ANNUAL PLASTICITY
OF THE TROPHIC NICHE OF THE BRIDLED TERN
ONYCHOPRION ANAETHETUS IN CUBA

PLASTICIDAD ANUAL DEL NICHO TRÓFICO
DEL CHARRÁN EMBRIDADO *ONYCHOPRION ANAETHETUS*
EN CUBA

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SUMMARY.—The trophic ecology of the Bridled Tern *Onychoprion anaethetus* is poorly understood despite its great abundance in tropical and subtropical regions. Important breeding colonies are located in the Caribbean, where significant human disturbances occur and where coverage by marine protected areas is still largely insufficient. Bridled Tern populations are likely to experience considerable variation in trophic niche throughout their annual cycle, especially between the non-breeding and breeding phases as they change their feeding areas. In this study, we assessed the year-round variability of the Bridled Tern isotopic niche (δ^{15}N and δ^{13}C) from two breeding areas in North Central Cuba, as a proxy of its trophic niche. Feathers, down and blood samples were taken from adults and chicks, representing four life cycle phases of this species (non-breeding, pre-laying, incubation and chick-rearing). Overall, Bridled Terns occupied a narrow and relatively plastic isotopic niche, along the studied life cycle phases. The largest variability occurred between the non-breeding and the pre-laying phases, showing a marked reduction of the niche breadth. Patterns of niche variability differed among breeding areas only during the incubation phase. Considering that adult females of Bridled Tern rely on few prey species during the pre-laying, this life cycle phase is a period of high vulnerability for the Cuban colonies.—Garcia-Quintas, A., Barbraud, Ch., Bustamante, P., Lorrain, A., Denis, D. & Lanco, S. (2024). Annual plasticity of the trophic niche of the Bridled Tern *Onychoprion anaethetus* in Cuba. *Ardeola*, 71: 277-290.

Key words: δ^{13}C, δ^{15}N, Caribbean seabirds, Foraging ecology, Tropical terns.

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RESUMEN.—La ecología trófica del charrán embridado *Onychoprion anaethetus* es poco conocida a pesar de su gran abundancia en regiones tropicales y subtropicales. En el Caribe se localizan importantes colonias de cría, donde se producen perturbaciones humanas significativas y donde la cobertura de áreas marinas protegidas es muy insuficiente. Es probable que las poblaciones de charrán embridado experimenten una considerable variación en su nicho trófico a lo largo de su ciclo anual, especialmente entre las fases no reproductiva y reproductiva, porque cambian sus áreas de alimentación. En este estudio evaluamos la variabilidad anual del nicho isotópico del charrán embridado (δ^{15}N y δ^{13}C) en dos áreas de cría del centro norte de Cuba, como representante de su nicho trófico. Se tomaron muestras de plumas, plumón y sangre de adultos y pollos, representando cuatro fases del ciclo vital de esta especie (no reproductora, prepuesta, incubación y cuidado de pollos). En general, los charranes embridados ocuparon un nicho isotópico estrecho y relativamente plástico, a lo largo de las fases del ciclo vital estudiadas. La mayor variabilidad se produjo entre la fase no reproductora y la fase previa a la puesta, mostrando una marcada reducción de la amplitud del nicho. Los patrones de variabilidad del nicho difirieron entre las zonas de cría solo durante la fase de incubación. Considerando que las hembras adultas de charrán embridado dependen de pocas especies de presas durante la prepuesta, esta fase del ciclo vital es de alta vulnerabilidad para las colonias cubanas.—Garcia-Quintas, A., Barbraud, Ch., Bustamante, P., Lorrain, A., Denis, D. y Lanco, S. (2024). Plasticidad anual del nicho trófico del charrán embridado *Onychoprion anaethetus* en Cuba. *Ardeola*, 71: 277-290.

Palabras clave: δ^{13}C, δ^{15}N, aves marinas caribeñas, charranes tropicales, ecología de forrajero.

INTRODUCTION

The Bridled Tern *Onychoprion anaethetus* is a pantropical seabird species that breeds on small islands in the Pacific, Atlantic and Indian Oceans (Bretagnolle & Benoit, 1997; Labbé *et al*., 2013; Tayefeh *et al*., 2017), as well in large seas (e.g. Caribbean, Red) and gulfs (e.g. Arabian, Guinea, Fonseca, Persian; Hulsman & Langham, 1985; Komar & Rodríguez, 1996; Tayefeh *et al*., 2014). This species usually forages from floating groups of *Sargassum* and macro-algae in oligotrophic waters of low salinity and low productivity (Kohno & Kishimoto, 1991; Dunlop, 2011; Labbé *et al*., 2013). It feeds on a variety of prey, such as small fishes and marine invertebrates, although it may also consume insects (Kohno & Kishimoto, 1991; Dunlop & Surman, 2012; Moser & Lee, 2012). Adults have different foraging habitats during the breeding and non-breeding phases, as they migrate and shift their feeding habits between both stages (Labbé *et al*., 2013; Tayefeh *et al*., 2017).

