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Antonio Garcia Quintas

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# THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Écologie des Communautés

École doctorale : Biodiversité, agriculture, alimentation, environnement, terre, eau

Unité de recherche MARBEC

## Écologie de la reproduction et conservation des Laridés (mouettes et sternes) de Cuba dans un contexte anthropique

Présentée par Antonio GARCIA QUINTAS

Le 13 septembre 2023

SOUS LA DIRECTION DE SOPHIE LANCO BERTRAND ET DENNIS DENIS ÁVILA

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DE MONTPELLIER

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*“La gratitud, como ciertas flores, no se da en la altura y mejor reverdece en la tierra buena de los humildes”*

*José Martí*

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## Abstract

The breeding ecology of tropical seabirds remains poorly known even though understanding the ins and out of this critical life stage is essential for assessing the state of tropical marine ecosystems, or for evaluating marine spatial plans and the (re)design of marine protected areas. Within the Caribbean basin, Cuba stands out for hosting a large number of breeding seabirds, but also for lacking critically of ecological information on them. While collecting observations at sea may still be challenging, a combined use of classical, modern and state-of-the-art field and analytical methods allows extracting more out of the existing data. This thesis addressed ecological and conservation aspects of the Laridae family (gulls and terns) in Cuba, this family of seabird species being the best represented in this tropical archipelago. The selection and suitability of breeding macro- and micro-habitats were evaluated using machine and deep learning methods on multispectral Landsat satellite images. Oceanographic variables at broad spatial scales were shown to be critical for breeding site selection, as well as vegetation and substrate for nesting site selection. Spatio-temporal trophic niche plasticity and overlap were assessed in Laridae breeding communities using the isotopic niche ( $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$ ) as a proxy. Interspecific trophic segregation was detected based on the breadth and overlap of the isotope niches. This allowed a better understanding of the successful sympatric nesting of Laridae in Cuba, considering that adults forage in common areas within poorly productive tropical marine waters. The breeding phenology of several Laridae species and the effects of laying asynchrony on egg morphometry were characterised. Phenological patterns (from field observations and camera trap monitoring) were remarkably synchronous, while most egg morphometric variables (obtained by digital photo processing) did not reflect differences between early and late clutches. Lastly, optimisation models – used as a supporting decision tool - were implemented to evaluate the priority areas for the conservation of Laridae breeding habitats. The overlap of these priority areas with Cuba's current system of marine protected areas was found to be remarkably low. In general, the potential of Laridae as sentinels of Cuba's coastal ecosystems is highlighted. Research priorities are also identified, such as spatial foraging patterns and prey consumption by these seabirds, as well as the assessment of marine pollution risks from metals and other persistent organic pollutants.

**Keywords:** Seabirds; Tropical ecosystems; Conservation; Habitat modeling; Anthropogenic disturbance; Trophic ecology

## Résumé

L'écologie de la reproduction des oiseaux marins tropicaux reste mal connue, alors même que la compréhension des tenants et aboutissants de cette étape critique du cycle de vie est essentielle pour évaluer l'état des écosystèmes marins tropicaux, ou pour évaluer les plans d'aménagement de l'espace marin et la (re)conception des zones marines protégées. Dans le bassin des Caraïbes, Cuba se distingue par le fait qu'elle accueille un grand nombre d'oiseaux marins nicheurs, mais aussi par le manque criant d'informations écologiques à leur sujet. Bien que la collecte d'observations en mer reste encore délicate, l'utilisation combinée de méthodes de terrain et analytiques classiques, modernes et de pointe permet d'extraire davantage des données existantes. Cette thèse aborde les aspects écologiques et de conservation de la famille des Laridés (mouettes et sternes) à Cuba, cette famille d'oiseaux marins étant la mieux représentée dans cet archipel tropical. La sélection et l'adéquation des macro- et micro-habitats de reproduction ont été évaluées à l'aide de méthodes d'apprentissage automatique et profond utilisant des images satellites Landsat multispectrales. Les variables océanographiques à de larges échelles spatiales se sont révélées essentielles pour la sélection des sites de reproduction, de même que la végétation et le substrat pour la sélection des sites de nidification. La plasticité et le chevauchement spatio-temporels des niches trophiques ont été évalués dans les communautés reproductrices de Laridés en utilisant la niche isotopique ( $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$ ) comme proxy. La ségrégation trophique interspécifique a été détectée sur la base de l'étendue et du chevauchement des niches isotopiques. Cela a permis de comprendre le succès de la nidification sympatrique des Laridés à Cuba, alors que les adultes s'alimentent dans des zones communes au sein d'eaux marines tropicales peu productives. La phénologie de reproduction de plusieurs espèces de Laridés et les effets de l'asynchronie de ponte sur la morphométrie des œufs ont été caractérisés. Les schémas phénologiques (issus des observations sur le terrain et du suivi par pièges photographiques) étaient remarquablement synchrones, tandis que la plupart des variables morphométriques des œufs (obtenues par traitement numérique des photos) ne reflétaient pas de différences entre les nichées précoces et tardives. Enfin, des modèles d'optimisation - utilisés comme outil d'aide à la décision - ont été mis en œuvre pour évaluer les zones prioritaires pour la conservation des habitats de reproduction des Laridés. Le recouvrement de ces zones prioritaires avec le système actuel de zones marines protégées de Cuba s'est avéré remarquablement faible. D'une manière générale, le potentiel des Laridés en tant que sentinelles des écosystèmes côtiers de Cuba est mis en évidence. Des priorités de recherche sont également identifiées, telles que les schémas de recherche de nourriture dans l'espace et la typologie des proies consommées par ces oiseaux de mer, ainsi que l'évaluation des risques de pollution marine par les métaux et d'autres polluants organiques persistants.

**Mots-clés :** Oiseaux marins ; Écosystèmes tropicaux ; Conservation ; Modélisation de l'habitat ; Perturbation anthropique ; Écologie trophique



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## **Résumé en français**

### **Introduction**

Les oiseaux marins constituent l'un des groupes d'oiseaux les plus menacés au monde (Croxall *et al.*, 2012 ; Carr *et al.*, 2020) : selon l'UICN, 31% des 359 espèces d'oiseaux marins sont menacées au niveau mondial et 11% sont quasi menacées (Dias *et al.*, 2019). Leurs populations sont confrontées à de fortes menaces et pressions telles que la pêche, la mortalité accidentelle par les engins de pêche, le trafic maritime, la pollution par les hydrocarbures et les polluants organiques persistants, le développement des énergies renouvelables, l'introduction d'espèces exotiques dans les colonies de reproduction, le changement climatique et les perturbations liées au tourisme et aux activités récréatives (Thaxter *et al.*, 2012 ; Dias *et al.*, 2019 ; Mitchell *et al.*, 2020).

Les aires marines protégées (AMP) ont été utilisées comme des outils fondamentaux pour la gestion et la conservation des oiseaux de mer et de la biodiversité marine en général (Devillers *et al.*, 2015 ; Carr *et al.*, 2020 ; Schultz *et al.*, 2022). Cependant, malgré leur large acceptation au niveau mondial, de nombreuses AMP ont été critiquées et décriées pour leur inefficacité. Parmi les principaux problèmes, citons la permissivité des activités touristiques, récréatives et extractives au sein des AMP et la faible application des niveaux de restriction fixés (McGowan *et al.*, 2013 ; Devillers *et al.*, 2015). Une autre limite est l'adoption d'une approche statique de l'architecture des AMP, qui conduit souvent à la protection de zones trop petites et pas assez dynamiques par rapport aux processus écologiques variant dans l'espace et dans le temps qu'elles visent à protéger (Lescroël *et al.*, 2016).

La conception d'une AMP efficace pour les oiseaux marins nécessite la prise en compte de la variabilité annuelle de la disponibilité des proies (McGowan *et al.*, 2013), de l'étendue des zones nécessaire à leur alimentation (Yorio, 2009 ; Thaxter *et al.*, 2012) et de la dynamique des processus tels que la migration et la connectivité (Proudfoot *et al.*, 2020). Deux autres aspects clés pour une politique efficace de conservation de ces animaux très mobiles sont (i) la prise en compte des échelles spatiales des différentes phases de leur cycle de vie pour la conception des AMP en fonction de la dynamique des espèces à conserver (Yorio, 2009 ; Opper *et al.*, 2018), et (ii) la prise en compte des menaces et perturbations naturelles et anthropiques dans la conception et le cadre législatif des zones à protéger (Perrow *et al.*, 2015 ; Lescroël *et al.*, 2016 ; Lieske *et al.*, 2019).

Souvent au sommet des chaînes trophiques, les oiseaux de mer contribuent à réguler la taille et la santé des populations de leurs proies, tout en fournissant des sources de nourriture à d'autres prédateurs marins et terrestres. Le guano qu'ils produisent dans leurs colonies de reproduction fertilise également les substrats et augmente la productivité primaire, en particulier dans les écosystèmes côtiers (Jones *et al.*, 2008). Les oiseaux de mer sont d'importants transporteurs de nutriments marins vers les écosystèmes terrestres, ce qui augmente l'azote disponible et pourrait soutenir le réseau trophique pendant les périodes de reproduction et de non-reproduction (Gaiotto *et al.*, 2022). En outre, le lessivage du guano produit dans les colonies fournit de l'azote

aux récifs coralliens (ce qui pourrait contribuer à leur croissance) à proximité des sites de reproduction (Lorrain *et al.*, 2017 ; Linhares & Bugoni, 2022).

Les oiseaux marins jouent également le rôle d'espèces bio-indicatrices de l'état, des changements et de la santé des écosystèmes marins (Barrett *et al.*, 2007 ; Hindell *et al.*, 2012 ; Oppel *et al.*, 2018). Ils peuvent être considérés comme des sentinelles des effets du changement climatique et des perturbations humaines en mer. Plusieurs paramètres écologiques (par exemple l'abondance, la survie, la fidélité au site de reproduction, le succès reproducteur) des oiseaux marins sont sensibles aux variations naturelles et anthropiques. Ces animaux intègrent les effets de la pression climatique sur les niveaux trophiques inférieurs et les manifestent de manière facilement quantifiable (par exemple, par des modifications dans leurs phénologies de reproduction) (Hindell *et al.*, 2012). Ils reflètent également les anomalies des régimes climatiques et de la productivité océanique en fonction de leur sensibilité aux variations de l'offre trophique (Bost & Maho, 1993 ; Barrett *et al.*, 2007 ; McGowan *et al.*, 2013). Parallèlement, les paramètres de reproduction des oiseaux marins peuvent indiquer l'état et la structure d'âge des stocks de poissons d'importance commerciale, contribuant ainsi à la gestion des pêcheries (Piatt *et al.*, 2007 ; Einoder, 2009).

Les connaissances sur l'écologie des oiseaux marins nicheurs sont très inégales d'une région du monde à l'autre. En général, les oiseaux marins des régions polaires et tempérées ont été beaucoup plus étudiés que les espèces tropicales (Weimerskirch 2007). Ces dernières ont tendance à se spécialiser dans des tailles de proies, des périodes de recherche de nourriture et des aires de répartition spécifiques (bien qu'elles ne fassent pas preuve de fidélité stricte à une zone particulière en raison de la variabilité de la disponibilité des proies, en particulier des espèces pélagiques) (Catry *et al.*, 2008 ; Oppel *et al.*, 2015). L'étendue de leurs niches trophiques contraste souvent entre les périodes de reproduction (recherche de nourriture dans une zone restreinte autour du nid) et les périodes de non-reproduction (recherche de nourriture opportuniste) (Cherel *et al.*, 2008). De plus, ils ont tendance à se distinguer par leur période de reproduction (Surman & Wooller, 2003). Les adultes reproducteurs sont socialement monogames, partagent les soins à la couvée, pondent généralement peu d'œufs, voire un seul, et les poussins ont un taux de croissance lent (Langham, 1983). La coexistence et le succès reproducteur des oiseaux marins tropicaux reposent principalement sur des mécanismes intra et interspécifiques de ségrégation trophique et reproductive qui évitent ou réduisent la compétition.

Les Caraïbes abritent un grand nombre de colonies de reproduction d'oiseaux marins (Bradley & Norton, 2009), mais sont l'une des régions tropicales les moins étudiées. Dans cette région, il existe de fortes pressions anthropiques résultant d'activités économiques telles que le tourisme et la pêche, contrastant avec une couverture particulièrement faible des AMP (Croxall *et al.*, 2012). Bradley & Norton (2009) soulignent les menaces qui pèsent sur les oiseaux marins des Caraïbes, telles que le changement climatique et l'élévation du niveau de la mer, les modifications de la chimie des océans, l'augmentation du nombre d'ouragans et de tempêtes, la pêche à la palangre (captures accidentelles) et la pollution des océans (par le pétrole, les plastiques, les pesticides). Ces menaces et les tendances démographiques observées placent les

oiseaux marins des Caraïbes dans une situation très difficile, nécessitant des recherches et des mesures de conservation urgentes.

Cuba représente 48 % de la zone insulaire émergée des Caraïbes (Acosta *et al.*, 2011) et plus de 15 % de sa surface est constituée de zones humides (Mugica *et al.*, 2012). Les études sur l'écologie des oiseaux marins à Cuba sont rares et récentes. La plupart des études ornithologiques se concentrent sur les oiseaux terrestres et on sait peu de choses sur la taille et les tendances des populations, les événements de reproduction et les habitats de reproduction des oiseaux marins (Jiménez *et al.*, 2009). Ceci est principalement dû à des contraintes logistiques et économiques, en plus du fait que les écosystèmes tels que les écosystèmes marins sont difficiles à étudier en raison de leur extension et des conditions environnementales difficiles (Tremblay *et al.*, 2009).

