

BREEDING MICROHABITAT PATTERNS AMONG SYMPATRIC TROPICAL LARIDS

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ABSTRACT

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The selection of breeding microhabitat (nesting sites) affects successful reproduction in seabirds, yet the process of nesting-site selection in sympatric tropical species remains poorly known. During the 2021 breeding season, we assessed nesting-site selection among five larid species at three cays of Cuba and quantified explanatory variables. Random forest classification models were used to assess which landscape features among eight variables best explained site selection by each species. Patterns were clear for most species, especially the highly gregarious Roseate Tern *Sterna dougallii*, Royal Tern *Thalasseus maximus*, and Sandwich Tern *T. sandvicensis*. Patterns were consistent among the study cays. Dominant plant species, minimal distance to cay edge, vegetation cover, and substratum at nesting sites were among the more important explanatory variables. Interspecific differences in nesting-site selection may be important for the assemblage of multispecific colonies by reducing aggressive interactions, competition, and breeding failures.

Key words: gulls, terns, marine coastal ecosystem, nesting site, random forest, breeding colonies

INTRODUCTION

Habitat selection contributes significantly to the individual fitness and co-existence of animals (Orians & Wittenberger 1991, Trevail *et al.* 2021). The process is highly complex, with multiple origins derived from several selective pressures (Danchin *et al.* 1998). The complexity can lead animals to select poor habitats based on erroneous or incomplete information (Orians & Wittenberger 1991, Kokko *et al.* 2004). Among seabirds, the selection of nesting habitat is a multifactorial and relatively little known process (Córdoba-Córdoba *et al.* 2010, Clark *et al.* 2019). Two key aspects appear to be involved: colonial breeding—a highly specialized behavior—and the influence of spatial and temporal scales.

Colonial breeding, which refers to the phenomenon of a species breeding at high densities in areas with suitable resources and conditions, is quite common in birds and has been observed in ~13% of avian species (Rolland *et al.* 1998, Salas *et al.* 2020). Breeding habitat selection by seabirds operates at least at two spatial scales: selection of the breeding location (e.g., island, peninsula, beach, etc., hereafter called breeding macrohabitat) and the nesting site itself (i.e., the specific place of nest establishment, hereafter called breeding microhabitat). Interspecific colonial behavior (several species using the same island and its surrounding waters) is important at the macrohabitat scale, while species segregation is often exhibited at the scale of the microhabitat scale (Buckley & Buckley 1980, Fasola & Canova 1992).

Selection of the nesting site within suitable breeding habitat has long been recognized as important for breeding success (Robertson *et al.*

2001, Muzaffar *et al.* 2015). Substratum (Greer *et al.* 1988, Fasola & Canova 1992), geomorphology (Eveillard-Buchoux *et al.* 2019), vegetation (Raynor *et al.* 2012, Muzaffar *et al.* 2015), weather conditions, predation (Fasola & Canova 1992, Córdoba-Córdoba *et al.* 2010), space restrictions (Fasola & Canova 1992, Nunes *et al.* 2018), flooding risks (Greer *et al.* 1988, Raynor *et al.* 2012), and social interactions (Greer *et al.* 1988, Córdoba-Córdoba *et al.* 2010) are the most important factors involved; these depend on habitat characteristics and species requirements. Nesting-site selection in seabirds is thus complex and calls for a better understanding of the variables driving species-specific selection and segregation (Burger & Shisler 1978, Greer *et al.* 1988). Understanding the ecological factors driving nesting-site selection is ultimately a critical aspect for designing efficient conservation policies (Eveillard-Buchoux *et al.* 2019), as seabirds are among the most threatened birds in the world (Dias *et al.* 2019).

In the West Indies, Cuba is an important seabird breeding region (Bradley & Norton 2009). Laridae (gulls, terns, and skimmers) are the most common type of seabirds in Cuba, with 25 species registered but only nine of which breed within the archipelago (Jiménez *et al.* 2009, Navarro 2021). Ecological studies on the breeding ecology of these species in Cuba are scarce, and breeding and nesting habitats having been described only roughly (e.g., Rodríguez *et al.* 2003). A few small cays in the central-northern region of Cuba constitute important hotspots, especially Felipe de Barlovento, Felipe de Sotavento, and Paredón de Lado cays (Ruiz *et al.* 2014, Fig. 1). These sites support the largest larid colonies in Cuba, with Felipe de Barlovento hosting the greatest species richness of the entire archipelago (Ruiz *et al.* 2014, García-Quintas

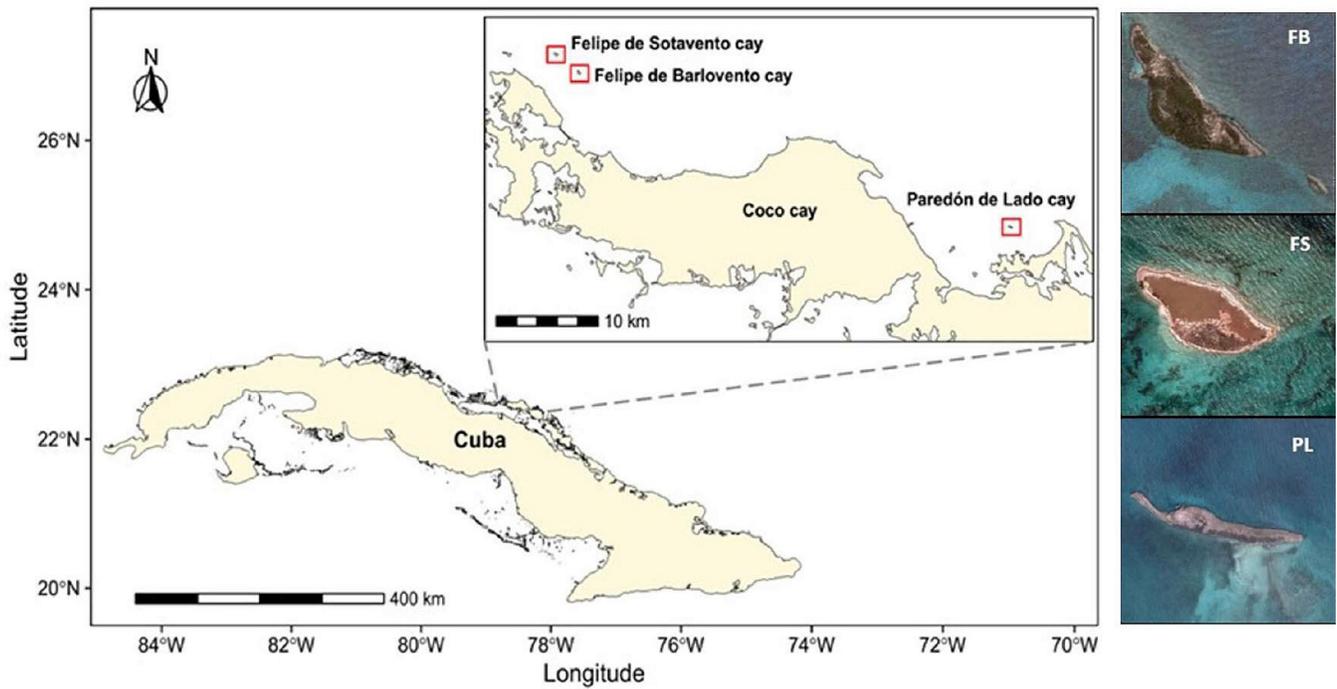


Fig. 1. Study area during the 2021 breeding season; red squares indicate the study cays. FB = Felipe de Barlovento cay, FS = Felipe de Sotavento cay, PL = Paredón de Lado cay

et al. 2020). Nevertheless, there is no information on nesting-site selection by Laridae in this area. We thus aimed to assess the nesting-site (breeding microhabitat) selection patterns of larid species in the cays of central-northern Cuba and to identify the most important variables explaining those patterns.

