BREEDING PHENOLOGY AND REPRODUCTIVE SUCCESS OF LARID SPECIES NESTING IN CUBA

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ABSTRACT

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Breeding phenology is a life history trait that influences reproductive success and population dynamics, yet it remains poorly studied in tropical seabird species. The Caribbean constitutes a breeding hotspot for seabirds, although information about their phenology and reproductive success is limited. We characterized the breeding phenology and reproductive success of seven larid species during the 2021 breeding season on three cays in Cuba. To document breeding phenological phases, we conducted weekly surveys and used camera traps. We also recorded the number of nests, eggs and fledglings. Overall, the breeding phenology of the studied species was seasonal and relatively synchronous, occurring primarily from May to August. The phenological pattern exhibited in this larid community may reflect increased prey availability during the rainy season in Cuba. Additionally, denser vegetation cover—resulting from higher rainfall—may offer greater protection against predators, particularly because most of the species are summer residents. Reproductive success was high (≥ 50% per pair) for Laughing Gull *Leucophaeus atricilla*, Sooty Tern *Onychoprion fuscatus*, and Roseate Tern *Sterna dougallii* in all cays, while Bridled Tern *O. anaethetus* and Royal Tern *Thalasseus maximus* exhibited variable reproductive performance between cays. Sandwich Tern *T. sandvicensis* exhibited moderate reproductive success (40%–49%). Landscape features at nesting sites appeared to strongly affect the reproductive success of both Bridled Tern and Royal Tern.

Key words: breeding performance, gulls, phenological phases, seasonality, terns, tropical seabirds

INTRODUCTION

The ecology of tropical seabirds remains incompletely understood, including their breeding phenology (e.g., Surman et al., 2012). Tropical seabirds display a mix of breeding patterns (synchrony, asynchrony, seasonality, periodic breeding, episodic breeding, aseasonal breeding), in contrast to temperate and polar seabird species, which typically breed seasonally and synchronously (Hamer et al., 2002). Knowledge of breeding phenology is essential to understand seabird ecology, as it directly impacts reproductive success and population dynamics (Lindén, 2018; Quintero et al., 2014). The timing of reproduction is crucial to reproductive success, as it is closely linked to local environmental conditions and prey availability (Brandl et al., 2019), although it also has a heritable component (Dobson et al., 2017; Moiron et al., 2020). Breeding phenology influences clutch size, chick growth, and depredation—all factors that can influence reproductive outcomes.
The reproductive success of seabirds is influenced by multiple factors. These include nesting-site selection (Muzaffar et al., 2015), age/experience (Sydeman & Emslie, 1992) and foraging characteristics (Lorentsen et al., 2019; Pulvirenti et al., 2023) of parents, egg morphology (Cram et al., 2019), and human disturbance (Byerly et al., 2021). The potential synergistic effects of these and other factors on reproductive success require rigorously designed studies to accurately assess the role of individual factors in breeding performance. Nevertheless, the basic measures of reproductive success have been used as primary indicators for evaluating the status and trends of seabird populations, as well as for identifying local environmental stressors (Barrett et al., 2007; Hazen et al., 2019).

Cuba is a tropical archipelago that hosts a large seabird community (Bradley & Norton, 2009), with the Laridae family (gulls and terns) being the most represented group (Jiménez et al., 2009). Nevertheless, breeding phenology of this seabird family remains largely unknown in the archipelago, despite being better studied in other tropical locations, including the Caribbean (e.g., Buckley et al., 2021; Gochfeld & Burger, 2020; Haney et al., 2020). Furthermore, some parameters of reproductive success have only been roughly and sporadically quantified in Cuban larids (e.g., Acosta et al., 2022). Therefore, this study aims to (1) characterize the breeding phenology and (2) assess the reproductive success of larid species at three locations in Cuba.