Despite being an abundant species, with a worldwide population being estimated between ~600,000–1,500,000 mature individuals, and cosmopolitan in the tropics and subtropics (Villard & Bretagnolle, 2010; Tayefeh *et al*., 2017), its ecology is relatively poorly known (Hulsman & Langham, 1985; Bretagnolle & Benoit, 1997). Most studies have focused on the description of new breeding locations, moulting patterns, diet, feeding and brood-attendance behaviour (e.g. Diamond, 1976; Kohno & Kishimoto, 1991; Komar & Rodríguez, 1996), and on estimating reproductive parameters such as nesting habitat, breeding population size, egg characteristics, chick care and growth, and breeding success (Hulsman & Langham, 1985; Bretagnolle & Benoit, 1997; Garavanta & Wooller, 2000; Villard & Bretagnolle, 2010; Tayefeh *et al*., 2017).

Knowledge of the trophic ecology of the Bridled Tern is limited to basic foraging characteristics and diet composition, mainly during reproduction (see Hulsman & Langham, 1985; Kohno & Kishimoto, 1991; Dunlop & Surman, 2012; Moser & Lee, 2012). Stable isotope analysis has been used to describe the foraging ecology, with δ^{15}N as a proxy of the trophic position and δ^{13}C as a

proxy of the feeding location, of the Bridled Tern in breeding colonies in the Seychelles archipelago (Catry *et al*., 2008) and on the Western Australian coast (Dunlop, 2011; Labbé *et al*., 2013), both in the Indian Ocean. Only Labbé *et al*. (2013) tackled the approach of the so-called isotopic niche, a concept of increasing application that integrates the stable isotopic ratios (δ values) as homologues of environmental variables associated with the ecological niche (Newsome *et al*., 2007). Thus, the isotopic niche joins the n-dimensions in a reduced number of axes constituting a proxy of the species' trophic niche (Grecian *et al*., 2015).

As a proxy of trophic niche, the isotopic niche may differ among seabird species according to their trophic plasticity, as determined by specific prey requirements/foraging strategies (Cherel *et al*., 2008; Bratton *et al*., 2022). Thus, generalist trophic species are expected to have a broader and more variable isotopic niche than specialists, favouring sympatric breeding of seabirds by reducing niche overlap (Morera-Pujol *et al*., 2018). Furthermore, the isotopic niche breadth may be influenced by individual specialisation within seabird species (Lisnizer & Yorio, 2019; Wiley *et al*., 2019). Between seasons, the isotopic niche of seabirds is usually broader during the non-breeding period than during the breeding period, considering the larger freedom of foraging movements of non-breeding adults, that are unconstrained by the frequent need of returning to land for brood care (Cherel *et al*., 2008). But it may also be possible to distinguish breeding phases from the isotopic niche, probably as a consequence of physiological and/or foraging strategy changes in seabirds (Labbé *et al*., 2013). The isotopic niche approach has recently been applied to Bridled Tern colonies in Cuba (Garcia-Quintas *et al*., unpublished data).

Within the Bridled Tern's wide geographical range, the Caribbean is an enigma in terms of feeding ecology. However, several breeding colonies of Bridled Terns are established in this region with important population sizes (~8,909–10,368 breeding pairs; Bradley & Norton, 2009), which are probably underestimated due to a lack of spatial and temporal coverage by breeding surveys. The stable isotope approach could serve as a starting point for assessing Bridled Tern trophic ecology in the Caribbean. This approach provides ways to explore the characteristics and variation of the trophic niche, as well as to highlight information gaps (Rader *et al*., 2017; Shipley & Matich, 2020). Analysing the seasonal variability of the isotopic niche can help characterise biogeographic or connectivity patterns, essential aspects for the conservation of migratory species (Newsome *et al*., 2007) such as the Bridled Tern. Assessment of isotopic niche temporal variation must involve stable isotope data from different tissues (such as blood and down/feathers), which cannot be directly compared due to their different fractionation factors (Hobson & Clark, 1992). However, the isotopic niche breadth representing different tissues can be compared, as it is a surface metric and therefore does not depend on the position in n-space. Regardless of whether or not the isotopic values of a tissue have been modified by a correction value, the niche breadth generated from these will be the same because it depends on the scattering pattern of the data and not on their positions.

To our knowledge, only one study has addressed the isotopic niche of this species in the Caribbean, in two breeding areas of North Central Cuba (i.e. Garcia-Quintas *et al*., unpublished data). In these areas, the Bridled Tern occupied a narrow and relatively plastic isotopic niche ($\delta^{15}N$ and $\delta^{13}C$) between the pre-laying and chick-rearing phases of the breeding season compared to other Laridae species. However, the year-round characterisation of its isotopic niche

remains unknown, although it could be important for the management and conservation of Bridled Terns in the Caribbean basin by contributing to the detection of critical stages during which the niche is restricted.

In this study, stable isotope analysis of different tissues was used to estimate the spatio-temporal variability of the Bridled Tern isotopic niche throughout its annual cycle from two breeding areas in North-central Cuba, and to infer its trophic plasticity. This work focused on four phases of the Bridled Tern annual cycle that differed in time constraints and energy costs, leading to likely dietary changes (Labbé *et al.*, 2013): non-breeding, pre-laying, incubation and chick-rearing. We expected the largest differences in Bridled Tern isotopic niche breadth to occur between the non-breeding phase and the other periods, due to contrasting foraging strategies: opportunistic vs central-place foraging (Dunlop & Surman, 2012; Labbé *et al.*, 2013).