While nesting-site selection by seabirds is influenced by several factors (García Borboroglu & Yorio 2007, Córdoba-Córdoba *et*

al. 2010), it is mainly recognized as a mechanism to reduce interspecific competition for space and predation risk (Buckley & Buckley 1980, Brooke *et al.* 2018). Based on field observations and monitoring in the aforementioned cays, it appears that predation pressure is minimal; there are few predators such as raptors, gulls, and terrestrial crabs. Thus we hypothesize that spatial competition could explain the nesting pattern of several larids in accord with heterogeneity of available microhabitats. We further hypothesized

TABLE 1
Ecological components measured to assess reproductive microhabitat (nesting-site) selection by five larid species in three cays in central-northern Cuba during the 2021 breeding season

Factor	Variable	Unit	Ecological meaning
Laying substratum	Substratum type (qualitative)	-	Essential to the nest/clutch support
Ground wetness	Normalized Difference Water Index (quantitative)	-	Represents the degree of wetness at the nesting place and the potential risk of flooding
Position inside the locality	Minimal distance to cay edge (quantitative)	m	Indicates the potential vulnerability of nesting sites to sea surges
	Horizontal vegetation cover (quantitative)	%	Related to the level of visibility of the nesting site to predators, to microclimatic conditions, and to potential aggression interactions between neighbors mediated by nest visibility
Vegetation	Minimal distance to vegetation patch (quantitative)	m	Associated with the use of that vegetation resource for nest safety
	Dominant plant species (qualitative)	-	Allows the detection of plant-larid associations for nesting, if they exist
Exposure level	Horizontal non-vegetation cover (quantitative)	%	Cover provided by any non-vegetation component such as rock or dead wood. Indicates the visibility level of the nesting site to predators and its direct exposure to the sun and rainfall
	Minimal distance to open area (quantitative)	m	Represents a measure of shelter (access level) and escape facility of adults facing threats

that nesting-site selection varies depending on whether species are sympatric. This strategy could allow co-existence, minimizing both competition for space and nest failures due to interspecific interactions. However, if nesting-site characteristics do not vary for a given species despite the presence of other larid species, this would suggest species-specific nesting-site selection processes that are influenced by other ecological factors.

STUDY AREA AND METHODS

Fieldwork was undertaken in three cays of the Sabana-Camagüey archipelago in the central-northern region of Cuba: Felipe de Barlovento (FB), Felipe de Sotavento (FS), and Paredón de Lado (PL, Fig. 1). In this region, the annual temperature averages 26.3 °C and monthly precipitation averages 88.5 mm. Easterlies with a mean annual wind speed of 14.5 km·h⁻¹ prevail year round (Meteorological Station 78339 of the Coastal Ecosystem Research Center, Cayo Coco, Ciego de Ávila, Cuba).

These very small cays (< 0.1 km²) are at low elevation and have sandy and rocky substrata with sparse vegetation. Plant cover is composed of button mangrove *Conocarpus erectus* (González-Leiva & González-Pérez 2021); grassland patches on FS are dominated by seaside oats *Uniola paniculata*. Plant richness in these cays is low (28 species total) without significant seasonal variation: 19 species have been observed on FS, 17 on FB, and 9 on PL (González-Leiva & González-Pérez 2021).

Data collection

We characterized the nesting sites of five larid species on FB, FS, and PL during the 2021 breeding season (Fig. S1 in Appendix 1, available on the website). The seabird species present were Laughing Gull *Leucophaeus atricilla* (LAGU) in FB and PL; Bridled Tern *Onychoprion anaethetus* (BRTE) in FB, FS, and PL; Roseate Tern *Sterna dougallii* (ROST) in FB; Royal Tern *Thalasseus maximus* (ROYT) in FB and PL; and Sandwich Tern *T. sandvicensis* (SATE) in FB. Brown Noddy *Anous stolidus* (BRNO, in FB and FS) and Sooty Tern *O. fuscatus* (SOTE, in FB and PL) were also present, but in low numbers (< 16 nests) and thus could not be included in the analysis. All species breed during the same period of the year, from May to August (Garrido & Kirkconnell 2011).

During the period 18–27 May 2021, we selected at least 30 nests for each species at each cay, except for ROYT at PL. Nest were selected to represent the range of ground cover heterogeneity. To characterize nesting sites, we assessed five ecological components through eight variables (Table 1). Briefly, 1) laying substratum was assessed via substratum type (sand, herb, branch, rock, land, padding, and combinations of these); 2) ground wetness was measured using the Normalized Difference Water Index (NDWI); 3) position at the site was measured in metres using the minimal distance to cay edge (defined as the fixed limit of the water-land interface, regardless the type of coast); 4) vegetation was measured using the amount of horizontal vegetation cover, the minimal distance to the nearest vegetation patch, and the dominant plant species; and 5) exposure level was measured by the amount of non-vegetation cover and the minimal distance to an open area. All variables were obtained during the fieldwork except for the satellite-derived NDWI (Gao 1996). NDWI is a spectral index that measures humidity level on surfaces, and it was used here as a proxy of breeding failure risk due to occasional flooding caused by

rain or waves. We considered all combinations of substratum type and dominant plant species. Distance variables were measured with a 30-m tape measure (precision ± 1 mm), and horizontal vegetation cover was estimated using a plastic tube with visual fields divided into