L'avifaune marine de Cuba est représentée par cinq ordres, 12 familles et 49 espèces (Navarro, 2021). La famille la mieux représentée est celle des Laridés, composée de 25 espèces de sternes et de mouettes, dont neuf se reproduisent localement (Jiménez *et al.*, 2009 ; Navarro, 2021). L'écologie des Laridés à Cuba est pratiquement inconnue. Les quelques études réalisées sur ce groupe correspondent à des inventaires d'individus et de colonies de reproduction, à des ajouts de nouvelles espèces (beaucoup rares ou occasionnelles) et à des caractérisations de base de l'utilisation de l'habitat et de certains paramètres du succès de la reproduction (*e.g.* Rodríguez *et al.*, 2003 ; Acosta *et al.*, 2022). Le suivi réalisé n'a pas été stable dans le temps, ou du moins il n'y a pas de publications qui le démontrent. L'efficacité de la conservation des oiseaux marins à Cuba n'a pas été évaluée, mais elle semble faible. Les AMP existantes sont principalement basées sur d'autres objectifs de conservation (poissons, récifs coralliens, requins, chéloniens, crocodiles), et celles qui ne le sont pas visent à protéger les sites de reproduction des oiseaux de mer, laissant au second plan les zones d'alimentation associées.

Étant donné le manque notable d'informations écologiques sur les Laridés à Cuba et l'incertitude quant à l'efficacité de leur conservation, toute recherche scientifique fournissant des informations écologiques sur ces oiseaux à Cuba est très précieuse. Les étapes telles que la reproduction sont souvent complexes (vulnérabilité accrue des adultes et des poussins, augmentation de la demande alimentaire et des efforts de recherche de nourriture, changements dans les schémas de déplacement des adultes, coûts énergétiques élevés) mais essentielles pour la préservation des populations d'oiseaux marins. Pour cette raison, cette thèse se concentre sur l'écologie de la reproduction des Laridés à Cuba, en mettant l'accent sur trois colonies multispécifiques situées dans une zone de reproduction importante dans le centre-nord du pays. Les objectifs sont les suivants :

**1. Caractérisation du modèle de sélection et prédiction de l'adéquation de l'habitat de reproduction des Laridés à Cuba.** L'habitat est un facteur essentiel pour comprendre l'écologie des espèces. Connaître la distribution spatiale, l'adéquation et la sélection des habitats de reproduction des Laridés peut également permettre d'évaluer la vulnérabilité des colonies aux ouragans et aux tempêtes tropicales, ainsi qu'à la pollution marine en fonction de la proximité des sources de polluants et de la circulation des courants marins. Cela contribuerait à

une gestion et une conservation plus efficaces des habitats de reproduction et d'alimentation des Laridés.

**2. Caractériser la niche trophique des Laridés cubains pendant la saison de reproduction.**

La caractérisation de la niche trophique (étendue, amplitude, chevauchement) peut contribuer à l'analyse des vulnérabilités des Laridés de Cuba en fonction de leurs besoins alimentaires et de leurs sites de recherche de nourriture. Cela peut également indiquer le niveau de risque de contamination en mer, étant donné que les espèces généralistes et exploitant les eaux de surface sont plus susceptibles d'ingérer des proies contaminées. En outre, la connaissance des patronstrophiques des Laridés pourrait aider à prévoir les impacts possibles des anomalies océaniques (par exemple, l'augmentation de la température de la surface de la mer, les changements chimiques océaniques). Ainsi, l'évaluation des niches trophiques peut être utile pour identifier et conserver les zones d'alimentation des Laridés se reproduisant à Cuba. L'analyse des isotopes stables de  $\delta^{13}\text{C}$  et  $\delta^{15}\text{N}$  peut fournir un premier aperçu des aspects fondamentaux de l'écologie trophique des Laridés cubains. Plus précisément, la niche isotopique est une approximation de la niche trophique.

**3. Décrire la phénologie de la reproduction et la morphologie des œufs des Laridés à Cuba.**

La connaissance de la phénologie de la reproduction des oiseaux marins est un aspect important pour le suivi régulier des espèces importantes et des sites de nidification, ainsi que pour la mise en œuvre de mesures de gestion et de conservation efficaces. La délimitation détaillée des phases phénologiques facilite la conception de programmes de surveillance visant à obtenir des informations intéressantes tout en minimisant les perturbations humaines dans les colonies de reproduction. Le suivi phénologique permet également de détecter des phénomènes reproductifs tels que l'asynchronisme de ponte, qui peut avoir un impact sur le succès reproducteur global des colonies. Les caractéristiques morphométriques des œufs pourraient être utiles pour évaluer ce phénomène et ainsi renforcer les mesures de gestion spécifiques visant à améliorer le succès de la ponte tardive dans les colonies. La description de la phénologie de la reproduction des oiseaux marins peut contribuer à la conception de protocoles standardisés pour le suivi de la reproduction de groupes tels que les Laridés, ce qui peut contribuer à l'optimisation des ressources dans les pays ayant des limitations logistiques et économiques, comme Cuba.

**4. Évaluer les zones prioritaires pour la conservation des colonies de reproduction des Laridés à Cuba, en tenant compte des plans de développement actuels et futurs.**

La conservation des oiseaux marins à Cuba et dans les Caraïbes est un défi. Ces animaux sont confrontés à des menaces importantes et sont peu protégés. L'incertitude quant au degré de couverture des zones de reproduction des Laridés par le système cubain d'aires marines protégées et la nécessité permanente d'actualiser les politiques de conservation requièrent de nouveaux outils d'aide à la prise de décision. Les approches de conservation à Cuba et dans les Caraïbes doivent prendre en compte les effets de deux des principales activités socioéconomiques de la région : la pêche et le tourisme côtier. Par conséquent, l'identification des zones prioritaires pour la conservation des Laridés reproducteurs devrait être basée sur le principe des impacts cumulatifs. De cette manière, il est possible d'améliorer l'efficacité de la gestion et de la conservation des zones protégées importantes pour ces oiseaux, et de promouvoir le développement durable du tourisme de nature.

## **Modélisation de l'habitat de reproduction**

### **Méthodes**

Les zones d'étude correspondent à deux échelles spatiales à Cuba : l'ensemble de l'archipel (pour le macrohabitat) et trois cayes dans le centre-nord (pour le microhabitat) qui font partie de l'un des principaux sites de reproduction des Laridés à Cuba. Toutes les informations disponibles sur les sites de reproduction des Laridés ont été compilées et filtrées à partir de publications scientifiques, de livres, de thèses, de rapports de projets et de données non publiées. Une base de données sommaire a été créée avec 49 sites de reproduction signalés, les années d'observation, les espèces reproductrices et les sources d'information. Dix-huit variables écologiques (terrestres et océaniques) potentiellement importantes pour la sélection du macro habitat de reproduction des Laridés ont été enregistrées sur les sites d'étude ainsi que sur d'autres sites aléatoires (en tant que mesure de la disponibilité de l'habitat). Un total de 136 images satellites Landsat de sites de reproduction et de sites aléatoires ont été sélectionnées et normalisées pour mesurer l'utilisation et la non-utilisation des macrohabitats. À l'échelle locale (cayes du centre-nord de Cuba), huit variables écologiques importantes pour la sélection des microhabitats de nidification ont été enregistrées pour les sites avec nidification et sans utilisation pour cinq espèces de Laridés.

La prédiction de l'adéquation du macro-habitat de reproduction à l'échelle du pays a été réalisée à l'aide d'un réseau neuronal convolutionnel (CNN, apprentissage profond) qui a été entraîné, validé et testé à partir de l'imagerie satellite Landsat (Figure 1). Des modèles de forêt aléatoire (Random forest ou RF, machine learning) sont utilisés pour évaluer quelles covariables environnementales (en considérant trois échelles spatiales - 10, 50 et 100 km) contribuent le plus à la sélection des macro- et micro-habitats de reproduction par les Laridés à l'échelle de Cuba et de la région centre-nord, respectivement (Fig. 1). Au niveau cubain, nous avons considéré les neuf espèces de Laridés se reproduisant à Cuba : Mouette atricille (*Leucophaeus atricilla*), Petite Sterne (*Sternula antillarum*), Noddi brun (*Anous stolidus*), Sternes fuligineuse (*Onychoprion fuscatus*), bridée (*Onychoprion anaethetus*), hansel (*Gelochelidon nilotica*), de Dougall (*Sterna dougallii*), royale (*Thalasseus maximus*) et caugek (*Thalasseus sandvicensis*). L'évaluation des microhabitats dans les cayes du centre-nord s'est concentrée sur le Mouette atricille et les Sternes bridée, de Dougall, royale et caugek.

### **Résultats**

Le CNN a montré de bonnes performances lors de l'entraînement, de la validation et des tests (scores F1 >85%). Les sites présentant la meilleure adéquation de l'habitat (probabilité > 0.75) couvrent 20.3 % de la zone de prédiction. Ainsi, l'analyse des données satellitaires à l'aide des CNN permet une bonne prédiction de l'adéquation de l'habitat, ce qui est crucial dans les régions tropicales qui ne disposent pas d'inventaires complets et réguliers des sites de reproduction des oiseaux de mer. Les macro-habitats de reproduction des Laridés sont des sites relativement proches des îles principales (Cuba et de la Juventud), avec une faible couverture végétale et une forte concentration en chlorophylle-a dans les eaux adjacentes, dans un rayon de 50 et 100 km

autour des colonies. Des valeurs de température de surface de la mer moindres ( $<30$  °C) aux distances susmentionnées ont été déterminantes pour la sélection de ces sites.

Cette étude illustre la complémentarité entre des approches de types réseaux de neurones (CNN) et forêts aléatoires (RF). Les RFs peuvent être considérées comme un bon outil explicatif, ordonnant l'importance de caractéristiques liées à des hypothèses écologiques a priori, tandis que le CNN permet d'évaluer la pertinence, sans a priori sur les métriques à utiliser, des images satellite optiques de l'habitat, et produit des prédictions précises de l'adéquation de l'habitat à grande échelle. Il s'agit d'une avancée significative pour les études sur l'écologie de l'habitat, qui élargit les perspectives d'analyses d'images à l'aide d'approches d'apprentissage profond. L'architecture profonde des CNN implique un coût de calcul élevé (Kattenborn *et al.*, 2021 ; Yuan *et al.*, 2020) mais, dans le même temps, sa polyvalence permet une grande généralisation avec une large applicabilité dans le domaine de la télédétection (Mahdianpari *et al.*, 2018 ; Ma *et al.*, 2019 ; Kattenborn *et al.*, 2021). Cependant, la compréhension écologique est encore limitée, car il n'y a pas d'indications explicites sur les métriques que les CNN utilisent pour maximiser la qualité de la prédiction. Sur la base des résultats des RFs et de l'analyse statistique, on peut déduire que des caractéristiques importantes telles que la végétation, le nombre de cayes/îlots et la couleur de l'océan (liée à la chlorophylle-a) ont été capturées par les données spectrales Landsat. La performance du CNN pourrait probablement être améliorée en incluant des informations sur la température de surface de la mer dans un rayon de 100 km (conformément aux résultats des RFs) et en s'entraînant sur des ensembles de données plus importants.

## **Modélisation des niches isotopiques**

### **Méthodes**

Cette étude a été réalisée dans des colonies de reproduction sur trois cayes du centre-nord de Cuba. Au total, 311 échantillons de duvet, de plumes et de sang ont été prélevés sur des poussins (six espèces) et des adultes (une espèce) de Laridés étudiés en vue d'une analyse ultérieure des isotopes stables en laboratoire. La niche trophique a été étudiée par l'analyse des isotopes stables de  $\delta^{13}\text{C}$  et  $\delta^{15}\text{N}$ . L'analyse des isotopes stables est l'une des méthodes biochimiques les plus utilisées pour étudier l'écologie trophique et les déplacements des oiseaux (Hobson 1990 ; Barrett *et al.* 2007 ; Ausems *et al.* 2020). Cette technique est basée sur la variation naturelle des rapports isotopiques stables de divers éléments chimiques, où les rapports isotopiques les plus lourds subissent des modifications par rapport aux formes plus légères en fonction des différences de taux de réactions métaboliques (Inger et Bearhop, 2008 ; Dunlop, 2011). Les valeurs de  $\delta^{15}\text{N}$  permettent de déduire le niveau trophique des organismes étant donné l'augmentation progressive et prévisible qui se produit lors du transfert trophique (Barrett *et al.*, 2007 ; Ramos *et al.*, 2020). Ainsi, les consommateurs présentent des valeurs de  $\delta^{15}\text{N}$  plus élevées que leurs proies (Forero & Hobson, 2003). Les applications courantes du  $\delta^{13}\text{C}$  ont été la description des zones d'alimentation et des sources de proies disponibles pour les espèces (Barrett *et al.*, 2007 ; Hong *et al.*, 2019). Elles sont basées sur la variation isotopique naturelle de ce composé parmi les producteurs primaires ayant différents types de photosynthèse, ce qui

conduit à l'existence de gradients dans diverses combinaisons de sources de productivité primaire (Quillfeldt *et al.*, 2005 ; Ramos *et al.*, 2020).

L'approche de niche isotopique (Newsome *et al.*, 2007) a été utilisée comme substitut de la niche trophique pour évaluer la plasticité trophique des Laridés. Les valeurs des isotopes stables et des niches ( $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$ ) des tissus échantillonnés et des espèces ont été utilisées pour évaluer les variations intra- et interspécifiques de la niche isotopique (fourchettes, amplitude, chevauchement) des espèces reproductrices (Fig. 2). Les échantillons de duvet des poussins reflètent le régime trophique des femelles avant la ponte, tandis que les échantillons de plumes intègrent le régime alimentaire des poussins fournis par les parents pendant l'élevage. Les isotopes du sang des adultes représentent les caractéristiques de la nourriture consommée et les zones de recherche de nourriture des oiseaux pendant l'incubation. En particulier, la variabilité interannuelle de la niche isotopique de la Sterne bridée a également été évaluée à partir d'échantillons de plumes, de duvet et de sang d'adultes et de poussins, représentant quatre phases du cycle de vie de cette espèce (non-reproduction, pré-ponte, incubation et couvaion) (Fig. 2).