MATERIALS AND METHODS

Study areas and sampling

Sampling of Bridled Tern tissues took place on Felipe de Barlovento, Felipe de Sotavento and Paredón de Lado cays, belonging to the Sabana-Camagüey archipelago, North-central Cuba (Figure 1). These cays are one of the most important breeding areas for seabirds in Cuba, both in terms of number of individuals and number of species (Jiménez *et al.*, 2009). The Bridled Tern is a summer visitor to Cuba (Garrido & Kirkconnell, 2011; Navarro, 2023) that normally breeds
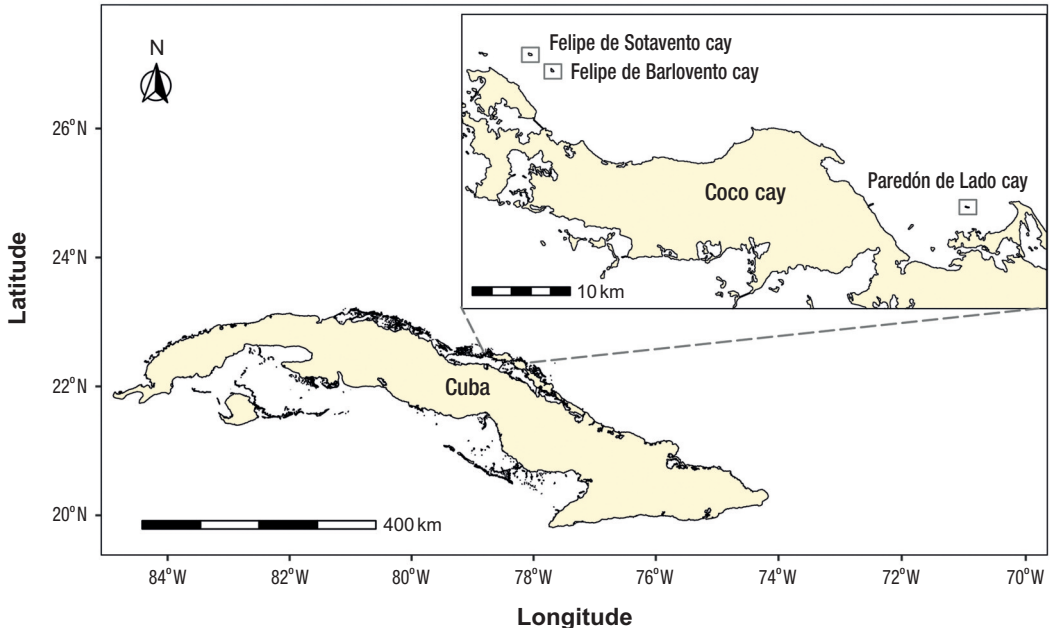

FIG. 1.—Locations of cays (grey squares) where Bridled Tern tissues were sampled during the 2021 breeding season in Cuba.
[Cayos de muestreo (cuadrados grises) de tejidos de charrán embridado durante la temporada reproductiva de 2021 en Cuba.]

on all three cays, according to Jiménez *et al*. (2009) and our own field observations. The tropical climate of this region shows a mean annual temperature of $26.3 \pm 0.4°C$, an average monthly precipitation of $88.5 \pm 18.1mm$ and average annual wind speed of $14.5 \pm 2.2km.h^{-1}$ (easterlies mainly). During the Bridled Tern breeding season in Cuba (May to August, Garrido & Kirkconnell, 2011) average temperature is $28.0 \pm 1.0°C$ and precipitations average $109.2 \pm 83.1mm$ (Meteorological Station 78339, Centro de Investigaciones de Ecosistemas Costeros, Cayo Coco).

During the 2021 breeding season we collected body feathers and blood from adults, as well as down and body feathers from chicks of Bridled Tern in all three study cays. Due to the geographical proximity of the Felipe de Barlovento and Felipe de Sotavento cays (Figure 1), only two breeding areas were considered for statistical analysis: Felipes (gathering Barlovento and Sotaven-

to) and Paredón de Lado. Thirty-five adults and 26 chicks were sampled in Felipes, and 30 adults and 30 chicks were sampled in Paredón de Lado (Table 1).

Adults were captured directly on or in the vicinity of their nests using a handle net during the incubation phase. Animal handling time was ~5-7 minutes, minimising the risk of nest abandonment by the parents. Feathers (5 or 6 per individual) were removed from the backs of incubating adults and stored in labelled plastic bags until analysis. Blood samples (0.6ml) were collected in heparinised capillary tubes after tarsal vein puncture with a needle. Blood samples were stored in Eppendorf tubes with 90% ethanol, given the impossibility of keeping them frozen in the field. This procedure does not significantly alter the subsequent isotope analysis in seabird tissue samples (Hobson *et al*., 1997; Catry *et al*., 2008). Bridled Terns undergo an annual moult prior to the breeding season (i.e. during non-breeding

TABLE 1

Stable isotope values (mean ± SD) in adult and chick tissues of Bridled Tern *Onychoprion anaethetus* from North-central Cuba during the 2021 breeding season.
[Valores de isótopos estables (media ± DE) en tejidos de adultos y pollos de charrán embridado Onychoprion anaethetus *del centro-norte de Cuba durante la temporada reproductiva de 2021.]*