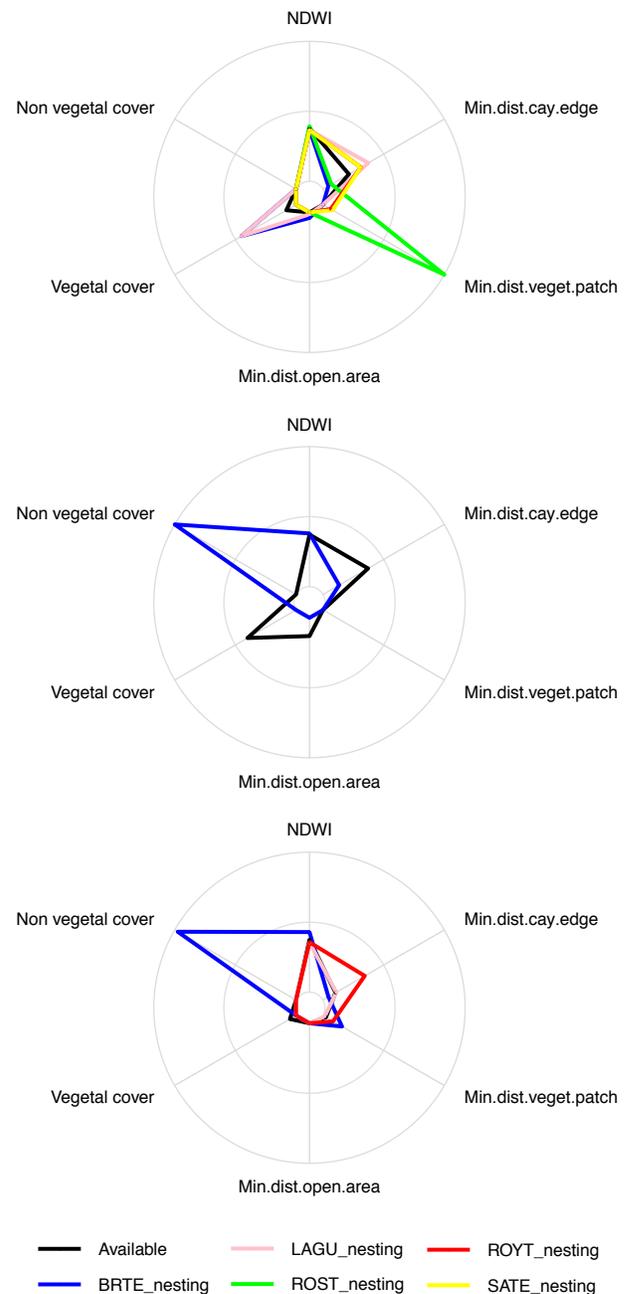


Fig. 2. Observed reproductive microhabitat selection patterns according to six quantitative variables for five species of larids nesting at Felipe de Barlovento (top), Felipe de Sotavento (middle), and Paredón de Lado (bottom) cays in central-northern Cuba during the 2021 breeding season. NDWI = Normalized Difference Water Index, Min.dist.cay.edge = minimal distance to cay edge, Min.dist.veget.patch = minimal distance to vegetation patch, Min.dist.open.aren = minimal distance to open area, LAGU = Laughing Gull *Leucophaeus atricilla*, BRTE = Bridled Tern *Onychoprion anaethetus*, ROST = Roseate Tern *Sterna dougallii*, ROYT = Royal Tern *Thalasseus maximus*, SATE = Sandwich Tern *Thalasseus sandvicensis*

TABLE 2
Quantitative variables describing the breeding microhabitat of
five species of larids and available sites in three central-northern cays in Cuba

Species	Variables ^a	Nesting sites	Available sites (<i>n</i> = 33)
Laughing Gull <i>Leucophaeus atricilla</i>	Cay: Felipe de Barlovento		(<i>n</i> = 30)
	Normalized difference water index	-0.27 (-0.29 to -0.24)	-0.24 (-0.26 to -0.18)
	Minimal distance to cay edge	28.64 (17.49–36.52)	16.38 (4.15–30.11)
	Minimal distance to vegetation patch ^b	7.04 (5.82–8.80)	6.75 (2.50–15.54)
	Inside the vegetation patch ^b	87%	61%
	Minimal distance to open area ^b	0.54 (0.43–0.63)	2.92 (2.27–3.07)
	Inside the open area ^b	43%	85%
	Percentage of vegetation cover ^b	75.0 (30.0–90.0)	75.0 (26.5–98.0)
	Without vegetation cover ^b	30%	42%
	Cay: Paredón de Lado		(<i>n</i> = 30)
	Normalized difference water index	-0.29 (-0.31 to -0.24)	-0.25 (-0.29 to -0.15)
	Minimal distance to cay edge	8.44 (4.19–15.06)	7.94 (3.01–14.93)
	Minimal distance to vegetation patch ^b	6.95 (2.20–13.25)	3.87 (1.15–14.60)
	Inside the vegetation patch ^b	33%	0%
	Minimal distance to open area ^b	0.55 (0.50–0.67)	0.0
	Inside the open area ^b	80%	100%
	Percentage of vegetation cover ^b	70.0 (15.0–75.0)	45.0 (16.3–78.8)
	Without vegetation cover ^b	70%	45%
	Percentage of non-vegetation cover ^b	25.0 (15.0–50.0)	50.0 (30.0–70.0)
Without non-vegetation cover ^b	83%	73%	
Bridled Tern <i>Onychoprion anaethetus</i>	Cay: Felipe de Barlovento		(<i>n</i> = 30)
	Normalized difference water index	-0.26 (-0.33 to -0.18)	-0.24 (-0.26 to -0.18)
	Minimal distance to cay edge	3.42 (1.51–5.21)	16.38 (4.15–30.11)
	Minimal distance to vegetation patch ^b	0.82 (0.67–0.96)	6.75 (2.50–15.54)
	Inside the vegetation patch ^b	93%	61%
	Minimal distance to open area ^b	1.05 (0.41–1.55)	2.92 (2.27–3.07)
	Inside the open area ^b	None	85%
	Percentage of vegetation cover ^b	72.5 (40.0–97.5)	75.0 (26.5–98.0)
	Without vegetation cover ^b	27%	42%
	Percentage of non-vegetation cover ^b	100.0 (62.5–100.0)	0.0
	Without non-vegetation cover ^b	60%	100%
	Cay: Felipe de Sotavento		(<i>n</i> = 30)
	Normalized difference water index	-0.24 (-0.30 to -0.10)	-0.26 (-0.28 to -0.15)
	Minimal distance to cay edge	10.22 (7.34–11.55)	28.50 (7.60–45.20)
	Minimal distance to vegetation patch ^b	1.30 (0.70–2.92)	7.52 (3.66–9.16)
	Inside the vegetation patch ^b	53%	64%
	Minimal distance to open area ^b	0.50 (0.40–0.80)	16.03 (6.12–22.55)
	Inside the open area ^b	63%	45%
	Percentage of vegetation cover ^b	80.00 (40.00–96.25)	84.0 (47.0–100.0)
Without vegetation cover ^b	73%	33%	
Percentage of non-vegetation cover ^b	100 (100–100)	0	
Without non-vegetation cover ^b	27%	100%	
Cay: Paredón de Lado		(<i>n</i> = 30)	
Normalized difference water index	-0.14 (-0.22 to -0.06)	-0.25 (-0.29 to -0.15)	
Minimal distance to cay edge	3.46 (2.29–4.47)	7.94 (3.01–14.93)	
Minimal distance to vegetation patch	24.55 (14.93–33.88)	3.87 (1.15–14.60)	
Minimal distance to open area ^b	0.20 (0.20–0.30)	0.0	
Inside the open area ^b	70%	100%	
Percentage of vegetation cover ^b	5.0 (2.7–47.5)	45.0 (16.3–78.8)	
Without vegetation cover ^b	90%	45%	
Percentage of non-vegetation cover ^b	97.5 (60.0–100.0)	50.0 (30.0–70.0)	
Without non-vegetation cover ^b	0%	73%	
Roseate Tern <i>Sterna dougallii</i>	Cay: Felipe de Barlovento		(<i>n</i> = 34)
	Normalized difference water index	-0.21 (-0.21 to -0.21) ^c	-0.24 (-0.26 to -0.18)
	Minimal distance to cay edge	5.31 (5.31–5.31) ^c	16.38 (4.15–30.11)
	Minimal distance to vegetation patch ^b	156.62 (156.62–156.62) ^c	6.75 (2.50–15.54)
	Inside the vegetation patch ^b	0%	61%
	Minimal distance to open area ^b	0.0	2.92 (2.27–3.07)
	Inside the open area ^b	100%	85%
	Percentage of vegetation cover ^b	0.0	75.0 (26.5–98.0)
Without vegetation cover ^b	100%	42%	