METHODS

Study areas

This study was conducted at three cays of the Sabana-Camagüey archipelago in the central-north region of Cuba (Fig. 1). Climatological

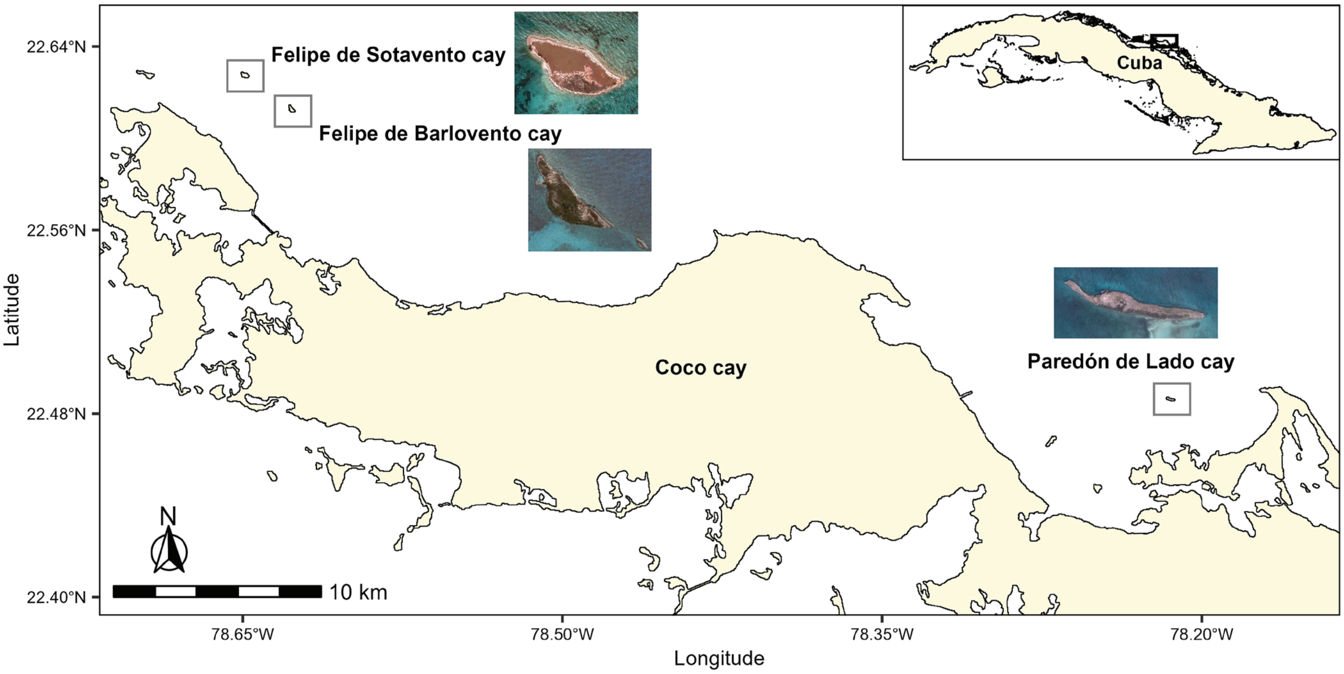

Fig. 1. Map of the study area showing three cays (enclosed in grey squares)—Felipe de Barlovento (FB), Felipe de Sotavento (FS), and Paredón de Lado (PL)—located in the Sabana-Camagüey archipelago in the central-north region of Cuba. The study was conducted during the 2021 breeding season.

data from Meteorological Station 78339 (located at the Coastal Ecosystem Research Center, Cayo Coco, Cuba), indicate that the region has a tropical climate, characterized by a moderate and stable thermal regime. The annual average temperature is 26.3 °C, and average annual precipitation is 88.5 mm. Prevailing easterly winds have an average annual speed of 14.5 km·h^{-1}. During the core breeding season of most seabirds in Cuba (May to August; Garrido & Kirkconnell, 2011), the average temperature rises to 28.0 °C, and average precipitation increases to 109.2 mm.