Age classes	Breeding sites	N	Tissue	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N mass ratio
Adults	Felipes	20	Feather	-17.14 ± 0.75	10.97 ± 1.05	3.16 ± 0.03
	Paredón de Lado	15	Feather	-17.39 ± 0.52	11.31 ± 0.81	3.15 ± 0.02
	Felipes	15	Blood	-17.58 ± 0.55	8.24 ± 0.29	3.42 ± 0.05
	Paredón de Lado	15	Blood	-17.34 ± 0.30	7.90 ± 0.16	3.43 ± 0.05
Chicks	Felipes	15	Down	-16.40 ± 0.34	9.05 ± 0.14	3.23 ± 0.07
	Paredón de Lado	15	Down	-16.11 ± 0.47	8.99 ± 0.14	3.20 ± 0.03
	Felipes	11	Feather	-15.75 ± 0.28	9.33 ± 0.40	3.14 ± 0.06
	Paredón de Lado	15	Feather	-15.83 ± 0.28	8.97 ± 0.31	3.17 ± 0.04

period; Bridge *et al*., 2007). Thus, the stable isotope values of feathers and blood samples reflected the characteristics of the foraging locations and prey consumed by Bridled Tern adults at the time of feather synthesis (Cherel *et al*., 2000) and 3-4 weeks prior to sampling for blood (Hobson & Clark, 1992; Bearhop *et al*., 2002), thus corresponding to the non-breeding and incubation phases, respectively.

Sampling of down (small handful) and feathers from the back of chicks followed the same procedure as for adults and was performed respectively after hatching and at different times during chick growth until fledgling. Stable isotopes of down samples reflected the characteristics of foraging areas and prey consumed by the mothers (adult females) during the pre-laying phase, while the body feathers reflected the food provided by both parents to the chicks during the chick-rearing phase (Klaassen *et al*., 2004; Ausems *et al*., 2020). All sampled birds were ringed for individual identification and to avoid pseudo-replication.

STABLE ISOTOPE ANALYSIS

Prior to stable isotope analyses, blood samples were oven-dried at 50°C for 24 hours and ground to a fine powder. Down and body feathers were cleaned to remove surface contaminants using a 2:1 chloroform and methanol solution followed by two methanol rinses. Then, they were oven-dried for 24 hours at 45°C and cut into small fragments with stainless steel scissors.

Approximately 0.3mg of blood, 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 analyser (Thermo Scientific Flash 2000) at La Rochelle University. Stable isotope values

are reported following the δ notation and expressed as ‰ according to the equation:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 10^3$$

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) indicate measurement errors <0.10‰ and <0.15‰ for δ^{13}C and δ^{15}N, respectively. The C:N ratios were always less than 3.5, indicating good lipid removal efficiency (Table 1).

DATA ANALYSIS

Four breeding phase-classes of individual combinations were considered to assess the spatiotemporal variation of the Bridled Tern isotopic (and trophic) niche: non-breeding (adults), pre-laying (adult females), incubation (adults) and chick-rearing (chicks). For non-breeding adults, the individual-area association was preserved for the purpose of following the annual cycle by groups of birds, but considering that the foraging areas of Bridled Terns during non-breeding phase are outside Cuba and are unknown. Statistical description of the isotope values was expressed as mean ± SD.

The isotopic niche breadth of δ^{15}N and δ^{13}C of Bridled Terns at each breeding phase (class of individual) was calculated by the Stable Isotope Bayesian Ellipses method via R-package SIBER (Jackson *et al*., 2011). This approach uses Bayesian inference based on the multivariate standard ellipses metric to quantify the isotopic *d*-space from the data. The ellipses represent the core of the isotopic niches and are derived from the variance and covariance of the bivariate data matrix. This

approach corrects for the effects of small samples by generating standard ellipse areas (SEAc) that facilitate comparisons among spaces of core isotopic niches (Jackson *et al*., 2011). SEAc was the metric used to estimates the isotopic niche breadth of Bridled Terns with ellipses fitted to 95% of data.

The spatial and temporal variations of the isotopic niche were assessed by comparing the SEAc between breeding areas by each phase-class of individuals (spatial differences) and between breeding phases-classes of individuals by breeding area (time variation), respectively. We first fitted Bayesian multivariate normal distributions to each group (i.e. each phase-class of individuals-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). Parameters of the built model included 1500 iterations, 1000 burnin, 10 thin and 2 chains within "parms" and R = 1 * diag(2), k = 2 and tau.mu = 0.001 as "priors" (further parameterisation details in Jackson & Parnell, 2023). Then, each ellipse area was calculated for 300 replicates of the fitted ellipses (the so-called Bayesian Standard Ellipse Areas, SEA.B).

To compare the isotopic niche in space and time we first calculated the mean and the 95% confidence intervals of the differences between SEA.B groups (metric [SEA.B 1] – metric [SEA.B 2]). We then calculated the probability of two-tailed no significant differences (null hypothesis) between the posterior distributions of the SEA.B groups: p = (1 – sum (metric [SEA.B 1] > metric [SEA.B 2]) / 300) * (1 – sum (metric [SEA.B 1] < metric [SEA.B 2]) / 300). Temporal comparisons (between phases) were made following the chronological order of the breeding phases. Significance was considered for p < 0.05. All data analyses were performed with R 4.1.1 (R Core Team, 2021).