TABLE 2 continued

Species	Variables ^a	Nesting sites	Available sites (n = 33)	
Royal Tern	Cay: Felipe de Barlovento	(n = 30)		
<i>Thalasseus maximus</i>	Normalized difference water index	-0.27 (-0.27 to -0.27) ^c	-0.24 (-0.26 to -0.18)	
	Minimal distance to cay edge	23.90 (23.90–23.90) ^c	16.38 (4.15–30.11)	
	Minimal distance to vegetation patch ^b	9.95 (9.00–11.62)	6.75 (2.50–15.54)	
	Inside the vegetation patch ^b	0%	61%	
	Minimal distance to open area ^b	0.0	2.92 (2.27–3.07)	
	Inside the open area ^b	100%	85%	
	Percentage of vegetation cover ^b	0.0	75.0 (26.5–98.0)	
	Without vegetation cover ^b	100%	42%	
		Cay: Paredón de Lado	(n = 19)	
		Normalized difference water index	-0.29 (-0.29 to -0.29) ^c	-0.25 (-0.29 to -0.15)
	Minimal distance to cay edge	26.39 (13.55–26.39)	7.94 (3.01–14.93)	
	Minimal distance to vegetation patch	13.00 (6.45–13.00)	3.87 (1.15–14.60)	
	Percentage of vegetation cover ^b	0.0	45.0 (16.3–78.8)	
	Without vegetation cover ^b	100%	45%	
	Percentage of non-vegetation cover ^b	0.0	50.0 (30.0–70.0)	
	Without non-vegetation cover ^b	100%	73%	
Sandwich Tern	Cay: Felipe de Barlovento	(n = 30)		
<i>Thalasseus sandvicencis</i>	Normalized difference water index	-0.27 (-0.27 to -0.27) ^c	-0.24 (-0.26 to -0.18)	
	Minimal distance to cay edge	23.90 (23.90–23.90) ^c	16.38 (4.15–30.11)	
	Minimal distance to vegetation patch ^b	12.34 (11.49–13.25)	6.75 (2.50–15.54)	
	Inside the vegetation patch ^b	0%	61%	
	Minimal distance to open area ^b	0	2.92 (2.27–3.07)	
	Inside the open area ^b	100%	85%	
	Percentage of vegetation cover ^b	0.0	75.0 (26.5–98.0)	
	Without vegetation cover ^b	100%	42%	

^a Values are median (quartiles). Distance units are in meters and percentages in %.

^b Variables with a large number of data = 0 are shown in two components: the variable itself (containing the values > 0) and the percentages representing the data = 0.

^c Idem values derived from variables that were recorded at a central point of the very dense colonies of Royal, Sandwich, and Roseate terns. Values were considered representative for all samples.

four (Wallace *et al.* 1996). NDWI values at nesting sites (previously georeferenced using a handheld GPS unit with a precision of ± 3 m) were calculated based on two Sentinel-2 L2A satellite images without cloud cover on 27 May (images available at <https://eos.com>, reference 17QQF) and 01 June 2021 (17QQE). In very dense colonies such as of ROYT, SATE, and ROST, some variables were recorded at a central point and considered to be representative for all samples.

We repeated the same procedure at 33 sites that were not used for nesting (“available sites”). Sites were chosen randomly at each cay as a measure of microhabitat availability. Their location was determined based on a zig-zag transect along the longitudinal axis of the cays. We divided transects into equal parts, and the split points were chosen as the location of the available sites (Fig. S1 in Appendix 1, available on the website). Environmental variables at the available sites were recorded during 04–06 May 2021 (the pre-laying period) to minimize disturbance at the colonies.

Data analysis

Quantitative variables were characterized by their median and quartiles, while qualitative variables were expressed as relative frequency. Zero-inflated microhabitat variables were summarized through separated proportions. We used random forest classification models (RFM) to assess the relative contribution of environmental variables to breeding microhabitat selection patterns (via the Gini index, Breiman *et al.* 1984). These models provide high accuracy and robustness to heterogeneous predictors (Ma *et al.* 2019). For RFM implementation,

we used 70% of the data to train vs. 30% to validate. Common metrics such as Overall Accuracy, Precision, Recall, and F1-scores were used to assess RFM performance. Sentinel satellite images were processed with ENVI 4.7 software (ITT Visual Information Solutions) while statistical analysis and modelling were undertaken with R 4.1.1 (R Core Team 2021) through RStudio 1.4.17 (RStudio Team 2021). The “randomForest” R package (version 4.6–14) (Breiman *et al.* 2018) was used to run the aforementioned models.

RESULTS

Spatial distribution of the larid breeding colonies showed a general tendency toward segregation (Fig. S2 in Appendix 1). Nesting-site selection patterns differed among species, with LAGU showing the largest ecological plasticity. LAGU nesting sites exhibited some variation between breeding macrohabitats depending upon cay characteristics and the more consistent patterns existing among sites located within vegetation patches (Table 2, Figs. 2–4). The general pattern of LAGU nesting sites revealed sites further inland from cay edges, in areas of high vegetation cover on FB but low cover on PL (Fig. 2). For this species, overall differences among nesting and available sites were weak (Table 3) and mainly explained by the dominant plant species, distance to cay edge, and ground wetness (via NDWI), independent of the study cay (Fig. 5).