Field studies were conducted on three cays: Felipe de Barlovento (FB), Felipe de Sotavento (FS), and Paredón de Lado (PL), each with an area less than 0.1 km^2 (Fig. 1). All three cays are characterized by a sandy-rocky substratum with sparse vegetation. The dominant plant formations include mosaics of sandy and rocky coastal vegetation, along with mangroves composed exclusively of *Conocarpus erectus* (González-Leiva & González-Pérez, 2021). Additionally, an extended grassland dominated by *Uniola paniculata* occurs in FS. Plant species richness is low, with a total of 28 species and no significant seasonal variation. Species counts by cay are 19 (FS), 17 (FB), and 9 (PL) (González-Leiva & González-Pérez, 2021). These cays constitute one of the most significant seabird breeding grounds in Cuba (Jiménez et al., 2009).

Fieldwork and breeding parameters

This study was conducted under Cuban Environmental License No. 04/2021, issued by the Oficina de Regulación y Seguridad Ambiental in the Ciego de Ávila Province, granting access to natural areas. Weekly surveys were undertaken in each study cay from May to August 2021 to monitor the breeding phenology of larids. Surveys were conducted exclusively between 09h00–10h00 to minimize disturbance. During each survey, we recorded the presence of adults, nests, eggs, chicks, and fledglings. Additionally, to identify the peak egg-laying period—defined as two consecutive surveys with a stable number of eggs—we counted the number of eggs per nest within a longitudinal 2-m-wide linear transect on FB. This transect was implemented on FB because this cay hosts the highest larid species richness among the study sites.

Once laying began, seven camera traps (WCB-00116, BirdCam Pro; Alabaster, United States) were placed near established colonies to obtain more detailed phenological information (e.g., duration of hatching and chick rearing). Cameras were installed within 0.5 m of nesting sites; however, in denser colonies, this distance was increased to 1.0 m. Each camera was programmed to take a photo (resolution: 2,592×1,944 pixels, flash disabled) 10 s after any activation of the motion sensor (set to low sensitivity). For loosely colonial species, one camera was placed per nest, whereas for highly gregarious species, one camera captured several nests within its field of view. The locations of the cameras were changed weekly to a different nesting site without repetition, continuing until the chicks fledged. This approach accounted for phenological variability among breeding pairs.

We considered seven phenological phases: (1) courtship, including any type of adult interaction involved in pairing; (2) copulation; (3) laying, from the first egg to a stable number of eggs; (4) incubation, from the first egg to the absence of eggs (failed or abandoned eggs were excluded); (5) hatching, between the first chick observed to the absence of eggs (failed or abandoned eggs were excluded); (6) rearing, parental care from hatching of the first egg to all chicks fledging; and (7) fledging, from the first fledging-age chick departing to the end of the monitoring period.

Once the peak of egg laying was identified, a total count of occupied nests (i.e., the number of breeding pairs) and eggs for each species on each cay was conducted. The total number of fledglings was recorded at the end of the monitoring period. Thereafter, the mean clutch-size (number of eggs pair) and reproductive success per egg and pair (i.e., percentage of fledglings relative to the number of eggs laid and breeding pairs, respectively) were calculated as measures of reproductive success. Reproductive success per pair can exceed 100% in species with clutches larger than one egg. Data visualization was performed using R 4.1.1 (R Core Team, 2021).

RESULTS

Seven larid species nested at the study sites: Laughing Gull *Leucophaeus atricilla* at FB and PL; Brown Noddy *Anous stolidus* on FB and FS; Sooty Tern *Onychoprion fuscatus* on FB and PL; Bridled Tern *O. anaethetus* on FB, FS, and PL; Roseate Tern *Sterna dougallii* on FB; Royal Tern *Thalasseus maximus* on FB and PL; and Sandwich Tern *T. sandvicensis* on FB. Brown Noddy *Anous stolidus* were not abundant and were directly monitored at only two nests.