RESULTS

Considering all tissues, the largest isotopic variability was detected in adult feathers of both areas and the blood of adults in Felipes breeding area (Table 1). The isotopic niche of this species was narrow in all contexts as the SEAc values were always $< 1‰^2$ (Figure 2). Isotopic niche breadth showed no significant differences between breeding areas

TABLE 2

Comparisons of isotopic niche breadth ($‰^2$, modelled by standard Bayesian ellipses areas) of the Bridled Tern *Onychoprion anaethetus*, by classes of individuals, between two breeding areas in Cuba at 2021. All comparisons followed the order Felipes breeding area > Paredón de Lado breeding area. Statistics and p-values (null hypothesis) were calculated from 300 replicates of ellipse area differences between breeding areas.
[Comparaciones de la amplitud del nicho isotópico ($‰^2$, modelado por áreas de elipses estándar bayesianas) del charrán embridado Onychoprion anaethetus, *por clases de individuos, entre dos áreas de cría de Cuba en 2021. Todas las comparaciones siguieron el sentido Área de cría Felipes > Área de cría Paredón de Lado. Los estadísticos y valores de p (hipótesis nula) se calcularon a partir de 300 réplicas de diferencias de áreas de elipses entre áreas de cría.]*

Classes of individuals	Mean (95% credible interval)	p_{H0}
Non-breeding adults	0.48 (−0.23, 1.18)	0.07
Pre-laying females	−0.06 (−0.21, 0.09)	0.15
Incubating adults	0.72 (0.24, 1.20)	<0.01*
Chicks	0.06 (−0.25, 0.37)	0.21

* Significant differences.

except during incubation (Table 2; Supplementary Electronic Material: Figure S1), when the niche of adults was broader in Felipes than in Paredón de Lado.

Annual differences in Bridled Tern isotopic niche breadth were significant between the breeding phases in both breeding areas,

except between pre-laying and incubation in Paredón de Lado (Table 3; Supplementary Electronic Material: Figure S1). The isotopic niche of non-breeding adults was significantly broader than that of pre-laying females and chicks. The isotopic niche of pre-laying females was narrower than that of incubating
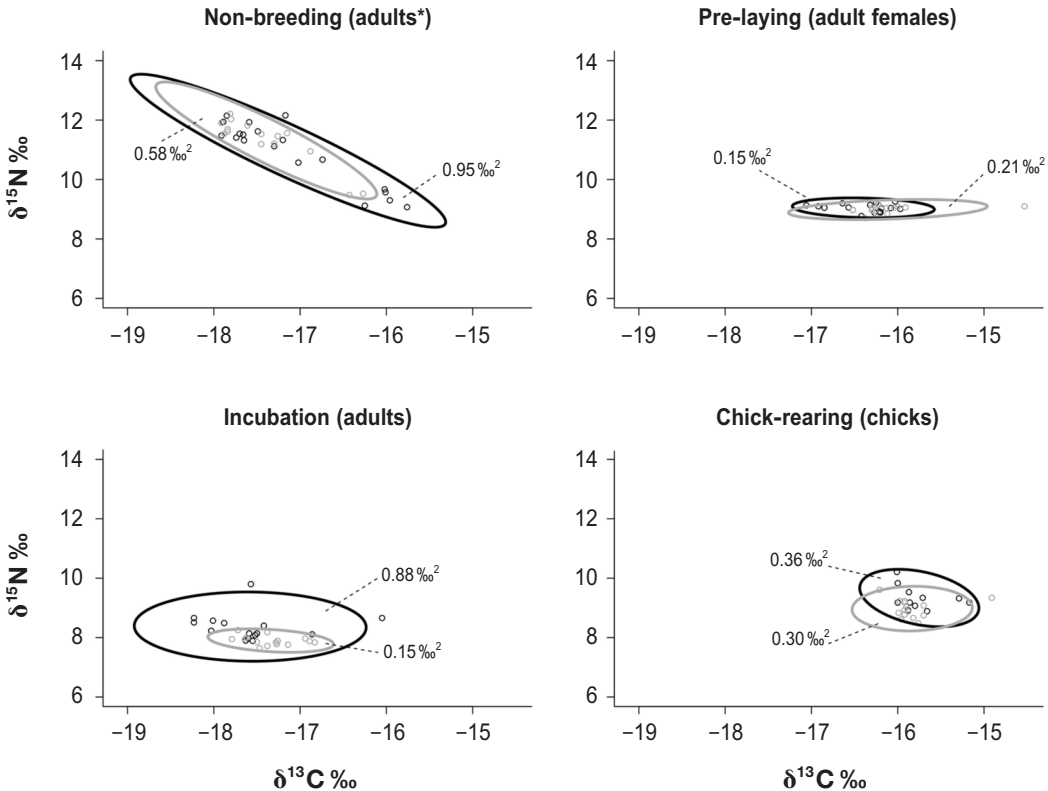
FIG. 2.—Bayesian standard ellipses for corrected sample sizes representing the isotopic niche breadths (‰², δ^{15}N and δ^{13}C) of Bridled Terns during four breeding phases from two breeding areas (Felipes black, Paredón de Lado grey) in North-central Cuba during the 2021 breeding season. Felipes breeding area combines the nearby Felipe de Barlovento and Felipe de Sotavento cays. * = For non-breeding adults, the individual-area association was preserved to follow the annual cycle by groups of birds, since the foraging areas during non-breeding phase are outside Cuba.
[Elipses estándares bayesianas para tamaños de muestra corregidos que representan la amplitud de los nichos isotópicos (‰², δ^{15}N y δ^{13}C) del charrán embridado durante cuatro fases de cría en dos áreas reproductivas (Felipes en negro y Paredón de Lado en gris) del centro norte de Cuba durante la temporada reproductiva de 2021. La zona de cría de Felipes reúne a los cayos cercanos Felipe de Barlovento y Felipe de Sotavento. * = Para los adultos no reproductores se conservó la asociación individuo-área para seguir el ciclo anual por grupos de aves, ya que las áreas de forrajeo durante la fase no reproductiva están fuera de Cuba.]

adults in Felipes breeding area. The incubating adults exhibited broader isotopic niches than chicks in Felipes but the opposite occurred in Paredón de Lado breeding area (Table 3; Supplementary Electronic Material: Figure S1).