## **Résultats**

La plasticité de la niche trophique semble être un mécanisme adaptatif important pour assurer le succès de la reproduction des Laridés se reproduisant en sympatrie dans le centre-nord de Cuba. La niche isotopique bivariée ( $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$ ) de cinq espèces diffère dans le temps (entre les phases de pré-ponte et d'élevage des poussins) et dans l'espace (entre les zones de reproduction), montrant des groupes trophiques généralistes et spécialistes. La ségrégation trophique interspécifique pourrait être due à des différences dans l'étendue et le chevauchement des niches, ainsi qu'à des stratégies d'alimentation spécifiques aux espèces (Cherel *et al.*, 2008 ; Liechty *et al.*, 2016 ; Gatto *et al.* 2019). Les modèles de variation isotopique des niches ont indiqué deux principaux modèles de plasticité trophique chez les reproducteurs : la contraction/expansion des niches et le déplacement des niches à travers différentes gammes de positions trophiques et/ou localités de recherche de nourriture. L'analyse des caractéristiques isotopiques et morphologiques des proies consommées, ainsi que l'évaluation des schémas de niche isotopique des prédateurs et des proies à différentes saisons de reproduction, peuvent aider à mieux comprendre les relations trophiques entre ces oiseaux de mer. Nos résultats sont cohérents avec ceux de Cherel *et al.* (2008) et Sebastiano *et al.* (2017) dans les colonies de reproduction d'oiseaux marins tropicaux qui incluent des Laridés.

Dans l'étude étendue au cycle annuel, la Sterne bridée occupe une niche isotopique restreinte et relativement plastique. La plus grande variabilité s'est produite entre les phases de non-reproduction et de pré-ponte, montrant une réduction marquée de l'étendue de la niche. Conformément aux résultats de Dunlop (2011) et Labbé *et al.* (2013), les valeurs  $\delta^{13}\text{C}$  des plumes des poussins sont plus élevées que celles du duvet, ce qui indique que la nourriture consommée par les poussins provient de zones de recherche de nourriture plus proches du rivage (zones enrichies en carbone en raison de la contribution des habitats benthiques) que celles exploitées par les femelles avant la ponte (Cherel et Hobson, 2007). La variabilité des niches diffère également entre les zones de reproduction. Considérant que la Sterne bridée dépend de peu d'espèces proies et que son aire de recherche de nourriture est réduite durant les phases de

pré-ponte et d'élevage des poussins (*e.g.* Catry *et al.*, 2008 ; Dunlop, 2011 ; Labbé *et al.*, 2013), ces deux phases du cycle annuel sont d'une grande vulnérabilité pour les colonies cubaines de cette espèce.

## **Description de la phénologie de la reproduction et de la morphologie des œufs**

### **Méthodes**

Cette étude a également été menée dans les colonies de reproduction des trois cayes du centre-nord de Cuba. Des échantillonnages hebdomadaires ont été réalisés et des pièges photographiques ont été placés sur les sites de nidification au cours de la saison de reproduction 2021 afin de décrire les patrons phénologiques (dates de début et de fin, et durée de chaque phase, pic de ponte) de la reproduction des espèces de Laridés étudiées (Fig. 3). Parmi les phases phénologiques identifiées, des stades de ponte précoce et tardive (Fig. 3) ont été détectés chez cinq espèces. La morphométrie des œufs précoces et tardifs a été caractérisée à partir de six variables obtenues par traitement numérique de photos (application Ovometrik mise en oeuvre dans le langage R) (Fig. 3), prises in situ dans les colonies selon le protocole standardisé de Ramírez-Arrieta *et al.* (2021). Ces variables ont ensuite été comparées entre les deux types d'œufs par espèce.

### **Résultats**

La phénologie de la reproduction est un élément crucial de l'écologie de la reproduction des oiseaux marins en raison de son influence sur la condition physique individuelle, le succès de reproduction et in fine la dynamique de la population (Dunn et Møller, 2014 ; Black *et al.*, 2018). En outre, les changements phénologiques interannuels de la reproduction des oiseaux marins peuvent refléter les changements du climat et des réseaux trophiques dans les écosystèmes marins (Hindell *et al.*, 2012). Dans cette étude, la phénologie de la reproduction des espèces est caractérisée par un schéma saisonnier et relativement synchrone, entre mai et août. Cela pourrait être dû à une plus grande disponibilité et accessibilité des proies pendant la saison des pluies à Cuba. Cependant, la variabilité interannuelle de ce trait doit être étudiée afin d'évaluer si la reproduction synchrone a lieu chaque année. Ce travail fournit la caractérisation la plus complète de la phénologie de la reproduction des Laridés à Cuba, compte tenu des informations générales existantes (*ex.* Rodríguez *et al.*, 2003 ; Garrido et Kirkconnell, 2011).

Seul les indices de forme des œufs de la Mouette atricille et de la Sterne bridée reflètent des différences entre les phases de reproduction précoces et tardives de ponte. La forme de l'œuf est un trait important du cycle biologique des oiseaux (Ramírez-Arrieta *et al.*, 2021) en raison de sa valeur adaptative par rapport aux caractéristiques du site de nidification, à la conservation de la chaleur, à l'efficacité de l'incubation, à la résistance structurelle de l'œuf et à l'échange gazeux (Denis et Olavarrieta, 2011 ; Chowdhury *et al.*, 2020 ; Ramírez-Arrieta *et al.*, 2021). La comparaison des autres variables n'a montré aucune différence ou a indiqué la nécessité d'augmenter la taille de l'échantillon. Cette grande similitude morphologique entre les œufs précoces et tardifs suggère que la morphométrie des œufs ne peut pas être utilisée comme



indicateur de l'asynchronisme de ponte intra-saisonnière chez les Laridés à Cuba. Néanmoins, en raison de la grande variabilité naturelle de la morphologie des œufs entre les couvées (Ricklefs *et al.*, 1978 ; Nedomová et Buchar, 2014), nous recommandons une réplification spatiale et temporelle de cette étude afin d'évaluer la variation morphologique des œufs de ces oiseaux marins tropicaux en fonction de la phénologie de la ponte.

## **Modélisation des zones prioritaires pour la conservation en tenant compte des plans de développement actuels et futurs**

### **Méthodes**

L'étude des zones de prioritaires pour la conservation des Laridés a été réalisée à l'échelle du pays, en considérant 4 variables décrivant les objets à conserver, et 13 variables décrivant les activités socioéconomiques (actuelles et futures), toutes spatialement explicites. Les caractéristiques de conservation ont été définies sur la base d'informations connues sur les colonies de Laridés et de l'avis d'experts. Les informations sur les coûts ont été obtenues auprès de diverses sources officielles liées aux secteurs de la pêche, de l'énergie et du tourisme. Des algorithmes de sélection systématique des sites de réserve de protection (utilisant la librairie d'optimisation JuMP, Dunning *et al.* (2017)) ont été mis en œuvre pour modéliser les zones de conservation prioritaires pour les habitats de reproduction des Laridés (Fig. 4) en tenant compte des quatre pressions humaines les plus importantes : la pêche, les parcs éoliens, le tourisme côtier et la pollution lumineuse nocturne. La fonction de coût global (entendue comme le coût que représenterait pour les activités anthropiques la mise en réserve d'une zone actuellement utilisée) est la somme pondérée de ces pressions humaines. Plusieurs scénarios de conservation ont été testés en fixant trois objectifs de protection (50, 75 et 90 %) pour les éléments de conservation considérés, ainsi que différents poids relatifs des pressions humaines dans la fonction de coût global. Des scénarios de conservation futurs ont également été modélisés en tenant compte du plan de développement des parcs éoliens à Cuba. Les zones modélisées ont été comparées aux zones marines protégées existantes afin de détecter les contraintes et les besoins de conservation (Fig. 4), conformément aux plans de développement cubains.

### **Résultats**

Les solutions de réserves de protection basées sur les objectifs de conservation de 50 % et 75 % sont très similaires entre leurs différents scénarios, tandis que des différences plus importantes ont été constatées avec les scénarios de l'objectif de conservation 90 %. Ces propositions de réserves couvrent des zones maximales d'environ 46 000, 82 000 et 120 000 km<sup>2</sup> pour les objectifs de conservation de 50, 75 et 90 %, respectivement. En général, les propositions de réserves de protection les plus coûteuses sont obtenues lorsque la pollution lumineuse nocturne est prioritaire, alors que l'inverse se produit pour le scénario où les parcs éoliens sont prioritaires, quelles que soient les valeurs des objectifs de conservation. Si l'on considère le futur plan de développement du parc éolien de Cuba, les schémas spatiaux des zones de conservation prioritaires sont très similaires aux scénarios des conditions actuelles du parc éolien calculés précédemment.

Ce travail examine les activités socio-économiques importantes pour le pays, et qui sont également des facteurs de stress pour les oiseaux de mer. Historiquement, l'un des plus grands problèmes de conservation pour les oiseaux de mer se reproduisant en colonies a été le dérangement humain (Anderson et Keith, 1980). Bien que certaines espèces puissent développer une tolérance à un certain degré de perturbation (Nisbet, 2000 ; Yorio *et al.*, 2001), cette accoutumance est spécifique à l'espèce et nécessite une planification appropriée des activités anthropogéniques (Schwemmer *et al.*, 2011). Ces résultats fournissent un outil pour aider les parties prenantes et les décideurs à développer et à affiner la planification durable de l'espace marin. La couverture finale et la localisation des zones à protéger dépendront des priorités gouvernementales à établir.

Dans les scénarios envisagés, plus de 70 % des zones de conservation prioritaires identifiées par le modèle pour les Laridés ne sont pas couvertes actuellement par les AMP existantes. En ce qui concerne les coûts des réserves de protection, les écarts les plus importants ont été observés lorsque le tourisme et la pêche avaient le poids le plus élevé, avec des objectifs de conservation de 50 % et 90 %, et lorsque le tourisme avait le poids le plus élevé avec un objectif de conservation de 75 %. Les lacunes les plus importantes en matière de couverture concernent les zones marines entourant les colonies de reproduction. Cela peut être dû à une perception inadéquate de l'écologie de la reproduction des oiseaux marins coloniaux, car ces espèces nécessitent des mesures de protection depuis le site d'établissement de la colonie jusqu'aux aires d'alimentation des adultes (Oppel *et al.*, 2018). En outre, il y a un fort chevauchement spatial entre les zones d'exploitation touristique et les AMP actuelles. L'une des principales critiques formulées à l'encontre des AMP concerne précisément l'étendue des activités humaines qui y sont autorisées et qui sont légalement soutenues par des catégories de gestion flexibles ou faibles (Driedger *et al.*, 2023 ; Lescroël *et al.*, 2016). Par conséquent, le lien entre l'écosystème marin, les perturbations humaines et les AMP doit être systématiquement évalué à l'aide d'informations détaillées et actualisées pour une conservation efficace.

En général, le potentiel de la méthode utilisée pour soutenir la prise de décision en matière de conservation est mis en évidence par sa flexibilité et sa capacité à intégrer les préoccupations écologiques et socio-économiques actuelles et futures, ce qui a d'ailleurs été appliqué pour concevoir divers scénarios dans les systèmes marins et terrestres (Brunel *et al.*, 2022 ; Proudfoot *et al.*, 2020). La capacité d'intégration de cette approche (objectifs et coûts de conservation) constitue une forme indirecte d'évaluation de l'impact humain cumulatif, qui permet d'orienter et de hiérarchiser les actions de gestion (Loiseau *et al.*, 2021). De plus, ce type d'outil a une valeur ajoutée face aux contraintes logistiques et financières souvent rencontrées dans les pays en développement, car il contribue fortement à l'utilisation optimale des ressources économiques et logistiques.

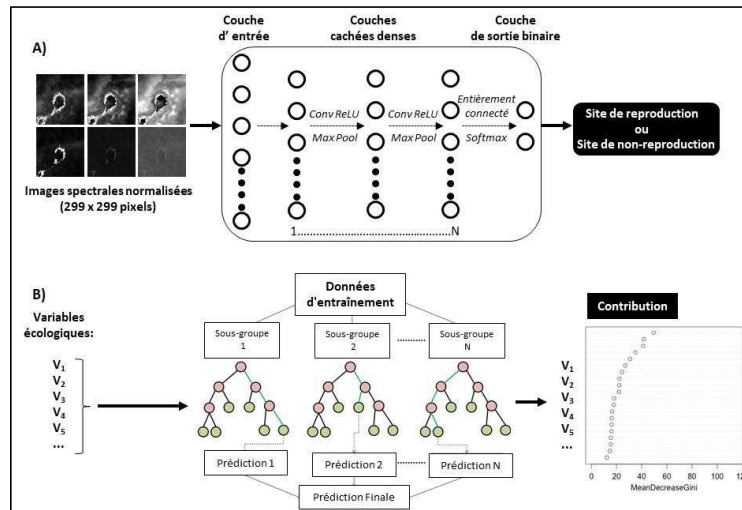
## **Conclusions**

Cette thèse fournit un ensemble de résultats qui contribuent à améliorer la connaissance scientifique de deux points de vue principaux. D'une part, elle comble d'importantes lacunes d'information sur l'écologie de la reproduction des Laridés tropicaux en général, et dans les Caraïbes en particulier. D'autre part, les approches méthodologiques appliquées à l'étude des

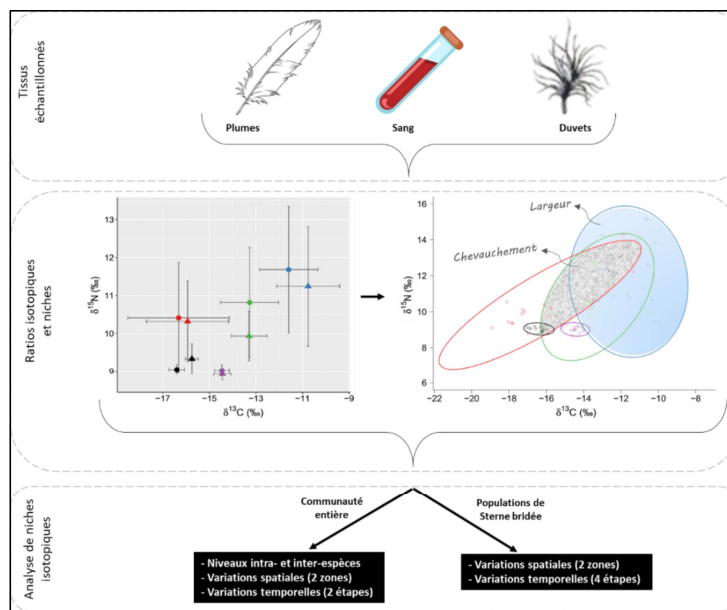
### Résumé en français

différents aspects de la reproduction et de la conservation des Laridés à Cuba exposent et/ou confirment leur efficacité au-delà de leurs utilisations traditionnelles. L'ensemble des recherches menées combine des approches de terrain et analytiques traditionnelles, modernes et de pointe pour aborder les processus écologiques qui caractérisent la reproduction des oiseaux de mer en général. L'objectif principal de cette recherche était de combler plusieurs lacunes dans les connaissances sur l'écologie de la reproduction du groupe d'oiseaux marins le mieux représenté à Cuba. Ainsi, la sélection de l'habitat (largement reconnue comme cruciale), les interactions trophiques basées sur des mécanismes de ségrégation et la dynamique phénologique pendant la reproduction sont des sujets essentiels pour comprendre l'écologie des oiseaux de mer. De plus, la conservation planifiée basée sur l'interaction homme-environnement est un moyen clair de protéger les ressources biologiques telles que les oiseaux de mer. Cette thèse ouvre également la voie à d'autres études pour répondre à d'autres questions de recherche importantes.