Breeding phenology

The peak of laying for all breeding species occurred during weeks 20–22, corresponding to 17 May–06 June (Fig. 2). Sampling with camera traps included nesting sites of five species where the effectiveness (i.e., the proportion of usable photos) of registered photos exceeded 70% (Table A1 in Appendix 1, available on the website).

Sooty, Roseate, and Sandwich Terns exhibited a high level of breeding synchrony, all reaching the laying peak three weeks after the onset of laying (Fig. 2). Bridled and Royal Terns required four weeks to reach their laying peak (Fig. 2). Laughing Gulls had a staggered laying pattern, taking five weeks to reach its peak (Fig. 2), making it the least synchronous species. Overall, there was a high degree of temporal overlap among respective phenological phases (Fig. 3). The main differences occurred in the relative durations of incubation, hatching, and chick-rearing periods. Laughing Gulls, along with Bridled, Roseate, Royal, and Sandwich Terns exhibited two separated laying periods that produced chicks in both. However, the Roseate Tern failed to produce chicks during the second laying period (Fig. 3).

Reproductive success

Laughing Gulls laid one to three eggs per nest, with two-egg clutches being more frequent on FB (44.60%) and FS (48.48%) than on PL (38.98%). In contrast, three-egg clutches predominated on PL (43.50%) compared to FB (38.85%) and FS (33.33%). Despite the relatively higher number of breeding pairs on FB, mean clutch sizes were remarkably similar across all cays. Reproductive success for this species was also comparable among the cays, with slightly higher values on FB (Table 1).

In their unique breeding population on FB, 73.53% of the Roseate Tern pairs produced the maximum clutch size of two eggs. In this species, reproductive success per egg was nearly half that measured per breeding pair (Table 1). The remaining species typically laid one-egg clutches and exhibited their lowest reproductive success values on PL—particularly Bridled and Royal Terns, whose success rates were less than half those