DISCUSSION

Compared to other Laridae species of Cuba, the Bridled Tern occupies a narrow isotopic niche (δ^{15}N and δ^{13}C) during its annual life phases (non-breeding and breeding) indicating a reduced trophic niche based on specialised diet and restricted foraging locations (e.g. Catry *et al*., 2008; Dunlop, 2011; Labbé *et al*., 2013; Garcia-Quintas *et al*., unpublished data). Given its narrow trophic niche (inferred from isotopes), this species exhibited a high temporal plasticity considering four specific phases. This trophic plasticity may constitute an adaptive safeguard to ensure the survival and breeding success of this specialist seabird species (Goodenough *et al*., 2022).

Among breeding areas (spatial variability), the only significant difference occurred between the SEAc of incubating adults, indicating a narrower isotopic niche of Bridled

TABLE 3

Comparisons of isotopic niche breadth (‰², modelled by standard Bayesian ellipses areas) of the Bridled Tern *Onychoprion anaethetus*, by breeding area, between four classes of individuals in Cuba in 2021. Comparison schemes follow the chronological order of the breeding phases represented by the classes of individuals. Statistics and p-values (null hypothesis) were calculated from 300 replicates of ellipse area differences between classes of individuals.
[Comparaciones de la amplitud del nicho isotópico (‰², modelado por áreas de elipses estándar bayesianas) del charrán embridado Onychoprion anaethetus, *por área de cría, entre cuatro clases de individuos en Cuba en 2021. Los esquemas de comparación siguieron el orden cronológico de las fases reproductivas representadas por las clases de individuos. Los estadísticos y valores de p (hipótesis nula) se calcularon a partir de 300 réplicas de diferencias de área de las elipses entre las clases de individuos.]*

	Comparisons	Mean (95% credible interval)	p_{H0}
Felipes breeding area	Non-breeding adults > Pre-laying females	1.06 (0.49, 1.59)	<0.01*
	Pre-laying females > Incubating adults	−0.73 (−1.18, −0.27)	<0.01*
	Incubating adults > Chicks	0.53 (0.01, 1.07)	<0.01*
	Chicks > Non-breeding adults	−0.85 (−1.43, −0.24)	<0.01*
Paredón de Lado breeding area	Non-breeding adults > Pre-laying females	0.50 (0.13, 0.85)	<0.01*
	Pre-laying females > Incubating adults	0.06 (−0.09, 0.20)	0.14
	Incubating adults > Chicks	−0.14 (−0.36, 0.06)	0.04*
	Chicks > Non-breeding adults	−0.41 (−0.78, −0.02)	<0.01*

* Significant differences.

Terns in Paredón de Lado than in Felipes breeding area. This difference in niche width appears to be based on both isotopes according to the ellipses arrangements (Figure 2). Thus, incubating adults at Paredón de Lado foraged within a smaller radius (from $\delta^{13}C$) and consumed a lower variety of prey (inferred from $\delta^{15}N$) relative to Felipes. This could result from different accessibility to feeding patches (floating vegetation and other floating objects, Kohno & Kishimoto, 1991) due to particular oceanographic and biogeochemical processes at each breeding area, which may imply different isotopic baselines even between geographically close localities (Rooker et al., 2008; Moreno et al., 2011) such as in this study. The calmer waters of Paredón de Lado breeding area (enclosed between cays) compared to Felipes (exposed to the open sea, Figure 1) could lead to a high accumulation of floating Sargassum sp. and seagrasses (which provide shelter for prey of Bridled Tern) in marine waters near the colony in the former area. In Felipes, incubating adults were able to forage away from colonies and then consumed a greater diversity of prey from dispersed feeding patches, considering that the restrictions on their movements due to central-place foraging must have been less important than during the chick-rearing phase.

Also, the spatial differences found in the trophic niche breadth (inferred from the isotopic niche breadth) of incubating adults may be a consequence of their nesting site characteristics at each breeding area. In contrast to Felipes breeding area, the nesting sites of Bridled Tern in Paredón de Lado have little or no vegetation cover (Garcia-Quintas et al., 2023) and are therefore very exposed to the intense heat typical of tropical regions. Thus, adults in Paredón de Lado might experience more acute heat effects (e.g. heat stress, dehydration) when incubating and, therefore, forage at shorter distances (conducive to a narrow trophic niche)

than in Felipes in order to enable frequent incubation exchange, this being a trade-off between adult survival and breeding success (see Cook et al., 2020).

Several significant differences in the breadth of the Bridled Tern isotopic niche (and hence trophic) among the phases of its annual cycle (temporal differences) were detected. The most remarkable variations occurred from the non-breeding to the pre-laying phase, and from the chick-rearing to the non-breeding phase, with non-breeding adults always showing the broadest trophic niche. Both temporal variations were to be expected because of the change in the foraging strategy between the non-breeding and breeding stages, corresponding to opportunistic and central-place foraging, respectively (Cherel et al., 2008; Lisnizer & Yorio, 2019). Opportunistic foragers had freedom of movement throughout their non-breeding areas (outside Cuban seas) and consumed a greater diversity of prey than during the breeding period.