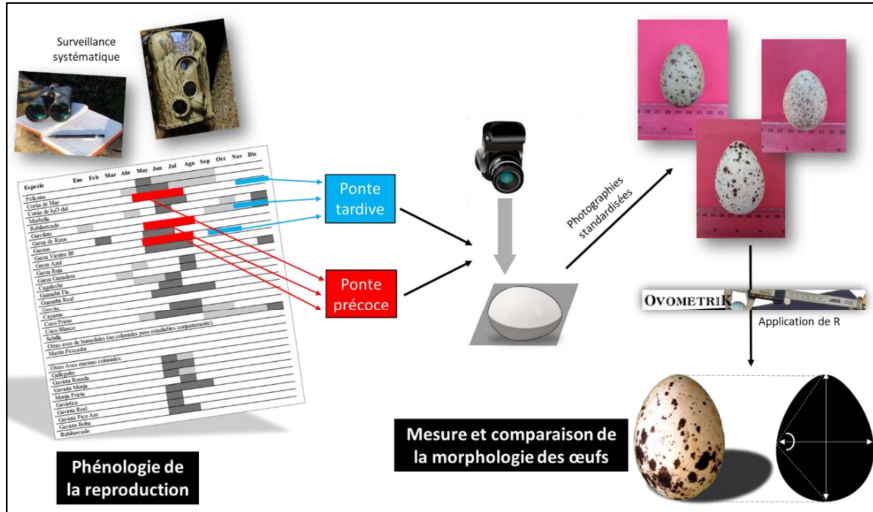
Enfin, un appel est lancé pour encourager le développement de nouvelles approches de la recherche en écologie marine à Cuba et dans les Caraïbes. Tout d'abord, la perspective de l'interrelation fonctionnelle entre le biote strictement marin, les conditions/phénomènes climatiques et océanographiques, et le biote dépendant des ressources marines (par exemple, les crocodiles, les oiseaux de mer) devrait être encouragée. Cela permettra de répondre à des questions de recherche plus larges dans le domaine de l'écologie marine tropicale. Deuxièmement, les approches numériques et prédictives de la recherche marine doivent être renforcées afin de mieux comprendre le fonctionnement de cet écosystème hautement dynamique. Nous devons aller au-delà du travail à l'échelle locale pour quantifier les ressources, les phénomènes et les processus à des échelles spatiales plus larges. Cela permettra d'obtenir des volumes importants de données pour évaluer et prévoir des scénarios, des situations et des anomalies dans l'environnement marin. En conséquence, des mesures régionales plus efficaces de gestion et de conservation de la biodiversité marine pourraient être mises en œuvre.



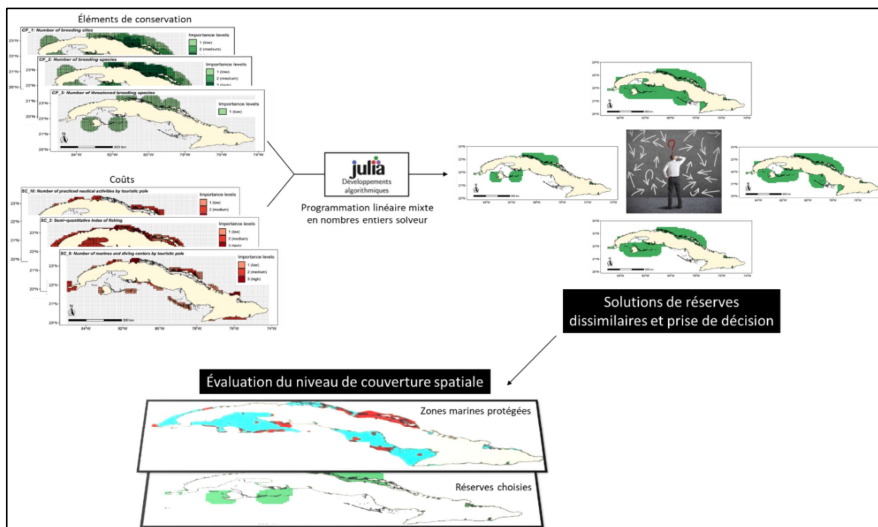
**Figure 1 :** Résumé graphique du chapitres 2 et 3 : approches complémentaires utilisées pour évaluer l'adéquation (A) et la sélection (B) des macro- et micro-habitats par les Laridés reproducteurs à Cuba. A) Structure générale et fonctionnement d'un réseau neuronal convolucional traitant des images satellites pour une prédiction de site de nidification, B) forêts aléatoires, analysant et pondérant l'importance des variables écologiques dans le processus de nidification.



**Figure 2 :** Résumé graphique des chapitres 4 et 5 : approche utilisée pour évaluer la variation intra- et inter-spécifique des niches trophiques (à l'aide des niches isotopiques) des Laridés se reproduisant à Cuba.

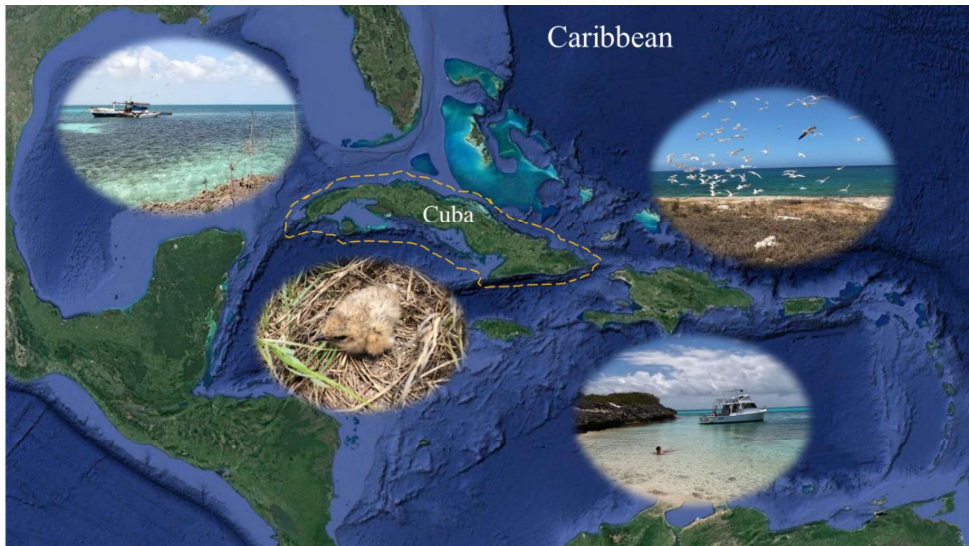


**Figure 3 :** Résumé graphique du chapitre 6 : procédure utilisée pour décrire la phénologie de la reproduction et la morphologie des œufs des Laridés se reproduisant à Cuba.



**Figure 4 :** Résumé graphique du chapitre 7 : procédure utilisée pour identifier les zones prioritaires pour la conservation des Laridés reproducteurs à Cuba, en tenant compte des pressions anthropogéniques.

**Chapter 1:**  
**General Introduction**



Although it may not appear so at first glance, seabirds are marine animals. These species obtain all or part of their food from the marine environment (Buckley & Buckley, 1980). However, the perception of little connection between seabirds and seas/oceans has long prevailed. Ornithologists viewed the sea as a flat, wet and relatively uniform environment over which birds flew and ate (Brown, 1980). Oceanographers and marine biologists, aware of the great dynamism of this environment, were reluctant to recognize that these flying animals, unable to reproduce at sea, were belonging to specific marine habitats or communities (Brown, 1980). However, in recent decades, this vision, challenged by the observations produced with modern technologies and methods, evolved with a better understanding of the interdependence between seabirds and marine-coastal ecosystems.

### **1.1 An aerial life on a drip from the sea: the great challenge for seabirds**

The interaction between the sea and seabirds is usually complex, involving a high degree of physical wear and energy cost. The marine environment is highly variable and dynamic due to oceanographic and climatological processes, which make the accessibility to trophic resources highly unstable and unpredictable both spatially and temporally (Pinaud *et al.*, 2005; Surman *et al.*, 2012; Englert Duursma *et al.*, 2018; Lorentsen *et al.*, 2019). Consequently, seabirds have had to adapt to the difficult conditions imposed by the marine environment to obtain food as they spend ~80% of their lifetime at sea (Bost & Le Maho, 1993). Several of their life history traits evidence their high specialization to life relying on the sea: long life span, fast growth, delayed maturity, low fecundity, high adult survival, wide mobility and reproduction in dense colonies (Furness & Monaghan 1987; Bost & Le Maho, 1993; Devney & Congdon, 2009; Yorio, 2009).

The breeding season is the most vulnerable phase in the annual cycle of seabirds, and at the same time, it is the phase in which they rely most heavily on terrestrial ecosystems. The reproduction implies many risks for the health and survival of adults and chicks (*e.g.* high degree of exposure to predators and adverse weather conditions, high energy cost during foraging to satisfy adult and chicks feeding needs, heavy dependence on the fluctuating availability of marine prey, greater exposure to human disturbances), while imposing important behavioral changes in adults with respect to the rest of the annual cycle (Buckley & Buckley, 1980; Vilchis *et al.*, 2006; Quintero *et al.*, 2014; Clay *et al.*, 2019). Adopting a central place foraging strategy and gathering in breeding colonies are among the most important behavioral changes for successful reproduction, and individuals need to breed in good synchrony with periods of important marine productivity.

Adjusting breeding time with favorable environmental conditions facilitates food acquisition that meet adult and chick requirements and maximizes breeding success (Brandl *et al.*, 2019). Central place foraging refers to foraging behavior within a specific radius around the breeding site (in contrast with wandering in vast areas as it may occur during the non-breeding season), imposed by the need for frequent return of adults to the nest site for the care and protection of eggs and chicks (Lamb *et al.*, 2017; Gatto *et al.*, 2019; Lorentsen *et al.*, 2019). This requires restrictions on movement, increased constraints for efficient prey capture and increased competition for food with other seabirds around the breeding site (Wakefield *et al.*, 2011;

Paredes *et al.*, 2012; 2015). Finally, colonial breeding constitutes a particular form of grouping where individuals breed in densely populated territories offering suitable nesting characteristics (Rolland *et al.*, 1998).

Coloniality is one of the most striking ecological phenomena occurring in 98% of seabird species (Forbes & Kaiser, 1994), and includes costs and benefits for breeders (Danchin & Wagner, 1997; Good, 2002). On the one hand, colonial breeding favors protection against predators (*e.g.* collective vigilance, group effect) and the efficient use of food resources based on shared information among individuals (Gorke & Brandl, 1986; Fasola & Canova, 1992; Doligez *et al.*, 2002; Weimerskirch *et al.*, 2010). However, it also increases the risk of predation by co-breeders (*e.g.* large gulls) as well as negative interactions leading to egg and chick losses, retarded chick growth and epidemic outbreaks (Fasola & Canova, 1992; Good, 2002). In particular, large concentrations of tropical pelagic seabirds could deplete food resources (mainly through competition between conspecifics) in the vicinity of their breeding colonies (“Ashmole’s halo” hypothesis, Birt *et al.*, 1987; Wakefield *et al.*, 2013).

## **1.2 Seabirds as marine ecosystem sentinels**

Seabirds have several characteristics that facilitate their study: they are highly visible animals (the other components of marine food webs often remain hidden underwater), easily quantifiable (they tend to forage in groups), breed in colonies (allowing for population censuses and monitoring) and are easy to capture offering the possibility to measure various demographic, behavioral and physiological parameters (Piatt *et al.*, 2007; Einoder, 2009).

As top predators in food webs, seabirds contribute to the regulation of the size and health of their prey populations, while also providing food sources for other marine and terrestrial predators. The guano they produce in their breeding colonies also fertilizes substrates and increases primary productivity, especially in coastal ecosystems (Jones *et al.*, 2008). Seabirds are important carriers of marine nutrients to terrestrial ecosystems, which increases available nitrogen and could support food webs during breeding and non-breeding periods (Gaiotto *et al.*, 2022). In addition, lixiviation of the guano produced in the colonies supplies nitrogen to the coral reefs (which could contribute to its growth) near to the breeding sites of seabirds (Lorrain *et al.*, 2017; Linhares & Bugoni, 2022).

