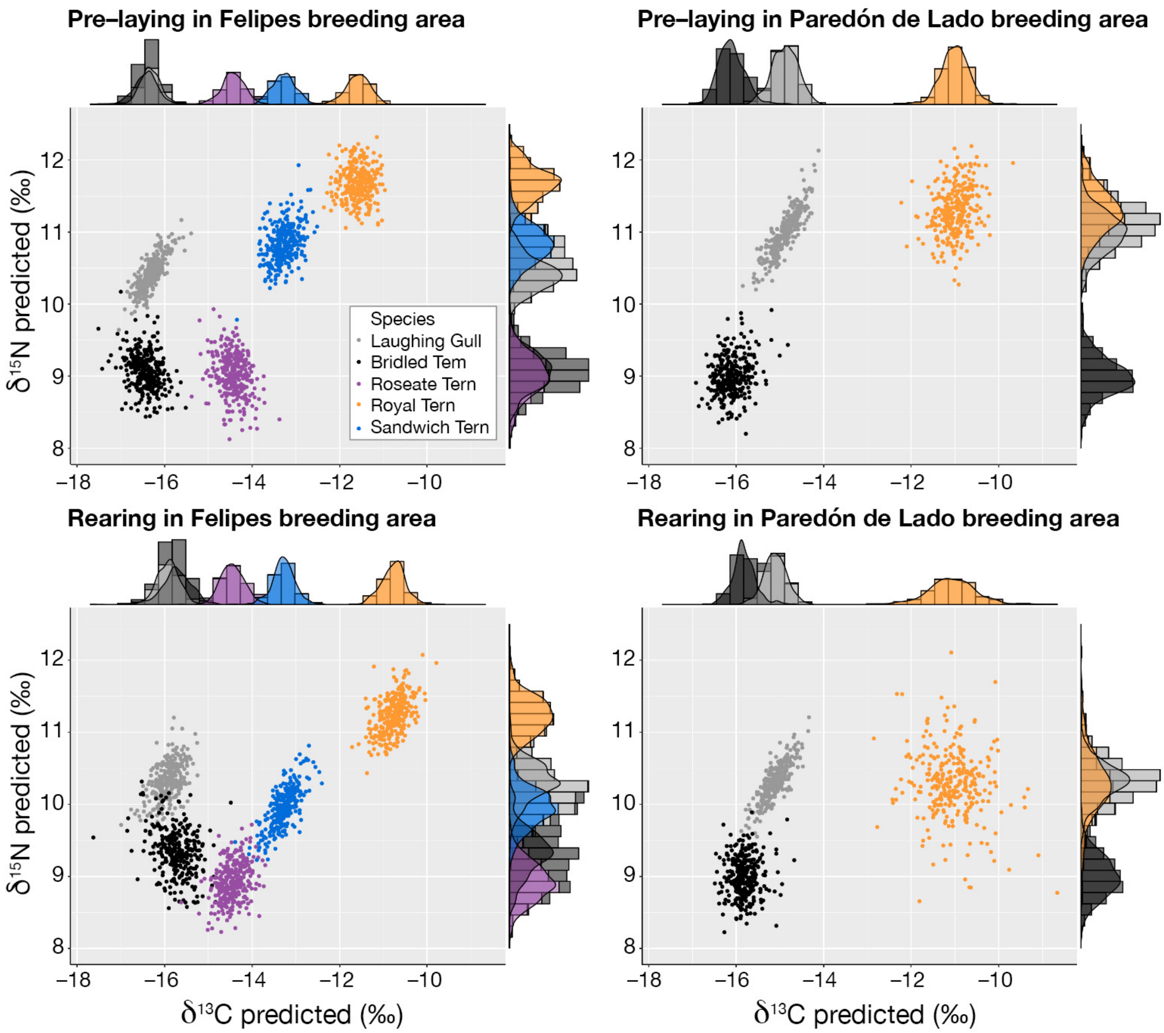

Fig. 4. Scatterplots and densigrams (density plots overlapped with histograms) of the standard Bayesian ellipse centroids representing the mean isotopic niche (δ^{15}N and δ^{13}C) positions of 5 Laridae species from 2 breeding areas in central-northern Cuba during 2 phases of the 2021 breeding season

4.2. Trophic niche plasticity

The realized niche plasticity can result from a broad array of mechanisms (Bolnick et al. 2003) that produce different patterns between generalist and specialist species. In this study, generalist and specialist Laridae species varied their trophic niches differently (from the isotopic niche variations between breeding areas and phases) as a potential response to local competition, foraging constraints, and density-dependent effects. Laughing gull, royal tern, and sandwich tern showed the greatest trophic niche plasticity, while the opposite was true for the specialists (bridled and roseate terns).