As did Labbé et al. (2013), we found that the largest isotopic variability and broadest niches occurred in adults during the non-breeding phase. This reflected a more varied diet (from large $\delta^{15}N$ ranges) of adults foraging to a larger extent in oligotrophic tropical waters (from large $\delta^{13}C$ ranges) before the breeding season. Furthermore, isotopic values representing the trophic niche of non-breeding adults in this study were consistent with those reported by Dunlop (2011) for adult Bridled Terns (but obtained from primary feathers) wintering in the Sulawesi Sea (western Pacific), while breeding in western Australia. Also our isotopic values were lower for $\delta^{13}C$ than those corresponding to non-breeding Bridled Tern adults in colonies in the Seychelles (~8% difference, Catry et al., 2008) and Western Australia (~2% difference, Labbé et al., 2013). Our $\delta^{15}N$ results were lower than those of adults from the Seychelles (~22% of difference)

but relatively similar to those from Western Australia. These isotopic differences could be due to the different structures of marine food webs in the different Bridled Tern wintering areas around the world and cannot be discussed further without knowledge of isotopic baselines (e.g. Graham *et al*., 2010).

Based on ellipses geometry (Figure 2), there was a high specialisation in prey (very small variation of δ^{15}N) by pre-laying adult females of Bridled Tern. It appears that females select specific food items (rich in lipids and proteins) during the presumed "pre-breeding exodus", which could be important to obtain adequate energy reserves and key biomolecules (e.g. albumin) to face the requirements of ovogenesis and the reproductive period (Jaeger *et al*., 2017; Bratton *et al*., 2022). This specialisation resulted in narrow trophic niches in both breeding areas. However, species niche breadth varied differently from the pre-laying to the incubation phase, probably according to prey accessibility and microhabitat characteristics at each breeding area. The significantly broader trophic niche (from SEAc) of incubating adults than that of pre-laying females at Felipes could derive from the lower accessibility to feeding patches at Felipes (implying a niche expansion, as explained above) than in Paredón de Lado, as well as by the more extensive vegetation cover at nesting sites (reducing heat stress of incubating adults) in the former (Garcia-Quintas *et al*., 2023). Thus, incubating adults in Felipes could forage far from their nests, increasing the species' trophic niche with respect to the pre-laying phase, represented by highly trophically selective adult females.

On the other hand, the change from the incubation to chick-rearing phase probably implies a strengthening of the constraints on adults due to central-place foraging. These constraints occur basically in the adult foraging ranges (Lorentsen *et al*., 2019), which may explain the geometry of the modelled ellipses (wider in the δ^{15}N range and narrower in the δ^{13}C range, Figure 2) for the chick-rearing phase in this study. This implies that the chicks' trophic niches were based on the consumption of diverse prey provided from locations closer to the colonies (e.g. Hulsman & Langham, 1985), and probably a different diet compared to incubating adults. Diet changes within the breeding season are common in Bridled Terns (Dunlop & Surman, 2012; Labbé *et al*., 2013) that are also dependent on local oceanographic conditions that influence the availability of feeding patches, that are usually ephemeral in tropical and subtropical marine ecosystems (Moser & Lee, 2012). As typically occurs, the Bridled Tern trophic niche breadth decreased from the incubation to the chick-rearing phase in Felipes breeding area (according to the SEAc) as a consequence of stronger restrictions on adult foraging movements during the second phase. However, the opposite variation pattern found in Paredón de Lado resulted from the consumption of more diverse prey by chicks than by incubating adults (see ellipse extensions along the δ^{15}N axis, Figure 2). This could be possible in a scenario of easy access to feeding patches (e.g. a large accumulation of floating vegetation near colonies) where central-place foraging constraints are trade-offs, as presumably occurs at Paredón de Lado.

The trophic ecology of the Bridled Tern remains insufficiently studied. Although a trophic specialist, this species exhibited a relatively plastic trophic niche throughout the year in Cuba. The narrower trophic niche breadth, based on the consumption of specific prey, during the pre-laying phase highlights this stage as one of high vulnerability within the annual cycle of Bridled Terns. This species can, by its diet, act as a bioindicator of contaminant levels that affect human health and coastal marine ecosystems (e.g. Burger & Gochfeld, 1991). Future evaluation of the Bridled Tern-prey isotope relationships

through bulk stable isotope analyses in prey and the quantification of contaminants (e.g. mercury) in the tissues of these animals at several sites in the still "poorly known" Caribbean Sea would be greatly valuable. This could be important for the assessment of health risks associated with socioeconomic activities, such as industry, fishing and tourism, carried out in coastal and marine areas of this region. In addition, long-term monitoring of the annual plasticity of the Bridled Tern trophic niche could contribute, together with indicators of breeding success, to detection of changes in marine food webs. This could be facilitated by the representativeness of the breeding colonies of this species in the Caribbean (Bradley & Norton, 2009).