A very consistent nesting-site selection pattern was found for BRTE (Table 3): nesting sites were located on sand, near to cay edges (i.e., the median distance of nesting sites was within the first quartile of

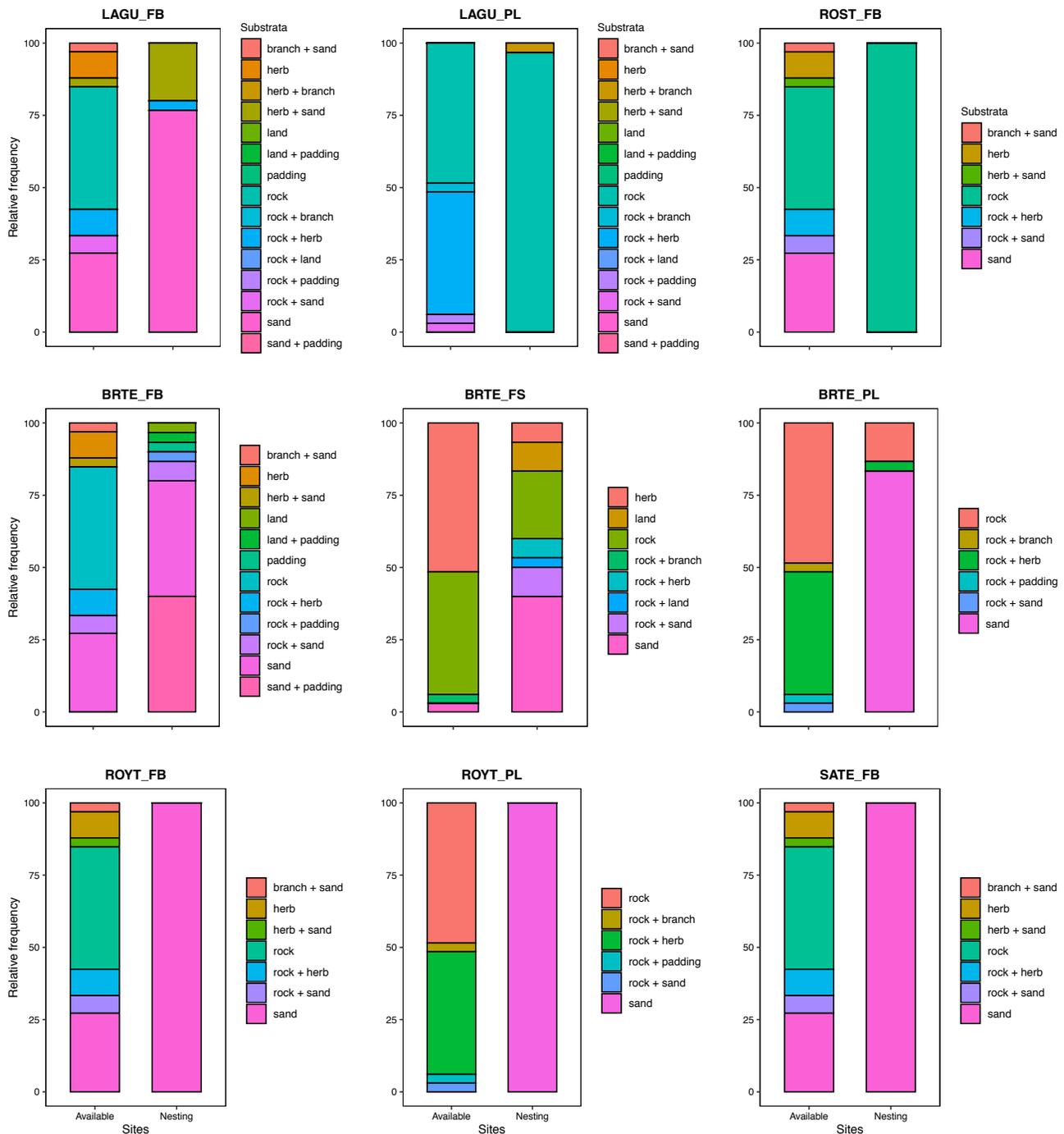


Fig. 3. Proportions of use and availability of substratum types used in nesting ($n = 30$ for each species by cay, except ROST_FB = 34 and ROYT_PL = 19) and at available sites ($n = 33$ by cay). LAGU = Laughing Gull *Leucophaeus atricilla*, BRTE = Bridled Tern *Onychoprion anaethetus*, ROST = Roseate Tern *Sterna dougallii*, ROYT = Royal Tern *Thalasseus maximus*, SATE = Sandwich Tern *Thalasseus sandvicencis*, FB = Felipe de Barlovento cay, FS = Felipe de Sotavento cay, PL = Paredón de Lado cay

distance on available sites), associated with button mangrove, and protected by high non-vegetation cover (mainly by rock; Table 2, Figs. 2–4). The selection pattern was similar among the three studied cays, despite their different landscapes (Fig. 2). Substratum type was the most important covariate explaining nesting-site selection of BRTE, followed by non-vegetation cover then minimal distance to cay edges (Fig. 5).

The highly gregarious species ROST, ROYT, and SATE exhibited clear selection patterns (Table 3) that differed among species. Nesting-site selection was easy to distinguish with respect to available sites on the cays due to the narrow ranges of values for some variables (Table 2, Figs. 3–4). Breeding microhabitat for ROST was marked by a high distance to vegetation patches, closeness to cay edge, and location above rocky substratum