Seabirds also play the role of bioindicator species of the state, changes and health of marine-oceanic ecosystems (Baird, 1990; Barrett *et al.*, 2007; Hindell *et al.*, 2012; McGowan *et al.*, 2013; Oppel *et al.*, 2018). Several life history traits (*e.g.* abundance, survival, breeding site fidelity, breeding success) of seabirds are sensitive to natural and anthropogenic variations (*e.g.* Barbraud & Weimerskirch, 2001; Genovart *et al.*, 2013; Champagnon *et al.*, 2018). As top predators, these animals integrate the effects of climate pressure on lower trophic levels and display them in easily quantifiable ways (*e.g.* changes in their breeding phenologies) (Hindell *et al.*, 2012). They reflect anomalies in climatic regimes and ocean productivity based on their sensitivity to variations in trophic supply (Bost & Le Maho, 1993; Barrett *et al.*, 2007; McGowan *et al.*, 2013). At the same time, seabird breeding parameters can indicate the status and age structure of commercially important fish stocks, thus contributing to fisheries



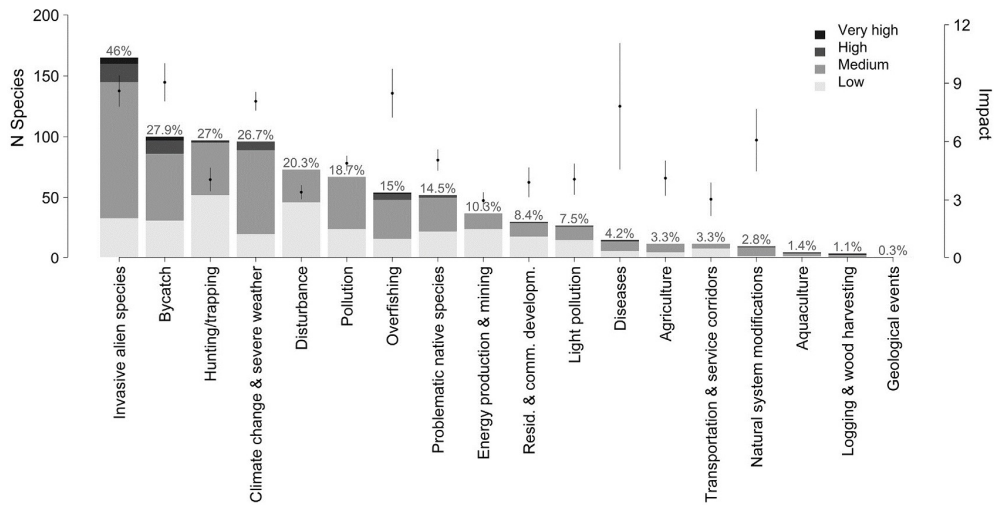
management (Piatt *et al.*, 2007; Einoder, 2009). In addition, some seabird species are excellent samplers of small fishes that are difficult to record by traditional sampling methods (Barrett *et al.*, 2007). Thus, for all the above reasons, seabirds are considered as sentinels of the effects of climate change and human disturbance on marine ecosystems (Hazen *et al.*, 2019).

### **1.3 Big threats and little protection: the issue for seabirds**

Seabirds are one of the most threatened groups of birds worldwide (Croxall *et al.*, 2012; Carr *et al.*, 2020): according to IUCN, 31% of the 359 seabird species are globally threatened and 11% are near threatened (Dias *et al.*, 2019). Their populations face strong threats and pressures such as fisheries removals, incidental death by fishing gear, marine traffic, pollution by hydrocarbons, persistent organic pollutants and heavy metals, development of renewable energy sources, introduction of alien species in breeding colonies, climate change, and disturbances from tourism and recreational activities (Vitousek *et al.*, 1997; Yorio, 2009; Thaxter *et al.*, 2012; Troisi *et al.*, 2016; Dias *et al.*, 2019; Mitchell *et al.*, 2020). The magnitude of the damage caused by these pressures has not been evaluated in depth, but the available estimates are alarming (Fig. 1.1), especially for the threatened species (Fig. 1.2).

For example, bycatch due to fishing gear causes damage or death to more than 150 000 seabirds annually (Anderson *et al.*, 2018). Also, several of the life history traits of seabirds (*e.g.* nests are easily accessible on the ground and in dense colonies constitute a fragility to catastrophic events) increase their vulnerability to human disturbance (Devney & Congdon, 2009; Yorio, 2009). Thus, enhancing the management and conservation of seabirds and their habitats is an imperative, given their importance for the preservation of global biodiversity and key ecosystem services within marine-coastal environments (Jones *et al.*, 2008).

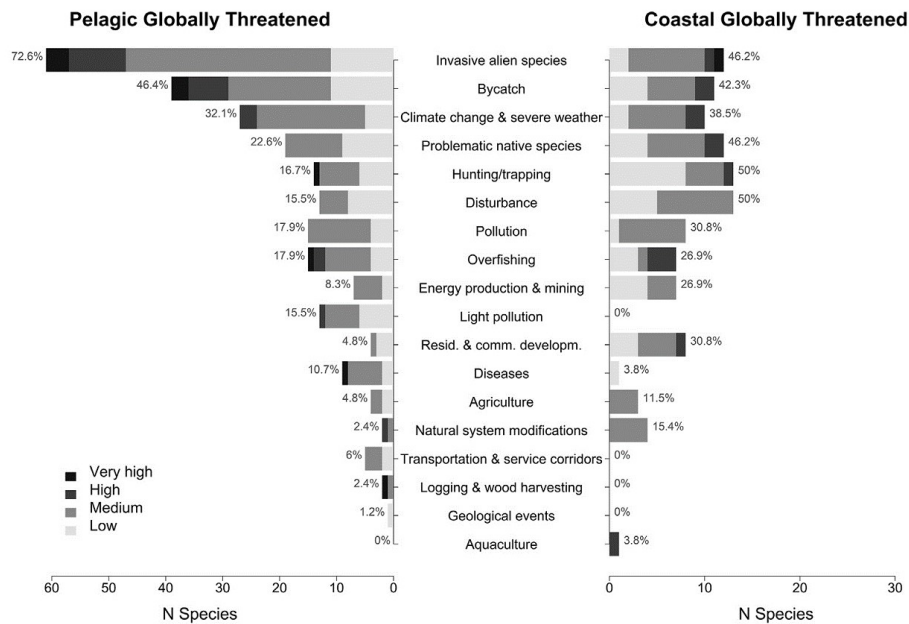
Marine protected areas (MPAs) are fundamental tools for the management and conservation of seabirds and marine biodiversity in general (Devillers *et al.*, 2015, 2020; Carr *et al.*, 2020; Schultz *et al.*, 2022). The recognition of the potential of MPAs has been maturing since the adoption of major international agreements for the conservation of marine and ocean biota. Among these is the Rio Declaration in 1982, which encourages countries to adopt holistic conservation approaches and sustainable practices to mitigate impacts on global marine biodiversity (Devillers *et al.*, 2015). Also, the establishment of international targets such as Aichi Target 11 of the Convention on Biological Diversity (CBD), aimed at protecting the world's marine and coastal ecosystems (Meehan *et al.*, 2020). This target initially planned to establish a marine-coastal protection coverage of 10% per country by 2020. Although it was not achieved extensively, it was reprogrammed toward an ambition of 30% protection of the oceans by 2030 (Devillers *et al.*, 2020; Schultz *et al.*, 2022; Driedger *et al.*, 2023).



**Figure 1.1.** Ongoing threats to all seabird species (ranked by the number of species affected). Left y axis: total number of species affected; Right y axis: average impact  $\pm$  SE. Values atop bars indicate the percentage of species affected (n=359). Taken from Dias *et al.* (2019).

Despite their wide acceptance worldwide, many MPAs have been criticized and highlighted for their inefficiency. Among the major problems are the allowances for tourism, recreative and extractive activities within MPAs and poor enforcement of levels of restriction (McGowan *et al.*, 2013; Devillers *et al.*, 2015). Another limitation is the adoption of a static approach to the architecture of MPAs, often leading to the protection of too small and not dynamic enough areas in comparison with the space-time varying ecological processes they intent to protect (Lescroël *et al.*, 2016).

For seabirds, the design of an effective MPA requires considering the annual variability in prey availability (McGowan *et al.*, 2013), the extent of the marine areas used for foraging (Yorio, 2009; Thaxter *et al.*, 2012), and the dynamics of processes such as migration and connectivity (Proudfoot *et al.*, 2020). Two other aspects are key to the effective conservation of highly mobile animals such as seabirds: consideration of the spatial scale for the design of MPAs according to the dynamics of the conservation targets (Yorio, 2009; Opper *et al.*, 2018), and the inclusion of natural and anthropogenic threats and disturbances in the design and legislative framework of the areas to be protected (Perrow *et al.*, 2015; Lescroël *et al.*, 2016; Lieske *et al.*, 2019). Finally, the level of bans within MPAs substantially influences their efficiency. It has been shown that fully or highly restrictive MPAs far outperform moderate and low regulation MPAs in preserving biodiversity and ecosystem services (Claudet *et al.*, 2020; Schultz *et al.*, 2022; Driedger *et al.*, 2023).



**Figure 1.2.** Ongoing threats to pelagic (n=84) and coastal (n=26) globally threatened seabirds; values atop bars indicate percentage of species affected. Taken from Dias *et al.* (2019).

#### 1.4 Seabirds in tropical regions

Tropical and subtropical marine ecosystems (excluding upwelling regions) tend to be characterized by low and seasonally stable primary production, yet the availability of their resources is usually considered as more difficult to predict than in temperate systems (Hockey & Wilson, 2003; Jaquemet *et al.*, 2008). Nevertheless, these ecosystems host assemblages of large or endemic seabird populations (Surman & Wooller, 2003; Jaquemet *et al.*, 2008; Harrison *et al.*, 2021), as well as many of their breeding sites.

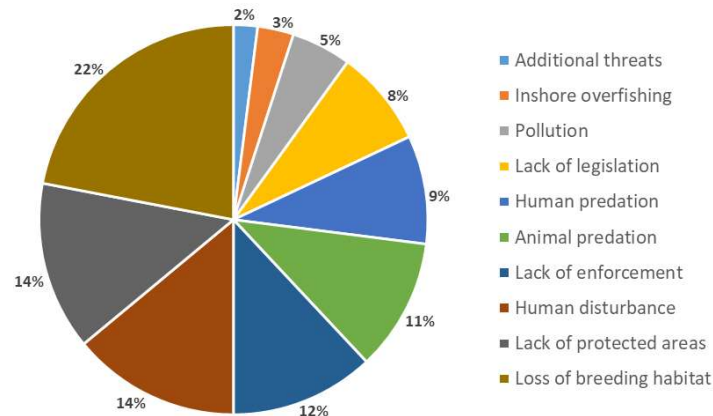
The coexistence and reproductive success of tropical seabirds is fundamentally based on intra- and interspecific mechanisms of trophic and reproductive segregation that allow to avoid or reduce competition. From a trophic point of view, tropical seabirds tend to specialize on diets with specific sizes, and specific foraging timing and ranges (although they do not show fidelity to specific areas due to the variability of prey availability, specially the pelagic species) (Catry *et al.*, 2008; Oppel *et al.*, 2015). The breadth of their trophic niches is usually contrasted between breeding (central place foraging) and nonbreeding (opportunistic foraging) periods (Cherel *et al.*, 2008). Niche partitioning relies also on breeding site selection, given the existence of diverse selection patterns among seabird species. In addition, tropical seabirds tend to segregate by breeding periods (Surman & Wooller, 2003). Breeding adults are socially monogamous, share the care of the brood, tend to lay few or a single egg and chicks often have a slow growth rate (depending on food availability and foraging skills of the adults) (Langham, 1983).

In general, the ecology of tropical seabirds has been poorly studied with respect to species from polar and temperate regions (Oro 2014). The Caribbean is home to a large number of breeding colonies of seabirds (Bradley & Norton, 2009), but it is one of the least studied tropical regions. This highlights the need for in-depth ecological studies on this avian group, as most Caribbean seabird species have experienced a reduction in their population size between 1984 and 2007 (Table 1.1; Bradley & Norton, 2009), which constitutes an alarm call.

**Table 1.1.** Variation of the population size of Caribbean seabirds between 1984 and 2007. Data from Bradley & Norton (2009).

Species	Change in Caribbean populations (%)
White-tailed Tropicbird	-59
Red-billed Tropicbird	+13
Masked Booby	-70
Brown Booby	-59
Red-footed Booby	+4
Brown Pelican	-61
Magnificent Frigatebird	-24
Laughing Gull	+71
Brown Noddy	+51
Sooty Tern	-36
Bridled Tern	+29
Least Tern	-25
Roseate Tern	-11
Common Tern	-16
Royal Tern	-54
Sandwich Tern	-45

Furthermore, this region is also the place for high anthropogenic pressures resulting from economic activities such as tourism and fisheries, which contrast with a particularly weak MPA coverage (Croxall *et al.*, 2012). Local and regional threats identified are diverse and require immediate attention (Fig. 1.3). Bradley & Norton (2009) listed the global threats affecting Caribbean seabirds that include climate change and sea level rise, changes in ocean chemistry, increase of hurricanes and storms frequency and intensity, long-line fishing and ocean pollution (by oil, plastics, pesticides). This set of local, regional and global threats and the observed population trends put the Caribbean seabirds in a very difficult situation, requiring urgent conservation actions.