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APPENDIX 1. Figure S1. Density plots of the standard Bayesian ellipses areas representing the isotopic niche (δ^{15}N and δ^{13}C) breadth of Bridled Tern *Onychoprion anaethetus* from two breeding areas and four breeding phases, central-north of Cuba, during the 2021 breeding season.
[Diagramas de densidad de las áreas de las elipses bayesianas estándar que representan la amplitud del nicho isotópico (δ^{15}N y δ^{13}C) del charrán embridado Onychoprion anaethetus *en dos áreas de cría y cuatro fases reproductivas, centro-norte de Cuba, durante la temporada reproductiva de 2021.]*

ANNUAL PLASTICITY OF THE TROPHIC NICHE OF THE BRIDLED TERN *ONYCHOPRION ANAETHETUS* IN CUBA

PLASTICIDAD ANUAL DEL NICHO TRÓFICO DEL CHARRÁN EMBRIDADO *ONYCHOPRION ANAETHETUS* EN CUBA

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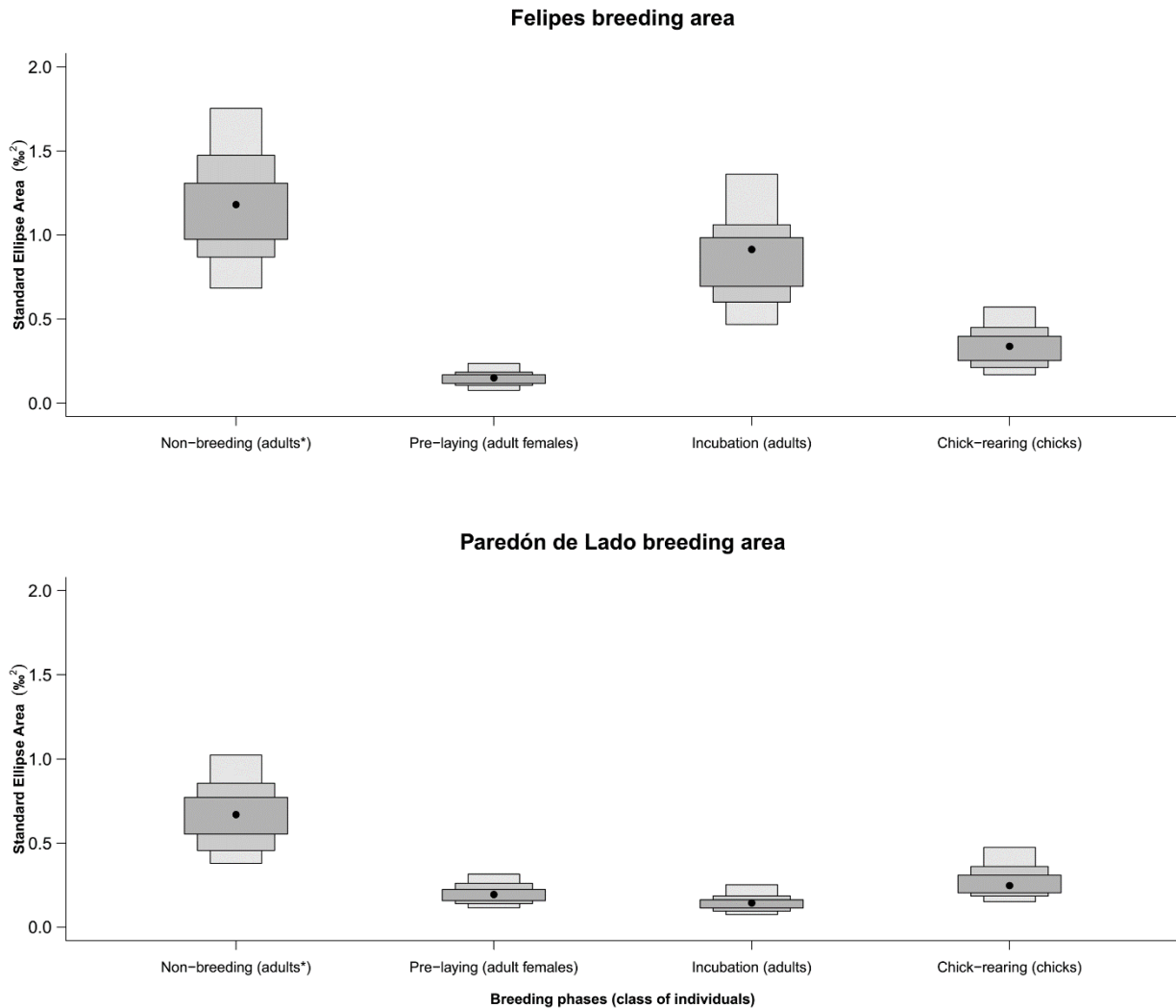* Corresponding author: agquintas86@gmail.com

APPENDIX 1

Felipes breeding area

Paredón de Lado breeding area

FIG. S1._Density plots of the standard Bayesian ellipses areas representing the isotopic niche (δ^{15}N and δ^{13}C) breadth of Bridled Tern *Onychoprion anaethetus* from two breeding areas and four breeding phases, central-north of Cuba, during the 2021 breeding season. Black dots represent their mode, shaded boxes representing 50, 75 and 95% confidence intervals from dark to light grey, respectively.

[Diagramas de densidad de las áreas de las elipses bayesianas estándar que representan la amplitud del nicho isotópico (δ^{15}N y δ^{13}C) del charrán embridado Onychoprion anaethetus *en dos áreas de cría y cuatro fases reproductivas, centro-norte de Cuba, durante la temporada reproductiva de 2021. Los puntos negros representan la moda, las cajas sombreados representan los intervalos de confianza del 50, 75 y 95 % del gris oscuro al claro, respectivamente.]*