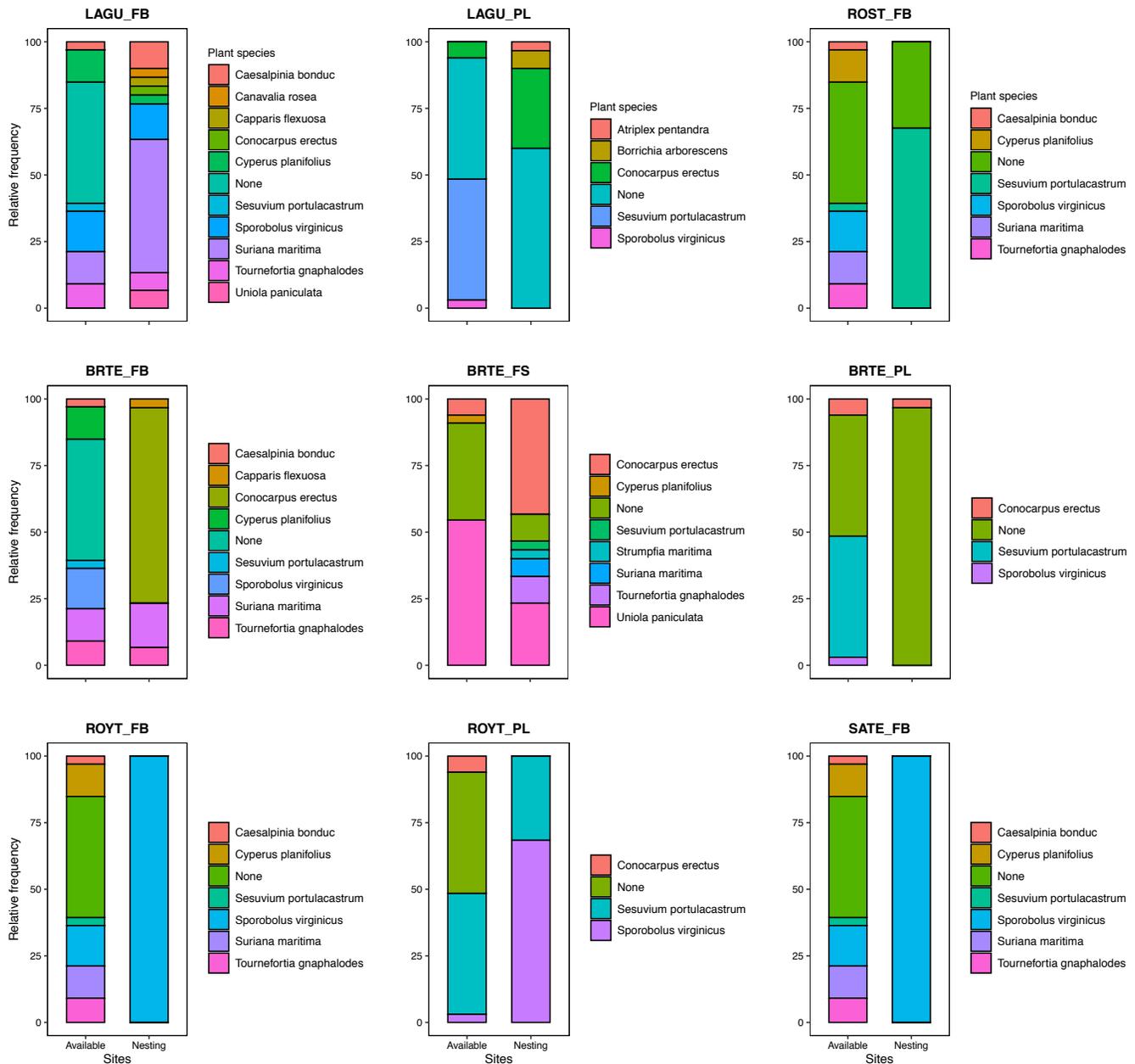


Fig. 4. Proportions of use and availability of the dominant plant species in nesting ($n = 30$ for each species by cay except ROST_FB = 34 and ROYT_PL = 19) and available sites ($n = 33$ by cay). LAGU = Laughing Gull *Leucophaeus atricilla*, BRTE = Bridled Tern *Onychoprion anaethetus*, ROST = Roseate Tern *Sterna dougallii*, ROYT = Royal Tern *Thalasseus maximus*, SATE = Sandwich Tern *Thalasseus sandvicencis*, FB = Felipe de Barlovento cay, FS = Felipe de Sotavento cay, PL = Paredón de Lado cay

without vegetation cover (Table 2, Figs. 2–4). Minimal distances to vegetation patches and to cay edges were the most important covariates for ROST (Fig. 5).

Similarly, ROYT and SATE exhibited clear nesting selection patterns that were similar among cays (Table 3). On FB, both species nested together while only ROYT nested on PL. Nesting sites for both species were on sand, mainly associated with seashore dropseed *Sporobolus virginicus* (a small and flexible herb), far from both cay edges and vegetation patches, and fully exposed (Table 2, Figs. 2–4). Nevertheless, covariates contributing to breeding microhabitat varied between the two species. For ROYT,

the dominant plant species and substratum type played fundamental roles in explaining the selection pattern, followed by minimal distances to cay edges and to vegetation patches (Fig. 5). The minimal distance to vegetation patches, dominant plant species, and substratum were the more important variables to SATE, but their relative importance was less compared to ROYT (Fig. 5).

DISCUSSION

Each of five larid species in the study exhibited contrasting patterns of microhabitat selection, revealing differences in their ecological plasticity. In this sense, LAGU could be considered to

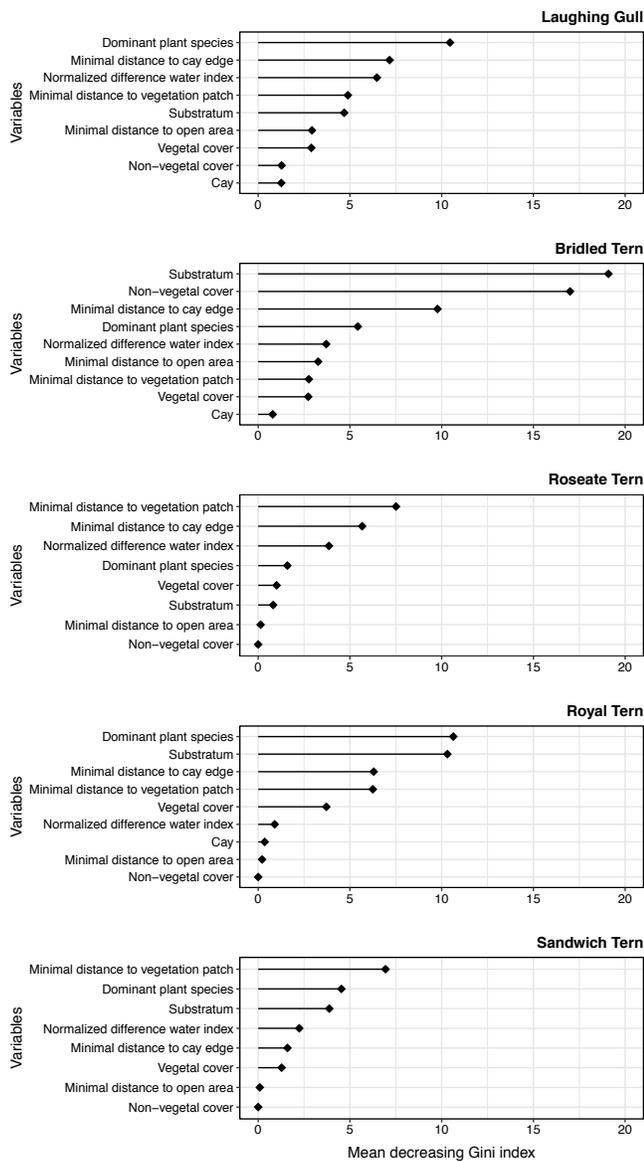


Fig. 5. Relative contribution (based on random classification forest classification models) of several variables that support the breeding microhabitat (nesting-site) selection patterns of five species of larids in three cays in central-northern Cuba during the 2021 breeding season. Laughing Gull *Leucophaeus atricilla*, Bridled Tern *Onychoprion anaethetus*, Roseate Tern *Sterna dougallii*, Royal Tern *Thalasseus maximus*, and Sandwich Tern *T. sandvicensis*.

be a generalist compared to other larid species. Although social interactions such as nesting-site defense and group adherence are important factors that influence the selection of reproductive microhabitat of LAGU and seabirds in general (Burger 1977, Greer *et al.* 1988), we found a loose selective pattern for the establishment of LAGU nests relative to microhabitat availability. The association of LAGU nesting sites with several plant species may indicate a protective role of plants. Some studies (Burger 1977, Burger & Shisler 1978, Greer *et al.* 1988) mentioned the association between the location of LAGU nests and vegetation as a means of protecting the brood and reducing visibility (and aggression) between neighboring pairs. Establishment of LAGU nests far from cay edges can reduce exposure to sea spray and

waves. It could also reflect the association with vegetation distribution, as few plants species grow near the waterline.