The movement restrictions imposed by the central-place foraging of adults (Ashmole 1963, Lamb et al. 2017) could explain the smaller trophic niche breadth (from SEAc differences) of laughing gull, royal tern (in PBA), and sandwich tern (in FBA) in the rearing phase compared to the pre-laying. Meanwhile, the similar trophic niche breadth of laughing gull and royal tern between breeding phases in FBA could be due to a density-dependent effect (Morera-Pujol et al. 2018). The larger size of their breeding population in FBA (311 pairs of laughing gull and 131 pairs of royal tern) compared to PBA (177 and 20, respectively) could imply a more intense competition for food during the central-place foraging period. The density-dependent effect may also explain the broader trophic niche of royal tern in FBA than in PBA while rearing. Considering the restrictions caused by central-place foraging, a wider trophic niche in FBA is expected to

Table 3. Paired overlap (%) of corrected standard ellipses representing the isotopic niches ($\delta^{13}C$ and $\delta^{15}N$) among 5 Laridae species at 2 breeding areas in central-northern Cuba, during 2 phases of the 2021 breeding season. Values in *italics* represent the rearing phase, and the other values represent the pre-laying breeding phase. The overlap corresponds to the ratio of overlapping area/non-overlapping area of ellipses

	Laughing gull	Bridled tern	Roseate tern	Royal tern	Sandwich tern
Felipes breeding area					
Laughing gull	–	*7.22*	*2.03*	*9.96*	*12.93*
Bridled tern	2.73	–	*4.43*	*0*	*1.15*
Roseate tern	0.11	0	–	*0.84*	*15.62*
Royal tern	15.91	0	0.26	–	*12.94*
Sandwich tern	29.98	1.45	3.09	42.53	–
Paredón de Lado breeding area					
Laughing gull	–	*5.39*	–	*6.26*	–
Bridled tern	3.06	–	–	*0*	–
Roseate tern	–	–	–	–	–
Royal tern	18.89	0	–	–	–
Sandwich tern	–	–	–	–	–

satisfy the increasing food demands of numerous royal tern chicks (Morera-Pujol et al. 2018, Trevail et al. 2019). Our study also confirmed the large trophic niche plasticity of laughing gull and royal tern considering that their trophic niches were broader than those found in colonies in French Guiana (Sebastiano et al. 2017) and Sinaloa (González-Medina et al. 2020). Also, the isotopic niche breath contraction between breeding phases of cayenne tern (a subspecies of sandwich tern) was found in the French Guiana colony (Sebastiano et al. 2017).

In FBA, royal tern in the rearing phase probably consumed prey from closer to shore than during the pre-laying phase, based on the significant difference in $\delta^{13}C$ predicted mean values (difference of 0.81‰, higher values during pre-laying). Laughing gull (in both breeding phases) likely consumed prey from closer to the coast in PBA than in FBA (higher $\delta^{13}C$ predicted mean values for PBA individuals). This greater accessibility for laughing gull to nearshore prey in PBA could be due to minor interspecific competition for foraging in nearshore waters (only royal tern as a potential competitor in PBA, while roseate, royal, and sandwich terns occurred in FBA) and/or easier prey capture (e.g. fishes, crabs) due to the calmer waters of PBA (enclosed between cays) compared to FBA (very exposed to the open sea) (Fig. 1). The avoidance or reduction of intra- and interspecific competition can sometimes explain dietary changes (Morera-Pujol et al. 2018, van den Bosch et al. 2019), that may occur in sandwich tern from the pre-laying to the rearing phase in FBA (considering the $\delta^{15}N$ predicted mean difference, 0.88‰). This species breeds in sympatry with royal tern in FBA, and their relatively similar prey consumption (McGinnis & Emslie 2001, Gatto et al. 2019) may lead to competitive interactions when breeding.