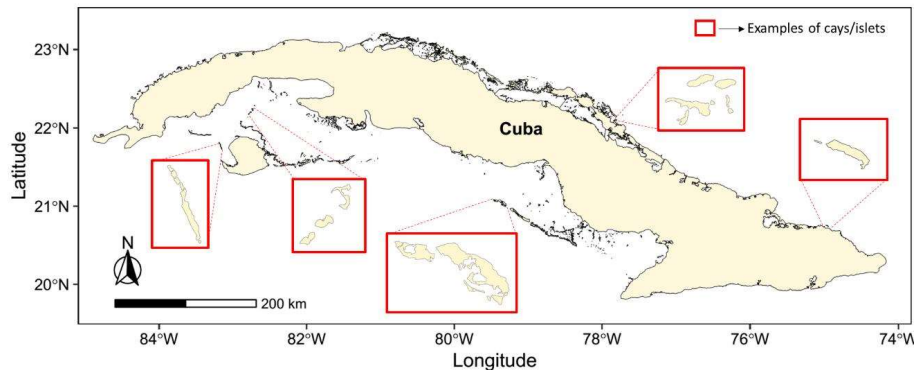
**Figure 1.3.** Distribution of local and regional threats for breeding seabirds in the Caribbean. Adapted from Bradley & Norton (2009).

Due to the need for immediate action, a set of conservation issues and proposals to initiate actions have been suggested (Bradley & Norton, 2009). At first place, capacity building, which includes an active role of the Society for the Conservation and Study of Caribbean Birds (SCSCB), the appointment of a coordinator for seabird work, and the strengthening of environmental education activities for the regional public. Second, the need to monitor priority species and sites was also highlighted, as well as the need to conduct surveys of new breeding sites. In addition, the significant loss of breeding habitats calls for strict conservation strategies at breeding sites. Thus, the need to protect additional breeding and foraging habitats, and to create and implement effective management planning for protected areas has been recommended. Finally, sustainable nature tourism has been identified as a key step to conserve the Caribbean seabirds. This implies the development of cooperation with regional tourism organizations and conservation NGOs, the evaluation of the ecosystem services and the creation of a protocol for sustainable ecotourism.

## 1.5 The study case: Larids in Cuba

### 1.5.1 Geographic and natural features on the Cuban coastal ecosystems

The Cuban archipelago (Fig. 1.4) is constituted by four island groups containing more than 1 600 islands, islets and cays: Los Colorados, Sabana-Camagüey (Jardines del Rey), Jardines de la Reina and Los Canarreos (Diccionario Geográfico de Cuba, 2000). Formally, cays are small, low-elevation, sandy, often flooded and largely mangrove-covered islands (Diccionario Geográfico de Cuba, 2000; Fig. 1.4); very common in the West Indies Sea and the Mexican Gulf. The main island of Cuba has 5 746 km of coastline and its extreme distances are: 1 250 km in length, 191 km maximum width and 31 km minimum width ([https://es.wikipedia.org/wiki/Geografia\\_de\\_Cuba](https://es.wikipedia.org/wiki/Geografia_de_Cuba)). The terrestrial surface of the Cuban archipelago is 109 884 km<sup>2</sup> while the coastal and territorial waters occupy 976 km<sup>2</sup> ([https://es.wikipedia.org/wiki/Geografia\\_de\\_Cuba](https://es.wikipedia.org/wiki/Geografia_de_Cuba)).



**Figure 1.4.** Map of the Cuban archipelago and zoomed-in examples of some of its cays and islets.

Cuba's climate is warm tropical, seasonally humid, with maritime influence and semi-continental traits (*www.insmet.cu*). Other climatic types are also reported in the country, such as in the southeastern coastal strip, which is classified as relatively dry tropical with little rainfall. The amount of sunlight received, the particularities of the atmospheric circulation and the influence of the physical-geographical characteristics of the national territory are identified as determining factors in Cuba's climate (*www.insmet.cu*). Due to its geographical position, Cuba is very close to the Tropic of Cancer, which conditions the reception of high sunlight throughout the year, determining the warm character of its climate. From November to April, weather variations are large, with abrupt changes in the daily weather, associated with the transit of frontal systems, the anticyclonic influence of continental origin and extratropical low pressure centers (*op. cit.*). From May to October there are few weather variations, with the more or less marked influence of the North Atlantic anticyclone (*op. cit.*). The most important changes are linked to the presence of disturbances in the tropical circulation (easterly waves and tropical cyclones).

Temperatures are generally high. Annual average values vary between 22°C and 28°C and are higher on the eastern coast (*op. cit.*). Values below 20°C are recorded in the highest parts of the mountains. The average maximum temperature ranges between 27°C and 32°C, and the average minimum temperature between 17°C and 23°C (*op. cit.*). The season from November to April is less hot and is known as "winter", while the warmer months of May to October are called "summer" (*op. cit.*).

The average relative humidity is high (~80%). Daily maximum, generally above 90%, occur at sunrise, while minimum drop to 50-60% at midday in the interior of the territory (*op. cit.*). The most humid areas are the western and central regions, together with the main mountain areas. East winds predominate (*op. cit.*). Maximum wind speeds occur during the passage of cold fronts, extratropical cyclones, local storms, hurricanes, among other phenomena. Also of interest are the local wind systems, with the presence of a central convective belt and the coastal influence of sea and land breezes, which strengthen or weaken depending on the predominant wind flow (*op. cit.*).

The most variable element in Cuba's climate is rainfall (*op. cit.*). There are two main seasons: the rainy season (from May to October) which cumulates approximately 80% of the total annual rainfall, and the dry season (from November to April). In the northeastern part of the eastern region and in the mountains, these characteristics vary and large volumes of rainfall occur from November to April. It is precisely in this part of the country where the largest rainfall areas are located, with values above 3 000 mm annually (*op. cit.*). However, on the southeastern coast, 600 mm or less annually are reported, with arid conditions. The largest rainfall volumes are associated with some of the most important meteorological phenomena (tropical cyclones, cold fronts, tropical waves) or have their origin in diurnal warming, almost always occurring in the afternoon in the form of short duration episodes. In the presence of large-scale meteorological systems, periods of heavy rainfall may occur, especially in the months of May-June and September-October (*op. cit.*).

Tropical cyclones strongly impact Cuba, both from environmental and socioeconomic point of views. The cyclone season in Cuba runs from June 1 to November 30, although some events have been recorded outside this period (Roura-Pérez *et al.*, 2018). Between 1791-2016, Cuba has been hit by 121 hurricanes: 59 category 1 (maximum winds = 119-153 km.h-1), 29 category 2 (maximum winds = 154-177 km.h-1) and 33 intense hurricanes (categories 3, 4 and 5 representing maximum wind ranges = 178-208, 209-251 and  $\geq 252$  km.h-1, respectively). The months of October (35.5%), September (31.4%) and August (15.7%) have had the highest frequency of hurricane occurrence (Roura-Pérez *et al.*, 2018).

Most of the cays and islets are dominated by clayey-alluvial and carbonate sediments from the Pleistocene (Diccionario Geográfico de Cuba, 2000). The vegetation on Cuba's cays is highly varied, taking as a reference the Sabana-Camagüey archipelago (the most extensive and heterogeneous in the country). Mangrove forests or mangroves predominate, in all their floristic and physiognomic variants (Menéndez *et al.*, 2014). In the rocky plains in the center of the larger cays, semi-deciduous and evergreen microphyllous forests are found (Menéndez *et al.*, 2014). Coastal scrub on sand and rock is highly represented. In areas with salt accumulation, halophyte communities are established, and in bare rocky spaces and sandy strips, rocky and sandy coastal vegetation complexes are located, respectively (Menéndez *et al.*, 2014). Other vegetation types less represented are swamp forests, freshwater vegetation and seasonally flooded savannas. In punctual sites there are plantations and crops, as well as secondary vegetation associated with human action (*op. cit.*).

## **1.5.2 Situation of the coastal ecosystems in Cuba**

### **1.5.2.1 Threats**

The main threats to Cuba's marine biodiversity come from the effects (current and predicted) of global climate change and anthropogenic activities. The expected impacts in Cuba from climate change are the increase in mean annual temperature, intensification and prolongation of drought periods, rise in mean sea level, and increase in the frequency and intensity of hurricanes (Planos *et al.*, 2013). These impacts could have important repercussions on Cuba's biota, characterized by a high degree of endemism and vulnerability. However, there are hardly

any studies aimed at assessing the possible effects of climate change on Cuban biota (Planos *et al.*, 2013). Blanco & Sánchez (2008) are the only authors reporting on climate impacts on waterfowl and seabirds. These authors predict that for these birds, the rise in sea level could reduce their nesting, feeding, resting and refuge habitats, limit the use of different feeding strategies, and change the arrival and concentration sites of migratory species. Thus, flooding, salinization and structural modification of coastal areas could severely affect seabird populations in Cuba, although more detailed quantitative studies are needed.

On the other hand, the main activities of socioeconomic interest that could produce alterations in coastal ecosystems (and seabird communities in particular) in Cuba are fisheries, tourism and the development of renewable sources (wind farms). These activities constitute government priorities aimed to ensure seafood supply/export, increase economic incomes and save energy carriers. Historically, fishing productivity on Cuba's insular shelf has been high, especially in Fishing Zone A (Fig. 1.5). However, lack of foresight and inadequate management caused that, since the 1980s, most of the country's fishery resources were fully exploited (Giménez *et al.*, 2016). Inappropriate practices such as overfishing, mangroves logging, use of aggressive fishing gear, reduction in the circulation of freshwater flows, illegal capture and trade of protected species, introduction of exotic species, marine pollution, and unsustainable coastal development have affected marine biodiversity and the productivity of fisheries in Cuba (González-Sansón *et al.*, 2009; Giménez *et al.*, 2016; Angulo-Valdes *et al.*, 2022). These effects could also extend to seabirds given their dependence on the consumption of marine resources, especially during periods of high demand such as the breeding season. However, the latter has not been evaluated and the breeding phenology of seabirds of Cuba remains largely unknown.

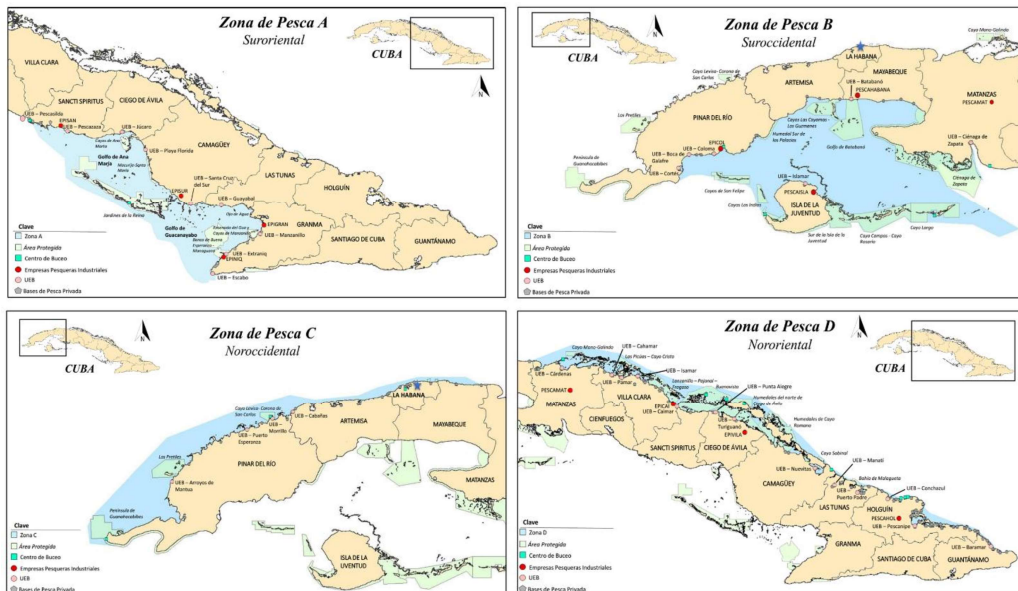


Figure 1.5. Sectorization of fishing zones (light blue areas) in Cuba. Source: Centro de Investigaciones Marinas, Cuba.



Sun and beach tourism is the main recreational modality offered by that sector in Cuba. That is why, there are several tourist poles in coastal areas throughout the archipelago where several activities are practiced, including sea and sun bathing on beaches, nautical tours, live-aboard trips, traditional and recreational fishing, scuba diving and snorkeling ([www.nauticamarlin.com](http://www.nauticamarlin.com), [www.gaviota-grupo.com](http://www.gaviota-grupo.com)). By 2020, there were 58 866 rooms in 178 hotels and other accommodation facilities in coastal areas of Cuba (Oficina Nacional de Estadísticas e Información de Cuba, updated inventory until 2020 of the Ministry of Tourism of Cuba). Average room occupancy (by domestic and international tourists) from May to August between 2017 and 2019 is estimated at 55%, while the number of tourists in the same period is estimated at 1 716 170 (Oficina Nacional de Estadísticas e Información de Cuba). During and after the Covid crisis, tourism activities experienced an abrupt decline, although there is a recent trend to recovery. Nevertheless, the characteristics of tourism-seabird interactions and their consequences on seabird behavior and populations have never been evaluated in Cuba.

The building of wind farms, together with other renewable energy sources, is part of the Cuban government's short- and medium-term strategy to reduce dependence on fossil fuels for energy production. All wind farms in operation (4), under construction (2) and planned (15) are framed in coastal areas. Several of them are in locations close to important seabird breeding areas, in addition to the fact that coastal areas are habitats commonly exploited by these animals. However, the negative impacts that wind turbines could have on seabirds in Cuba have not been quantified/estimated. Finally, a human disturbance that significantly affects seabirds is the night light pollution by artificial lights (Gineste *et al.*, 2017; Lieske *et al.*, 2019). This topic is of recent and growing interest in the world scientific community, but has not yet been studied within the ecological context of Cuba.