In agreement with Hulsman & Langham (1985), BRTE breeding characteristics (including nesting-site selection) can constitute an antipredator mechanism despite the apparent low predation pressure at the study areas. Indeed, this species appears to select well-hidden sites using a variety of resources such as vegetation, rocks, corals, and wood, depending of their availability. On islands in Australia and New Caledonia, BRTE used several types of vegetation and non-vegetation resources to protect nesting sites situated near the edges of the islands (Hulsman & Langham 1985, Bretagnolle & Benoit 1997, Villard & Bretagnolle 2010). We found a similar selection pattern for this species among the three cays we studied, providing further evidence for the predominant role of the substratum. Among the species we studied, BRTE used mostly vegetation and non-vegetation covers as borders and walls to protect nests, an important requirement for the selection of breeding microhabitats by seabirds (Eveillard-Buchoux *et al.* 2019).

For the RFM we used to assess the contribution of variables to nesting-site selection for ROST, ROYT, and SATE, performance indicators were high, possibly due to the high specialization of these species. Nesting sites selected by these species showed clear patterns, with the exclusive use of specific resources, such as substratum and nest-associated plant species, as well as a clear avoidance of vegetation patches. Moreover, the dense aggregation of these species reinforces the nesting-site selection criterion. This allows easy differentiation of nests from available sites through classifiers such as RFM.

ROST nesting sites were located in a rocky habitat, which provided pronounced walls for their nests, that was close to an isolated edge of FB and far from vegetation. This could be a protective strategy because ROST is one of the smallest larid species breeding in Cuba and probably suffers more predation risks from predators associated with vegetation. This species usually nests in sites that provide concealment (e.g., close to objects or vegetation), an advantageous mechanism for defending territories and protecting nest contents (Ramos & Monticelli 2012). The use of vegetation to cover ROST nesting sites can vary among regions (e.g., Ramos & Monticelli 2012, Tree *et al.* 2019), although this depends on the age of the breeding birds (Ramos & Monticelli 2012). Young pairs of ROST are likelier than older pairs to select nesting sites that are more hidden (Ramos & Monticelli 2012). Nevertheless, ROST in our study could select nesting sites far away from vegetation patches to avoid the interspecific competition for the best-covered sites.

Exclusive use of sand as a nesting substratum at sites with scarce or sparse vegetation characterized the selection pattern of ROYT and SATE (e.g., Fasola & Canova 1992, Raynor *et al.* 2012). At our study sites, both species selected sites having these characteristics plus an association with seashore dropseed. Although such nesting-site characteristics potentially increase vulnerability to disturbance and predation (due to higher exposure), ROYT and SATE colonies were dense, which facilitates defense against predators (Coulson 2002). However, the high performance of RFMs for these species may also reflect some degree of overfitting due to small sample sizes, although we found optimal indicators only in the more gregarious species. Thus, high performance of RFMs likely resulted from a combination of highly selective species and model overfitting. A

TABLE 3
Architecture and performance of the best random forest classification models to assess the breeding microhabitat (nesting-site) selection patterns for five larid species at three cays in the central-northern region of Cuba^a

Species	Number of trees	Number of variables tried by split	Out-of-bag estimate of error rate	Validation error rate	Overall accuracy	Precision	Recall	F1-score
Laughing Gull <i>Leucophaeus atricilla</i>	550	3	26.14	26.32	73.68	84.62	57.89	68.75
Bridled Tern <i>Onychoprion anaethetus</i>	100	3	4.55	5.26	94.74	100.00	90.32	94.92
Roseate Tern <i>Sterna dougallii</i>	50	2	0.00	0.00	100.00	100.00	100.00	100.00
Royal Tern <i>Thalasseus maximus</i>	50	3	0.00	0.00	100.00	100.00	100.00	100.00
Sandwich Tern <i>Thalasseus sandvicencis</i>	50	2	0.00	0.00	100.00	100.00	100.00	100.00

^a Performance indicators (Overall Accuracy, Precision, Recall, and F1-scores) are in %.

design based on a higher number of samples (i.e., nesting and non-nesting sites) at these or other ROST, ROYT, and SATE colonies could help to clarify this potential shortcoming.

Nesting-site selection often constitutes a species-specific strategy to maximize breeding success in seabirds (Orians & Wittenberger 1991, Muzaffar *et al.* 2015). Our results suggest the importance of substratum and dominant plant species as key variables among the larid species studied. Substratum plays an essential function for the nest stability and brood protection, especially for terns that do not build an elaborate nest. Except for ROST, all tern species selected sand as the predominant substratum, probably due to its soft and flexible consistency; ROST established their nests in rocky areas that naturally formed protective walls for the broods. LAGU built a basic nest structure above the selected substrata using surrounding vegetation, which is likely important for the stability of nests that typically contain more than one egg and for the protection of the brood. This could explain, to some extent, LAGU's higher plasticity in where it finds nesting sites compared to the tern species.

Vegetation characteristics are considered as a pivotal factor for nesting-site selection by many seabirds (Bukacinski & Bukacinski 1993), and we found that the plant species associated with nesting sites were among the most important variables in three of the five species we studied. The occurrence of a specific plant species at nesting sites probably results from the plants' dependence on the substratum type, although birds could select these sites based on the substratum-plant species combination. Beyond the specific plant, larids could select nesting sites with suitable vegetation cover to enhance protection and thermoregulation (shrubs), or substratum stabilization (herbs) to avoid the risk of eggs rolling and breaking.

Finally, the minimal distance to cay edges represented an important variable for all species except SATE, but with different patterns for each species (Figs. 2, 5). While BRTE and ROST established their nests near cay edges, LAGU and ROYT selected sites far from the edges. Additionally, nests within aggregations of LAGU and BRTE were situated further apart compared to the dense nesting of ROST, ROYT, and SATE. Thus, the spatial placement of nesting

sites exhibited a general interspecific segregation pattern by cay (based on field observations), likely reducing competition for sites, aggression, and eventual predation between breeding species (e.g., sometimes LAGU—the largest co-breeding species—attacked clutches of the other species).

In conclusion, nesting-site selection seems to determine the interspecific spatial patterns of nesting seabirds in our study. Studies focusing on the breeding microhabitats of one or two sympatric larids may be of limited value to our understanding of the mechanisms determining the co-existence of multiple sympatric breeding species (Burger & Shisler 1978). Larids often form mixed colonies, and we found that five species breeding in Cuba exhibited a clear and distinctive selection pattern of nesting sites that likely facilitates sympatric breeding. These species-specific patterns were defined mainly by the dominant plant species, minimal distance to cay edges, vegetation cover, and substratum at nesting sites. However, to better understand the nesting-site selection preferences of seabirds, other behavioral ecological factors need to be taken into account. In this sense the sociobiology—including intra and interspecific attraction and refusal relationships (Greer *et al.* 1988, Córdoba-Córdoba *et al.* 2010) and inter-annual site fidelity (Robert *et al.* 2014, Salas *et al.* 2020)—can influence the nesting-site selection patterns by larids. Quantification of breeding microhabitat requirements could contribute to defining protected areas within islands hosting seabird colonies, thus minimizing the impact of activities such as eco-tourism during the breeding season.