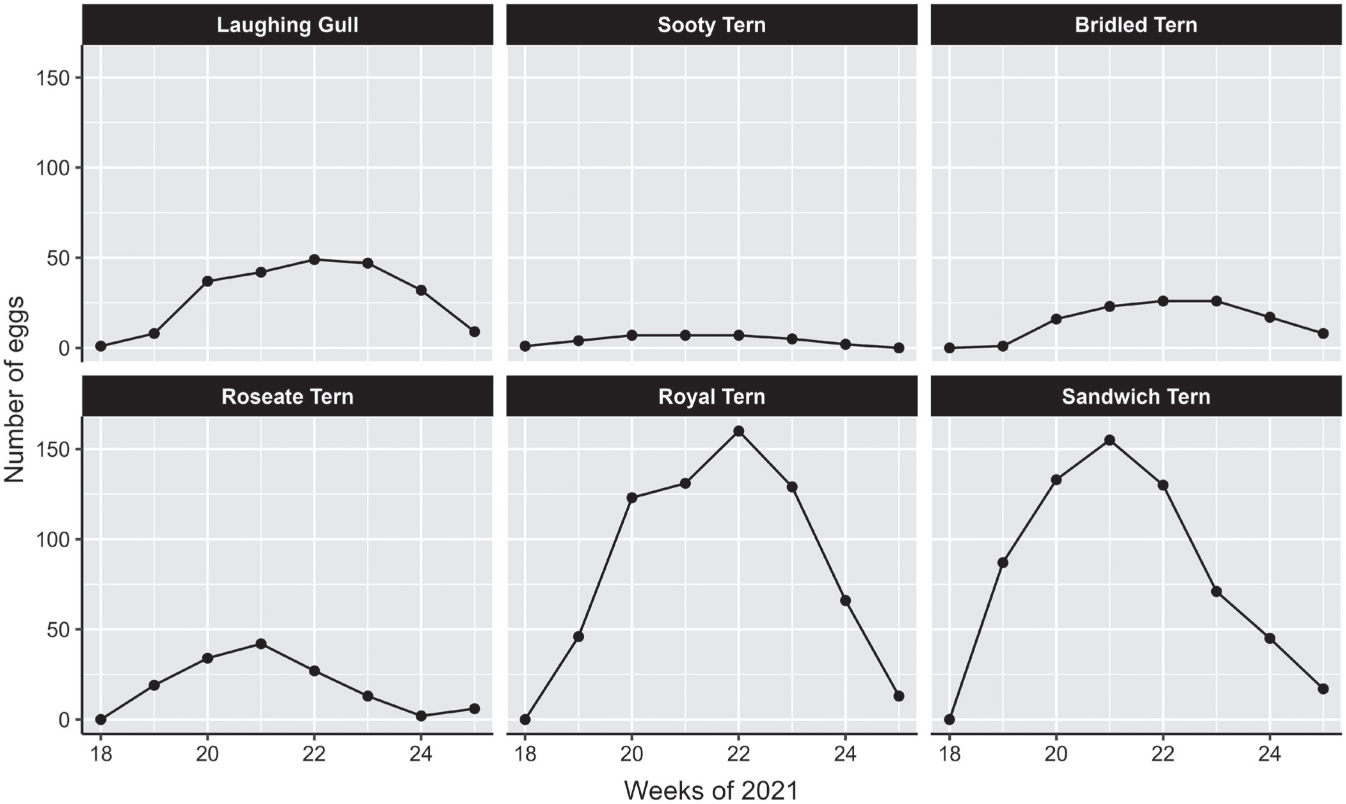

Fig. 2. Weekly egg counts of six larid species (Laughing Gull *Leucophaeus atricilla*, Sooty Tern *Onychoprion fuscatus*, Bridled Tern *O. anaethetus*, Roseate Tern *Sterna dougallii*, Royal Tern *Thalasseus maximus*, and Sandwich Tern *T. sandvicensis)* along a longitudinal transect at Felipe de Barlovento cay, central-north of Cuba, during the 2021 breeding season.