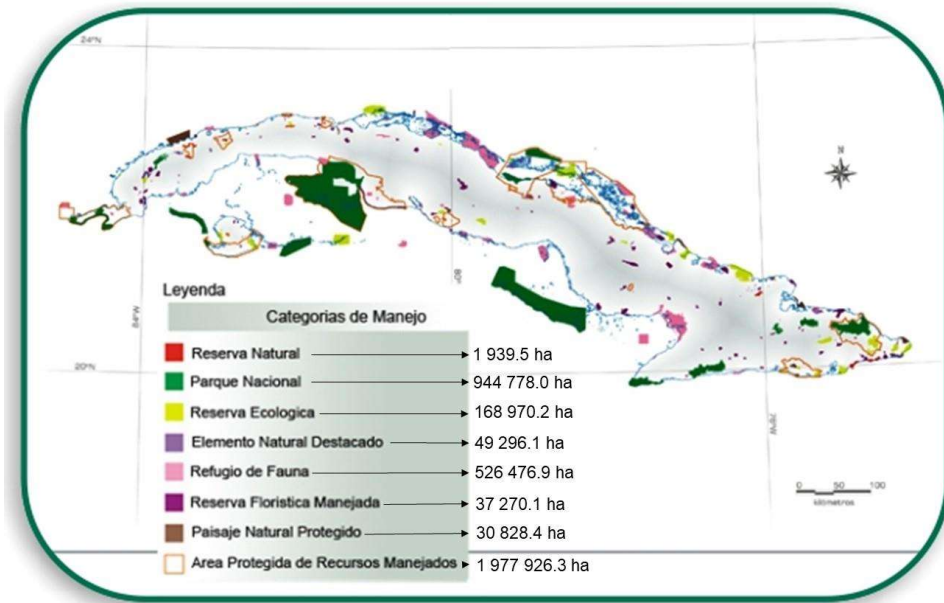
### **1.5.2.2 Environmental management and conservation**

The Ministry of Science, Technology and Environment (CITMA) is the main entity in charge of environmental management in Cuba, since part of its mission includes proposing and, once approved, leading and controlling the policy of the State and the Government in the areas of science and environment to contribute to the sustainable development of the country ([www.citma.gob.cu](http://www.citma.gob.cu)). The implementation and control of the approved environmental policies is the responsibility of various CITMA entities (*e.g.*, territorial delegations, Office of Environmental Regulation and Safety, Environmental Agency), the Cuban Forest Guard Corp (Ministry of Agriculture), as well as fisheries inspectors and agents of the Ministry of the Interior.

There are several instruments for environmental management and regulation supported by a legislative framework of ~14 regulations ([www.citma.gob.cu](http://www.citma.gob.cu)). Also, noteworthy are the National Environmental Strategy, the National Strategy and Program for Biological Diversity, the State Plan for Confronting Climate Change (2017), the Fisheries Law (2020), the Government Plan for the Prevention and Confrontation of Crimes and Illegalities Affecting Wild Flora and Fauna (2020), and the Law on the System of Natural Resources and the

Environment (2022). Nevertheless, despite all these instruments the management of marine resources still appears to be insufficient.

Regarding the conservation of natural and landscape resources, Cuba has a National System of Protected Areas composed of 119 protected areas (Fig. 1.6), 65 of which are MPAs (covering 43.6% of the total protected area). The National Center of Protected Areas (subordinate to CITMA) is in charge of the management and control of the protected areas in coordination with different entities and agencies of the Central State Administration (*e.g.* Flora and Fauna and Agroforestry Business Groups, NGOs, tourism organizations, administration councils). The protected areas are ranked in eight management categories according to their restriction levels. Thus, in descending order of restrictions are 3 Natural Reserves (1 MPA), 14 National Parks (10 MPAs), 23 Ecological Reserves (12 MPAs), 13 Highlighted Natural Elements (6 MPAs), 14 Managed Floristic Reserves (2 MPAs), 26 Fauna Refuges (20 MPAs), 12 Protected Natural Landscapes (5 MPAs) and 14 Protected Areas of Managed Resources (9 MPAs) (Fig. 1.6).



**Figure 1.6.** National System of Protected Areas of Cuba and surface covered by each one management category. Taken from the National Center of Protected Areas (<http://www.snap.cu/html/snap.htm>). The management categories are sorted (top to bottom) from maximum to minimum levels of restriction.

### 1.5.3 Background on seabird studies in Cuba

Within the insular Caribbean, Cuba stands out for its richness and abundance of seabirds. This archipelago constitutes 48% of the emerged insular area of the Caribbean (Acosta *et al.*, 2011) and more than 15% of its surface is made up of wetlands (Mugica *et al.*, 2012). Six of these wetlands were declared Ramsar Sites between 2001 and 2002 (Mugica *et al.*, 2006; Fig. 1.7).

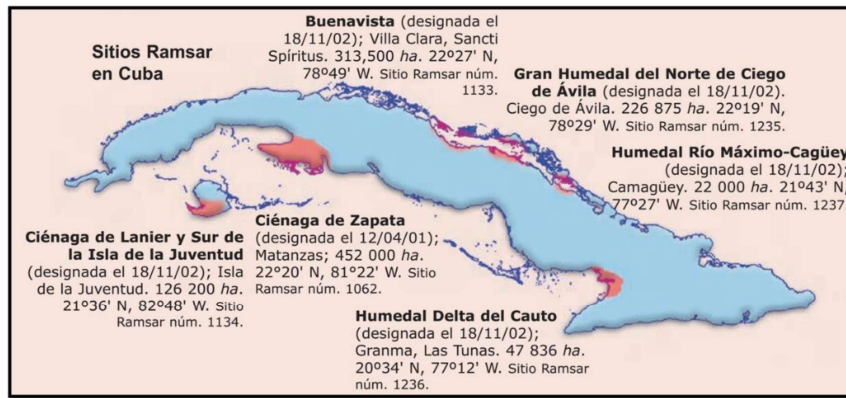


Figure 1.7. Ramsar Sites of Cuba. Taken from Mugica *et al.* (2006).

Studies on seabird ecology in Cuba are scarce and recent. Mugica *et al.* (2012) summarizes that ecological research on waterbirds (including seabirds) in Cuba began in the 1980s (Fig. 1.8A) and is poorly represented in the scientific literature (Fig. 1.8B). Most of the publications focus on 11 Cuban wetlands and are addressed to inventories, new records and understanding of the biology of Cuban waterbirds (including reproduction, conservation, migration, distribution and morphometry) (Mugica *et al.*, 2012; Figs. 1.8& 1.9). These studies correspond only to four of the six Cuban wetlands of international importance (Ramsar sites; Zapata, Birama, Río Máximo and Lanier marshes) (Fig. 1.9). The most important area in terms of number of publications is the Sabana-Camagüey archipelago (Fig. 1.9).

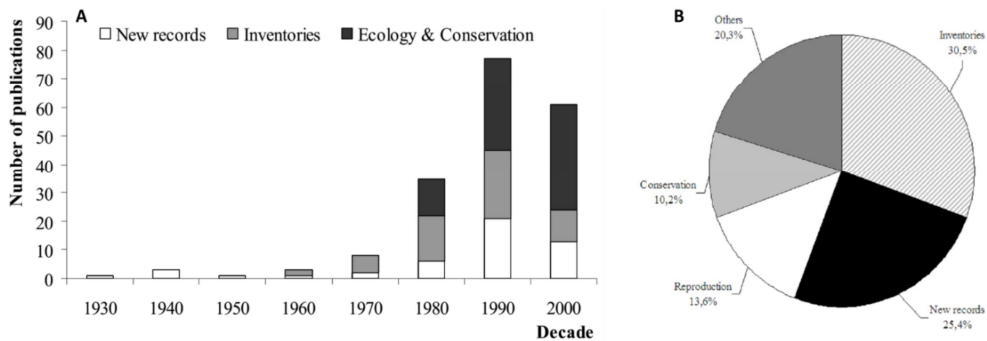
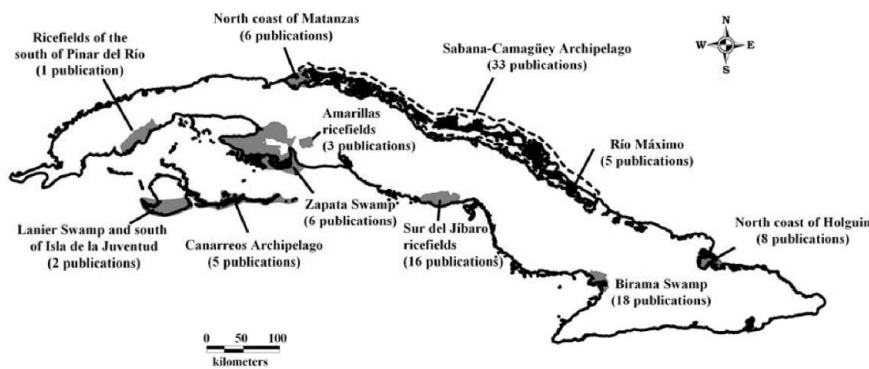


Figure 1.8. **A:** Distribution of publications on Cuban waterbirds (including seabirds) by decade, categorized by type of study. **B:** Percentage of published reports on Cuban waterbird communities classified by research topics from 1930 through 2006. Taken from Mugica *et al.* (2012).

Cuba's marine avifauna is represented by five orders, 12 families and 49 species (Navarro, 2021). The best represented family is Laridae, composed by 25 species of gulls and terns in the archipelago (Navarro, 2021). Only nine of these reproduce locally (Jiménez *et al.*, 2009; Navarro, 2021). The Laridae family is one of the best represented in cays and coastal areas. It is a cosmopolitan group, widely distributed throughout the world, from the tropics to the poles,

with species typically marine or pelagic, long-distance migrants (Garrido & Kirkconnell, 2011). Larids are generally flying birds with long, narrow wings, small legs, usually webbed. Many of them feed in flight, dive shallow to capture prey or swim at the surface. Other general characteristics of the family include the presence of a supraorbital salt excretory gland and a reduced or absent hind toe (Blanco *et al.*, 2001). Plumage coloration is usually white, grey and white, black and white or brown, especially in juveniles (Blanco *et al.*, 2001).

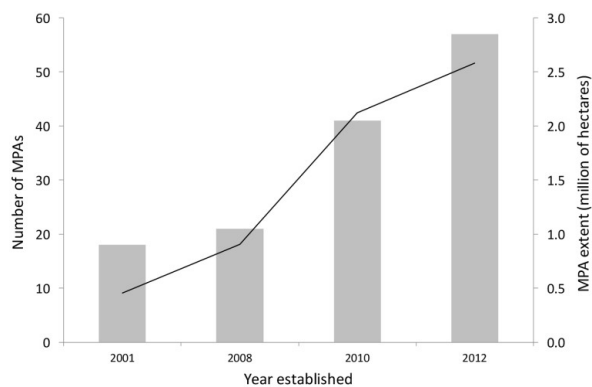


**Figure 1.9.** Number of publications on waterbirds (including seabirds) in 11 Cuban wetlands, between 1930-2006. Taken from Mugica *et al.* (2012). The main topics of these studies are summarized in the Fig. 1.8.

Gulls and terns are seabirds adapted to foraging at the surface or in a very shallow layer of the water column (Schwemmer *et al.*, 2009; Robertson *et al.*, 2014). Both groups of larids have important differences, mainly in their trophic ecology. Gulls tend to show a generalist behavior as they consume a high number of items of marine and even terrestrial origin (when food is scarce), use several foraging strategies (*e.g.* from the air, walking, swimming and short and shallow dives) and exploit several types of habitats within the sea-land gradient (Hunt, & Hunt, 1973; Schwemmer *et al.*, 2009; Washburn *et al.*, 2013). In addition, many species of gulls have acclimated to urbanized environments and consume waste and debris generated by anthropogenic activities (Washburn *et al.*, 2013). Terns are more specialized and consume prey from the sea surface, such as small fish and cephalopods (Langham, 1983; Schwemmer *et al.*, 2009). These birds tend to forage within a relatively short range from breeding colonies, use long periods for this activity and capture prey by flying over the sea surface or shallow immersion (Bugoni & Vooren, 2004; Robertson *et al.*, 2014). This implies a significant energy expenditure and increases the sensitivity of terns to food scarcity. Both gulls and terns tend to form breeding colonies in remote land fragments, although with species-specific particularities.

The ecology of larids in Cuba is practically unknown. The few studies carried out on this group correspond to inventories of individuals and breeding colonies, additions of new species records (many rare or occasional) and basic characterizations of breeding habitat use and some parameters of breeding success (*e.g.* Rodríguez *et al.*, 2003; Acosta *et al.*, 2022). The monitoring carried out has not been consistent and constant over time, or at least there are no publications that prove it. The main causes of this knowledge gap seem to be logistical and

economic limitations, the absence of specialists in this topic, and a poor holistic vision of the functioning of the coastal-marine ecosystem. In addition, there are difficulties in studying marine ecosystems due to their extension and harsh environmental conditions (Tremblay *et al.*, 2009). Furthermore, the effectiveness of seabird conservation in Cuba has not been evaluated, although it appears to be low. Existing MPAs are based primarily on other conservation values (fish, coral reefs, sharks, chelonians, crocodiles), which are not aimed at protecting seabird breeding sites, thus leaving foraging areas in the background. Despite the sustained increase in the number of MPAs and their coverage in Cuba (*e.g.* Fig. 1.10), the problem of insufficient effective protection of seabird breeding colonies has remained.



**Figure 1.10.** Number of marine protected areas established in Cuba (gray bars) and total hectares covered (black line) from 2001 to 2012. Taken from Perera-Valderrama *et al.* (2017).