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Appendix 1

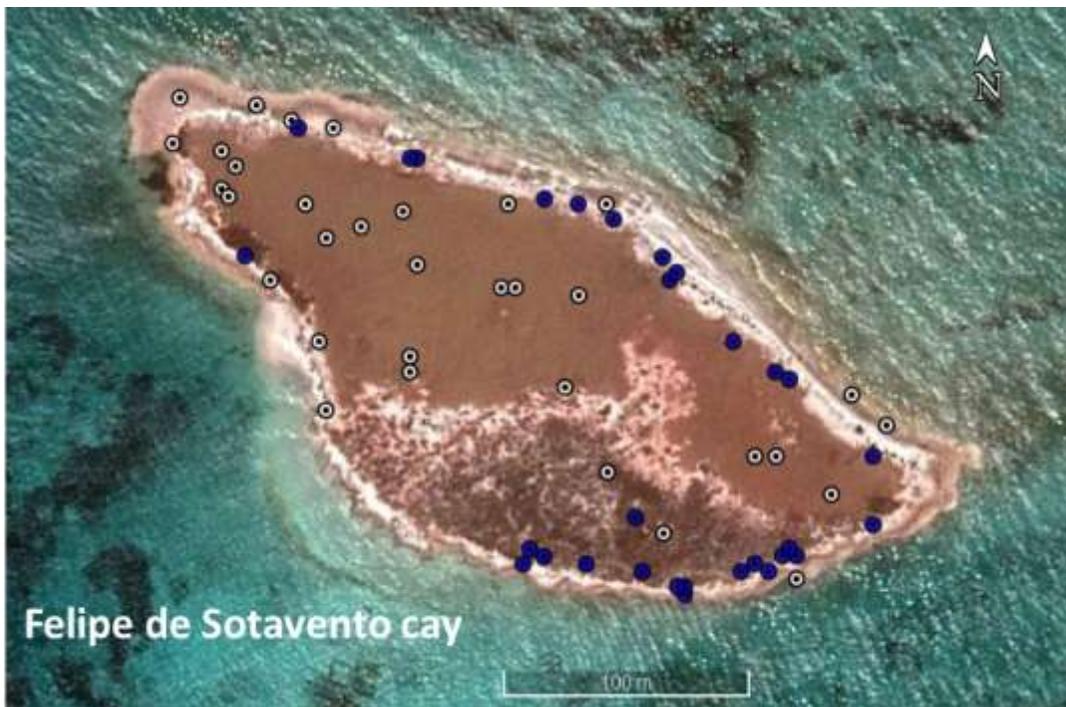


Fig. S1. Position of the sampling points (nesting and non-nesting sites) used to assess the breeding microhabitat selection of five Laridae species at three central-northern cays in Cuba during the 2021 breeding season. White = random points (non-nesting sites), red = Laughing Gull *Leucophaeus atricilla* nesting sites, blue = Bridled Tern *Onychoprion anaethetus* nesting sites, pink = Roseate Tern *Sterna dougallii* nesting sites, yellow = mixed Royal *Thalasseus maximus* and Sandwich *T. sandvicensis* tern nesting sites, green = Royal Tern nesting sites. Most of nesting sites of Roseate, Royal, and Sandwich terns are represented by a central point inside breeding colonies.

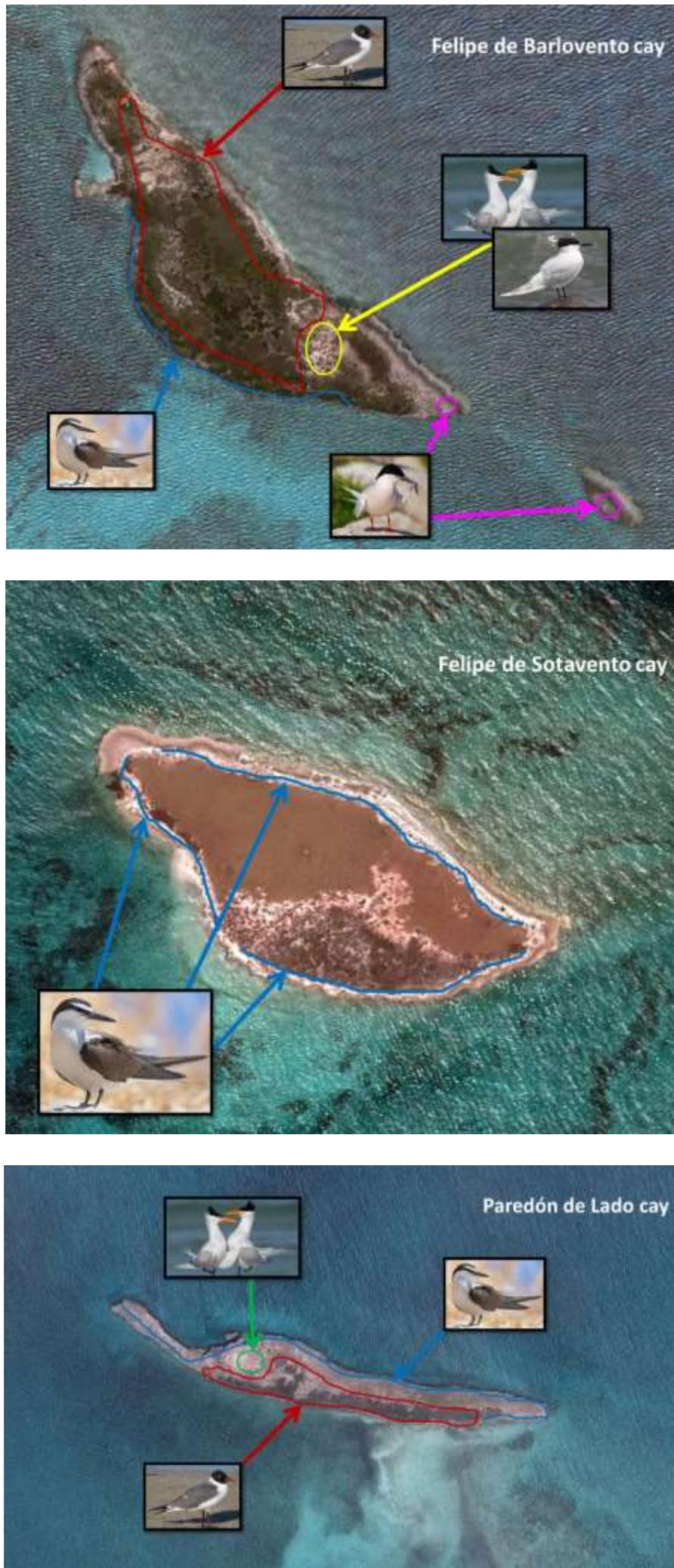


Fig. S2. General spatial distribution of the breeding colonies of five Laridae species at three central-northern cays in Cuba during the 2021 breeding season.