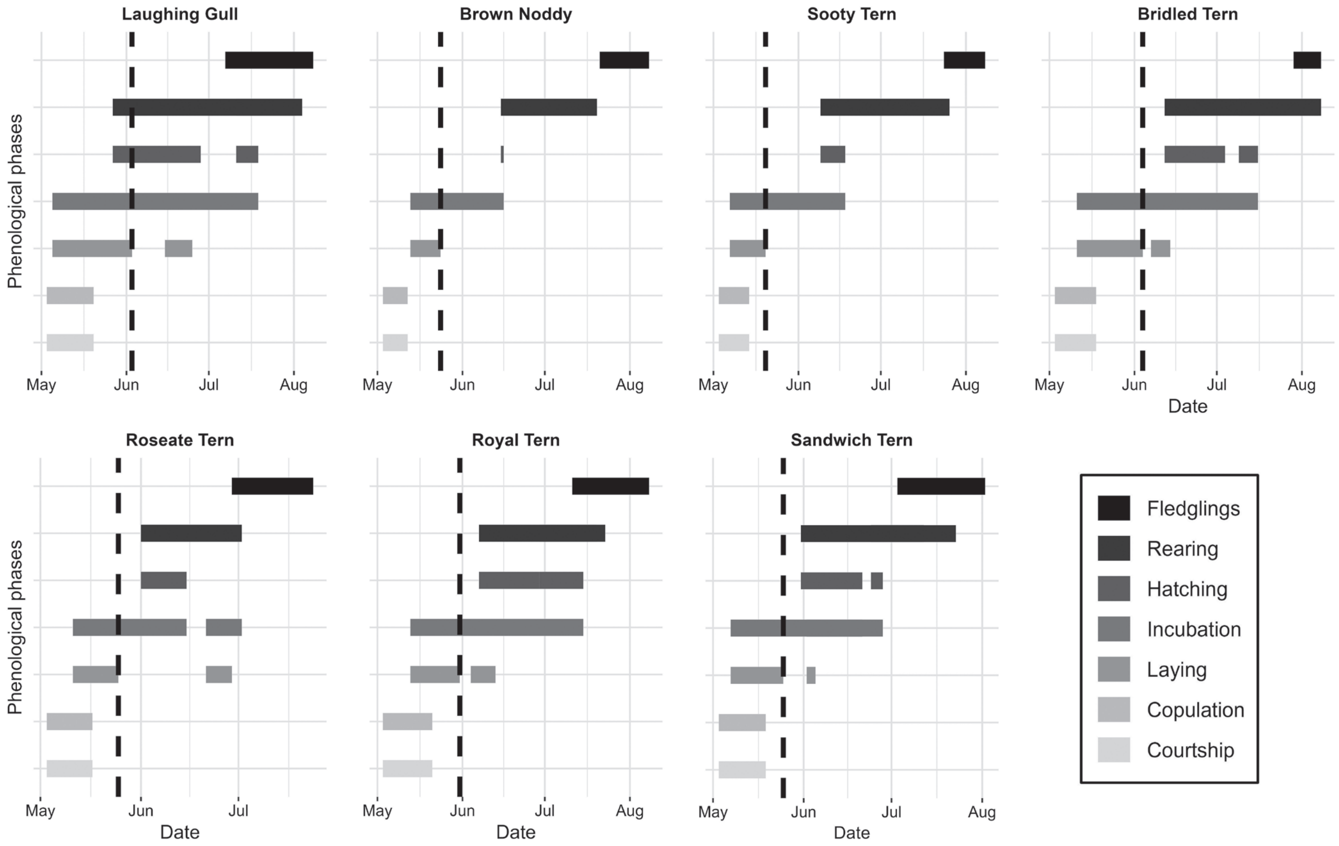

Fig. 3. Breeding phenology of seven larid species at three cays in central-north Cuba during the 2021 breeding season. Dashed black lines indicate the laying peak based on n = 40, 2, 7, 26, 34, 160, and 155 clutches for, respectively, Laughing Gull *Leucophaeus atricilla*, Brown Noddy *Anous stolidus*, Sooty Tern *Onychoprion fuscatus*, Bridled Tern *O. anaethetus*, Roseate Tern *Sterna dougallii*, Royal Tern *Thalasseus maximus*, and Sandwich Tern *T. sandvicensis*.

TABLE 1
Reproductive parameters of seven species of larids on three cays of north-central Cuba, during the 2021 breeding season

Cay	Species[a]	No. nests (= pairs)	No. eggs	Mean clutch size	No. fledglings	Reproductive success per egg (%)	Reproductive success per pair (%)
Felipe de Barlovento	Laughing Gull	278	618	2.22	320	51.78	115.11
	Brown Noddy	1	1	1.00	0	0.00	0.00
	Sooty Tern	15	15	1.00	9	60.00	60.00
	Bridled Tern	37	37	1.00	28	75.68	75.68
	Roseate Tern	34	59	1.74	24	40.68	70.59
	Royal Tern	131	131	1.00	81	61.83	61.83
	Sandwich Tern	159	159	1.00	72	45.28	45.28
Overall	7	655	1,020	1.56	534	52.35	81.53
Felipe de Sotavento	Laughing Gull	33	71	2.15	28	39.44	84.85
	Brown Noddy	1	1	1.00	1	100.00	100.00
	Bridled Tern	83	83	1.00	58	69.88	69.88
Overall	3	117	155	1.32	87	56.13	74.36
Paredón de Lado	Laughing Gull	177	400	2.26	173	43.25	97.74
	Sooty Tern	2	2	1.00	1	50.00	50.00
	Bridled Tern	76	76	1.00	21	27.63	27.63
	Royal Tern	20	20	1.00	6	30.00	30.00
Overall	4	275	498	1.81	201	40.36	73.09

[a] Laughing Gull *Leucophaeus atricilla*, Brown Noddy *Anous stolidus*, Sooty Tern *Onychoprion fuscatus*, Bridled Tern *O. anaethetus*, Roseate Tern *Sterna dougallii*, Royal Tern *Thalasseus maximus*, and Sandwich Tern *T. sandvicensis*

recorded at the other cays (Table 1). Brown Noddies were successful in only one nest at FS, but this species was poorly represented in the study areas.