Lastly, the stability in the breadth and position of the isotopic niches of roseate and bridled terns suggests a high trophic specialization. However, the significant expansion of the bridled tern's trophic niche breadth from pre-laying to rearing in the FBA may be attributed to a density-dependent effect, considering its breeding population size in this area (120 breeding pairs compared to only 76 in PBA). Density-related trophic niche expansion typically occurs in large populations (Morera-Pujol et al. 2018). The high and increasing food demand of the chicks in FBA, the restrictive central-place foraging of adults, and the specialized feeding over oligotrophic marine waters (Dunlop 2011) could have caused strong intra-specific competition and therefore the aforementioned increase in the trophic niche breadth of bridled tern in FBA between phases. It is also possible that parents of both species may exhibit individual specialization in different areas/prey. Consequently, the chicks of these species may be fed with a greater variety of prey from several sources, thereby exhibiting a broader niche than the pre-laying females.

4.3. Trophic niche overlap

Generally, isotopic niche overlap was low (Fig. 3), indicating that trophic niche partitioning may facilitate sympatric breeding among Laridae species in Cuba, as is typical for tropical breeding seabirds (Cherel et al. 2008, Sebastiano et al. 2017, Clay et al. 2019). This niche partitioning could also be a consequence of competition (Morera-Pujol et al. 2018) or an anticompetitive mechanism (Navarro et al. 2017, van den Bosch et al. 2019).

At the community level, the reduced isotopic niche overlap from pre-laying to rearing (also found by Sebastiano et al. 2017) in both breeding areas suggests that the studied species tended to maximize their trophic segregation during the chick-provisioning phase. This could help to reduce competition by the food available in partially shared foraging areas (due to central-place foraging in this phase), thus ensuring the successful growth and development of a greater number of chicks. The trophic niche overlap between species was low or moderate, suggesting a low probability of competition. The differentiated responses to interspecific competition of trophic generalist and specialist species (see Morera-Pujol et al. 2018) may also facilitate their sympatric breeding. Furthermore, the absence or very low trophic niche overlap detected between bridled and roseate terns implies the avoidance of strong competition between these trophic specialists.

The moderate overlap between the trophic niches of royal and sandwich terns when pre-laying at FBA could derive from their usual sympatric breeding (McGinnis & Emslie 2001, Gatto et al. 2019). However, despite both species having similar trophic requirements and feeding strategies (Table 1), the overlap of their trophic niches may not have major negative implications, as both species often exhibit different consumption patterns (e.g. prey size, consumption rates) at different feeding locations (McGinnis & Emslie 2001, Catry et al. 2008, Gatto et al. 2019).

Differences in foraging strategies, prey consumed, and generalist/specialist behavior may also support that species with narrow niches, nested within the broad niche of others, are not under high competitive stresses for food. For example, the specialists bridled and roseate terns were probably little affected, even though their niches were highly contained within those of laughing gull and sandwich tern, respectively, considering the contrasting trophic characteristics between them (Table 1). Consequently, the overall balance of the interaction between these pairs of species appears to lean towards low overlap.

5. CONCLUSIONS

Trophic niche plasticity appears to be an important adaptive mechanism to ensure the successful reproduction of Laridae breeding in sympatry in north-central Cuba. The bivariate isotopic niche ($\delta^{15}N$ and $\delta^{13}C$) of the 5 studied Laridae species varied among pre-laying and rearing phases, and among breeding areas showing generalist and specialist trophic species groups. Species with large isotopic niches (trophic generalists) exhibited high plasticity, adapting to the availability of resources (that might be different between breeding areas due to different ecological/oceanographic characteristics, or in the different phases due to the constraints of central-place foraging in the rearing phase) and to probable intra- and interspecific competition for prey and foraging locations. In our study, the overlap of trophic niches between species was low or moderate, indicating a low probability of competition. A thorough understanding of the trophic relationships among these seabirds could be obtained in the future by analyzing the isotopic and morphological characteristics of the prey consumed, and also by assessing the isotopic niche patterns of both predators and prey in different breeding seasons. Nevertheless, knowledge of species-specific trophic niche plasticity of Laridae could be incorporated into management plans of marine protected areas in Cuba which host breeding colonies of Laridae that might be more sensitive than other species (i.e. bridled and roseate terns), thus contributing to tropical seabird conservation.

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