DISCUSSION

Breeding phenology

Breeding phenology is a crucial component of seabird reproductive ecology, as it influences individual fitness, reproductive success, and population dynamics (Black et al., 2018; Dunn & Møller, 2014). Moreover, inter-annual phenological variation can reflect changes in weather and marine food webs (Hindell et al., 2012). Our study provides a more comprehensive characterization of larid breeding phenology in Cuba, highlighting the relative breeding synchrony among species. Although limited, previous studies (e.g., Garrido & Kirkconnell, 2011), along with our findings, indicate that larid reproduction in Cuba is generally seasonal and relatively synchronous, occurring from May to August. However, breeding phenology should be studied over consecutive years to assess annual variation in the degree of synchrony. Furthermore, the sample size (number of clutches) should be increased to more thoroughly characterize the breeding phenology of Brown Noddies and Sooty Terns in Cuba.

The breeding phenology of the species studied in Cuba was consistent with patterns observed across the Caribbean. Similar to other populations at the regional scale (Buckley et al., 2021; Gochfeld & Burger, 2020; Shealer et al., 2020), the highly gregarious Roseate, Royal, and Sandwich Terns began their relatively early and extended laying periods primarily in May, with most hatching occurring in June (extending to the first half of July for the Royal Tern). The Sooty Tern began nesting in early May, with an incubation period that fell within the range reported for populations in the Greater Antilles (Schreiber et al., 2020). The breeding season of the Bridled Tern in the Caribbean typically extends from late April to September, although timing may vary between localities (Haney et al., 2020). Consistent with this, we observed the laying peak beginning in early June. A similar pattern was observed for the Laughing Gull, although its laying peak in early June occurred slightly later than in some Caribbean and North American localities (Burger, 2020).

The seasonal and synchronous character of larid breeding phenology observed in our study may be attributed to several factors related to the region's climate and prey availability. For example, the breeding period occurred during the rainy season (May–October), a time characterized by relatively stable daily meteorological conditions (influenced by the North Atlantic Anticyclone, www.insmet.cu). The most significant variations in weather during this period are caused by atmospheric circulation disturbances, such as easterly waves and tropical cyclones.

Seabirds may adjust their breeding phenology in response to cues from local weather conditions (Surman et al., 2012). In our study area, stable weather during the rainy season results in calm sea surface conditions, which may enhance prey capture for larids that rely on surface dipping and shallow diving. Prey availability and abundance may also increase during this season. In tropical regions, high rainfall is often associated with greater food availability for birds (Quintero et al., 2014), which could explain the synchronized reproduction of larids in the Caribbean basin. Rainfall could increase runoff to the sea, which is likely to increase nutrient inputs to coastal marine food webs.

In addition, frequent rain influences vegetation cover by promoting the growth of annual plants and increasing leaf cover. As a result, vegetation cover on the cays increases during the rainy season. Since high vegetation cover and the presence of certain plant species are important variables for the selection of breeding microhabitats for most of these seabirds (Garcia-Quintas et al., 2023), this may be another factor contributing to the seasonal and synchronous breeding phenology observed in this study. Finally, the residency status of each species may also play a role. The Brown Noddy, along with the Sooty, Bridled, Roseate, and Sandwich Terns, are primarily summer residents in the region (Garrido & Kirkconnell, 2011), and must synchronize their breeding to ensure that offspring are able to fly south at the end of the season. In contrast, the Laughing Gull and Royal Tern are permanent residents (Garrido & Kirkconnell, 2011), allowing them to take full advantage of the favorable climatic conditions and the benefits of colonial breeding.

Despite the relative synchrony and seasonality in laying, five of seven studied species had two distinct laying periods. In general, the first period was longer than the second, which aligns with the advantages of early nesting (e.g., Dobson et al., 2017; Dunn & Møller, 2014; Moiron et al., 2020). The shorter duration of the second period, involving a smaller number of individuals, may reflect females that were unable to secure a nesting site and mate early in the season, those that failed during the first laying attempt, and/or younger or less experienced females.

Reproductive success

The species in this study exhibited three general patterns of reproductive performance. First, Laughing Gulls, Sooty Terns, and Roseate Terns had high reproductive success (≥ 50% per pair), although Laughing Gulls and Sooty Terns had relatively low reproductive success per egg. Second, Bridled and Royal Terns showed contrasting reproductive outcomes, with breeding success rates on PL being less than half that recorded on FB and FS. Finally, Sandwich Terns displayed moderate reproductive success (40%–49% per pair), despite the high number of breeding pairs on FB.

Laughing Gull clutch sizes in this study were at least 19% smaller than those reported at a colony in Tampa Bay, Florida (Dinsmore & Schreiber, 1974). However, they were comparable to clutch sizes reported at a colony on an island in Sinaloa, Mexico (González-Medina et al., 2009), where reproductive success per pair was more than twice that observed in this study. Sooty Tern reproductive success in the Seychelles (~50%; Feare, 1976) was similar to that observed at PL and moderately lower than at FB. The breeding success of Roseate Terns was relatively similar to that estimated for Cedar Beach, but lower than at Bird Island, both in the northeastern United States (Burger et al., 1996). These comparisons suggest that these species are capable of high reproductive performance depending on local conditions and the presence or absence of negative factors such as hurricanes, disease outbreaks, or introduced predators. The high reproductive success per pair observed in our study may be associated with the active defense of nest sites (observed in Sooty Terns) or the production of larger clutch sizes (> 1), which is common in Laughing Gulls and Roseate Terns (Burger et al., 1996; González-Medina et al., 2009; Garrido & Kirkconnell, 2011). These strategies may help offset their relatively low reproductive success per egg.

Bridled Tern reproductive success at FB and FS was ~20% lower than at One Tree Island, Australia (Hulsman & Langham, 1985), but relatively similar to that observed at colonies on Penguin Island, Australia (Garavanta & Wooller, 2000), New Caledonia (Villard & Bretagnolle, 2010), and Nakhilu Island, Persian Gulf (Tayefeh et al., 2017). At FB, Royal Tern achieved > 30% reproductive success compared to colonies at Isles Dernieres Barrier Island Refuge in the northern Gulf of Mexico (Owen & Pierce, 2014). However, the reproductive performance of the Bridled and Royal Terns in PL was notably low, not exceeding 30%. This may be attributed to two primary factors, aside from any potential limitations in chick food supply (Garcia-Quintas et al., 2024). First, the small size of the Royal Tern colony at PL likely led to weak collective defense against predators (a reduced group effect), leading to increased loss of eggs and chicks. Second, low vegetation cover in PL (Garcia-Quintas et al., 2023) may have increased exposure to aerial predators and climatic extremes (e.g., strong heat and rain), negatively affecting egg and chick survival in both species. In this context, the higher incidence of three-egg clutches of Laughing Gulls in PL may represent a reproductive trade-off, potentially enhancing breeding success under the same conditions. Finally, Sandwich Terns achieved reproductive success similar to that reported at the Isles Dernieres Barrier Island Refuge (Owen & Pierce, 2014), suggesting stable reproductive performance when breeding in sympatry with Royal Tern in nearby regions.

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AUTHOR CONTRIBUTIONS

AGQ: Conceptualization (lead), investigation (lead), visualization (lead), writing—original draft (equal), writing—review and editing (equal). DD: Conceptualization (equal), investigation (equal), visualization (equal), supervision (equal). CB: Visualization (equal), writing—original draft (equal), writing—review and editing (equal), supervision (equal). SL: conceptualization (equal), writing—original draft (equal), writing—review and editing (equal), supervision (lead).

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