#### 1.5.4 Basic characteristics of the studied species

This thesis focuses on the larid species that breed along the Cuban archipelago. It is necessary to clarify that previous publications (*e.g.* Rodríguez *et al.*, 2003; Jiménez *et al.*, 2009) refer that there are 10 breeding species of larids. However, recently a confusion between Common Tern (*Sterna hirundo*) and Roseate Tern (*Sterna dougallii*) has been identified (due to limitations of the identification materials and the similarity between both species when breeding (Nisbet, 2020)) and corrected. Thus, the following nine larids species are breeding in Cuba:



Laughing Gull (LAGU, *Leucophaeus atricilla*)

Photo: BRH Photography, 2018

Chapter 1: General Introduction

It is a common resident in coastal areas throughout the year and the only gull that breeds in Cuba, mainly in the northern area. It is of medium body size, ranging between 38-43 cm. Adults have a white belly, the back is light gray and wings are dark gray with black tips; legs and bill are usually black and may turn red during the breeding season. LAGU breed from approximately April to July in mixed colonies with other seabirds. It uses a wide variety of habitats for nesting, in small offshore rocky cays, in marshes, in reef hollows, always using grasses or vegetation debris for nest construction (Garrido & Kirkconnell, 2011). It lays two to four eggs, light to dark gray and generally spotted (Garrido & Kirkconnell, 2011). Both sexes incubate from 22-26 days. This species feed on fishes, snails, insects, seabird eggs and discards.



Brown Noddy (BRNO, *Anous stolidus*)

Photo: Antonio Garcia Quintas, 2021

BRNO has a dark brown plumage all over the body except for the upper part of the head and forehead, which are silvery-white. It is distributed in tropical and subtropical seas around the world and is also a fairly pelagic bird. In Cuba it is a common summer resident and it breeds in keys of the north coast and the Hicacos Peninsula. It feeds on fishes, shrimps and squids, usually in the open sea where it congregates to capture its prey from the surface (Garrido & Kirkconnell, 2011). The breeding period runs from May to August, adults build nests in bushes with branches and fill them with shells or alternately use stone mounds where they also deposits remains of mollusk shell (Garrido & Kirkconnell, 2011). The BRNO lays a single white or beige egg with purplish and gray spots generally concentrated towards one side (Valdés, 1984), which is incubated for 35 days.



Sooty Tern (SOTE, *Onychoprion fuscatus*)

Photo: Jacques de Seville, 2012



Bridled Tern (BRTE, *Onychoprion anaethetus*)

Photo: birdsofsaudi Arabia.com

SOTE and BRTE look very similar to each other. They are easily distinguished from other species by their dark color on the back. Both are white ventrally and have a dark mask covering the eyes. The differences between them are not very conspicuous: BRTE color is lighter dorsally (brownish-gray) and has a white collar between the mantle and the crown, while SOTE is darker dorsally and the head color continues with the back color. The white spot on the forehead is longer in BRTE and extends beyond the eyes. In addition, SOTE is slightly larger (43-45 cm) than BRTE (35-38 cm) and looks slenderer because the tail is longer. BRTE is widely distributed in tropical seas and exploits less pelagic habitats than SOTE. The latter can be found hundreds of miles offshore, getting close to land only to breed or when weather conditions are severe. Sooty tern remains in flight almost all the time during the non-breeding period. They nest in large mixed colonies between May and August, on islands or cays, they do not build nests (Garrido & Kirkconnell, 2011). Eggs, usually only one, are laid under rocks or on the sand (Valdés, 1984). The largest reported colony of BRTE in Cuba included about 280 individuals (Blanco *et al.*, 2001). Both species feed on fishes and squids (Garrido & Kirkconnell, 2011).



Least Tern (LETE, *Sternula antillarum*)

Photo: Dave Martin, 2010

This is the smallest species of the group (21.5-24 cm), its small size making it unconfoundable with the other species. In Cuba it is a common summer resident, mainly in the western region and adjacent cays (Garrido & Kirkconnell, 2011). The greatest concentration of nesting sites occurs in the Sabana-Camagüey archipelago. The plumage is gray on top and white on the belly, the legs are yellow and the bill is yellow with a black tip. Adults have black head and nape and white forehead. It feeds on small fish and invertebrates that it catches on the surface of the water. It usually nests in monospecific colonies and sometimes breeds in mixed colonies with other larid species and other shorebirds. The breeding period is from May to July. Adults rarely build nests as they take advantage of the ripples of the ground with abundant sand to nest and delimit the nest site with mollusk shells or herbaceous debris (Garrido & Kirkconnell, 2011). The clutch size is one to three light beige eggs with brown and gray spots (Blanco *et al.*, 2001).



Gull-billed Tern (GBTE, *Gelochelidon nilotica*)

Photo: scottishdude, 2009

It is a white larid (36 cm length) with a very pale gray mantle and rump; the bill is black and thick, and the legs are black and long. It has a wider wing than most terns and a slightly forked tail (Garrido & Kirkconnell, 2011). The breeding plumage includes a black cap. It was long considered an uncommon winter resident and transient in Cuba (Garrido & Kirkconnell, 2011), but two small breeding colonies were later detected in the Sabana-Camagüey archipelago. It feeds mainly on crustaceans, insects and frogs (Garrido & Kirkconnell, 2011).



Roseate Tern (ROST, *Sterna dougallii*)

Photo: US Fish and Wildlife

This small species (39 cm) has an elongated, slender appearance and white coloration with a uniform pale gray mantle (Garrido & Kirkconnell, 2011). The tail is white and markedly forked. The wings are short, allowing rapid flight and short flapping. During the breeding season, adults show a black cap, black bill with red base, orange-brown legs and white forehead and crown (Garrido & Kirkconnell, 2011). In Cuba it nests in small cays from May to July. It lays a cream-colored egg with dark spots and feeds on small fish and mollusks (Garrido & Kirkconnell, 2011).



Royal Tern (ROYT, *Thalasseus maximus*)

Photo: Owen Deutsch

ROYT is among the largest (46-56 cm) larid species in Cuba. It is a bimodal resident (*i.e.* populations with both permanent and migratory summer individuals) and abundant on coasts and cays, being the most common tern species along with Laughing Gull. The plumage is predominantly white, with light gray back and wings, black legs and bright orange bill. It has a cap of elongated black feathers in the form of a crest that varies seasonally, so that individuals can be found with white, black or spotted foreheads depending on the time of year and age. Juveniles have a yellow bill and legs and a brownish spotted back. The breeding period is from May to July, breeding in mixed colonies usually with the Sandwich Tern (Garrido &



Kirkconnell, 2011). It prefers to nest on the higher coasts of the northern and southern cays. It does not build a nest as such, it lays a single egg which is deposited in a depression in the ground (Valdes, 1984; Blanco *et al.*, 2001). The eggs are somewhat oval, light cream or white with brown and gray spots.



Sandwich Tern (SATE, *Thalasseus sandvicensis*)  
Photo: Mihai Baciu

SATE nests in cays far from the coast. It is of medium size (41-46 cm) with a light gray plumage that from a long distance looks white, a crest of black feathers similar to the ROYT and a very long and thin black beak with a yellow tip; the legs are also black. It feeds on fish, crustaceans, marine worms and squid, captured by diving into the water from the air (Garrido & Kirkconnell, 2011). It breeds in mixed colonies generally with ROYT, LAGU and ROST in cays on the north and south coasts of the island. It nests from May to July, on the rocky ground and lays a cream-pink egg sometimes with dark brownish spots in a ground ripple that may be surrounded by shells (Garrido & Kirkconnell, 2011).

### **1.6 Objectives of the thesis**

The major lack of ecological information on seabirds in Cuba and the uncertainty about the effectiveness of their conservation has already been highlighted. As larids constitute the largest seabird community in Cuba and as they exploit large extensions of marine habitats, because of their local abundance, wide mobility and high trophic position in marine food webs, any scientific research that provides ecological information on these birds breeding in Cuba will be highly valuable for the preservation of seabird populations and for the conservation of marine ecosystems. Thus, this research is focused on the breeding ecology of larids in Cuba, with an emphasis on three multi-species colonies located in an important breeding area in the central-northern part of the country. In particular, the specific objectives are to:

#### 1. Characterize the site selection pattern and predicting the suitability of breeding habitat for larids in Cuba

Habitat is an essential factor for understanding the ecology of species. In this sense, two fundamental questions are: where are the habitats used by a species? and what environmental variables determine the selection of these habitats? For Cuba's larids, the answers to these questions can contribute to the reduction of threats such as breeding habitat loss by anthropic causes or the consequences of climate change (*e.g.* the rise in sea level can affect nesting sites and alter the morphology of cays and islets that harbor colonies). Knowledge of the spatial

distribution of the breeding habitats of these seabirds can also serve to evaluate vulnerabilities of colonies to hurricanes and tropical storms (which cause coastal flooding, strong winds that devastate landscapes, high bird mortality), as well as marine pollution (fuels, heavy metals, plastics) depending on the proximity to polluting sources and of marine currents. All this would contribute to a more effective management and conservation of the breeding and feeding habitats of Cuba's larids, which is one of the priorities identified for the conservation of Caribbean seabirds (Bradley & Norton, 2009).

These topics are addressed in chapters 2 and 3 using machine learning methods and historical records of larids colonies in Cuba. Random forest models are used to evaluate what environmental covariates (18 land and marine variables, considered at three spatial scales - 10, 50 and 100 km) seabird may use to select their breeding macrohabitat (Chapter 2) and microhabitat (Chapter 3) at the scale of Cuba and the north-central region, respectively. In chapter 2, a convolutional neural network (deep learning tool) is also used to predict (for non-monitored sites) breeding macrohabitat suitability at the country scale from Landsat satellite images information. Also, during the 2021 breeding season, the nesting-site selection among five larid species was assessed and quantified using eight explanatory variables at three cays of Cuba (Chapter 3).

## 2. Characterize the trophic niche of the Cuban larids during the breeding season

The characterization of the trophic niche (ranges, breadth, overlap) can contribute to the analysis of species vulnerabilities according to their food requirements and foraging sites. For seabirds, this can also indicate the risk level of contamination at sea, considering that trophic generalists and foragers over large areas are more likely to ingest contaminated prey. In addition, knowledge of seabird trophic patterns could help predict possible impacts on seabirds due to ocean anomalies (*e.g.*, sea surface temperature rise, ocean chemical changes). Thus, assessing the trophic niche can be useful to identify and conserve the feeding areas of the larids that breed in Cuba. This would contribute to the priority of strengthening the conservation of foraging habitats of Caribbean seabirds (Bradley & Norton, 2009). The analysis of stable isotopes of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  can offer an initial perspective on basic aspects of the trophic ecology of Cuban larids.

Chapters 4 and 5 address this objective. In general, the trophic niche was investigated by stable isotope analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Stable isotope analysis is one of the most widely used biochemical methods for studying the trophic ecology and movements of birds (*e.g.* Hobson 1990; Cherel *et al.*, 2000; Barrett *et al.* 2007; Meier *et al.* 2017; Ausems *et al.* 2020). This technique is based on the natural variation of the proportions of stable isotopes of several chemical elements, where proportions of heavier isotopes experience modifications relative to lighter forms depending on differences in rate of metabolic reactions (Inger & Bearhop, 2008; Dunlop, 2011).  $\delta^{15}\text{N}$  values allow to infer the trophic level of organisms based on the gradual and predictable increase that occurs during trophic transfer (Barrett *et al.*, 2007; Layman *et al.*, 2007; Ramos *et al.*, 2020). Thus, consumers show higher values of  $\delta^{15}\text{N}$  than their prey (Forero & Hobson, 2003). Common applications of  $\delta^{13}\text{C}$  have been the description of foraging areas and sources of available prey (Barrett *et al.*, 2007; Hong *et al.*, 2019; Ausems *et al.*, 2020).

These are based on the natural isotopic variation of this compound among primary producers with different photosynthetic types, which leads to the existence of gradients in several combinations of primary productivity sources (marine vs terrestrial, benthic vs pelagic, neritic vs oceanic) (Quillfeldt *et al.*, 2005; Hong *et al.*, 2019; Ramos *et al.*, 2020). The isotopic niche approach (Newsome *et al.*, 2007) was used as a proxy of the trophic niche to assess the trophic plasticity of breeding species.

In Chapter 4 we used the stable isotopes values and niches ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of five Laridae species at two breeding locations in Cuba to assess the intraspecific variations and interspecific overlap of the isotopic niches from data on chicks' down and feathers. Down samples reflected female trophic regime before laying, while feather samples integrated the trophic regime of chicks provided by the parents during rearing. Chapter 5 deals with the annual isotopic variability of Bridled Tern. The trophic ecology of the Bridled Tern 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 the 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 chapter we assessed the year-round variability of the Bridled Tern isotopic niche ( $\delta^{15}\text{N}$  vs  $\delta^{13}\text{C}$ ) 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 (non-breeding, pre-laying, incubation and rearing).

### 3. Describe the breeding phenology and egg morphology of larids in Cuba

Urgent actions for the conservation of Caribbean seabirds include regular monitoring of important species and nesting sites (in terms of abundance, conservation status, threats) and the implementation of more effective management and conservation actions for these species (Bradley & Norton, 2009). In this sense, knowledge of the breeding phenology of the species is an important aspect. The detailed delimitation of the phenological phases facilitates the design of monitoring schemes aimed at obtaining information of interest while minimizing human disturbance (by census actions, sampling of tissues, food items and ectoparasites) in the breeding colonies. Phenological monitoring also allows to detect reproductive phenomena such as laying asynchrony, which can have repercussions on the overall breeding success of colonies. The morphometric characteristics of the eggs could also be useful to evaluate this phenomenon and thus enhance specific management actions to improve the success of late broods. Lastly, the design of a standardized protocol for monitoring the reproduction of seabirds, such as larids, can be very useful for the optimization of resources in countries with logistical and economic limitations, such as Cuba. The description of the breeding phenology of the species can contribute substantially to this end.

These objectives are the object of Chapter 6. Weekly field sampling and camera trapping were carried out to describe the breeding phenological patterns of the larid species. From the phenological phases identified, early and late laying times were detected in some species studied. This mismatch in laying causes the phenomenon of intraseasonal laying asynchrony

(*e.g.* Dobson *et al.*, 2017; Moiron *et al.*, 2020) and has been little studied in general. However, it has been documented that the eggs corresponding to both clutches tend to show remarkable differences, leading to larger probabilities of success in the case of the earliest (*e.g.* Bridge *et al.*, 2007; Fernández & Reboreda, 2008). Thus, applying the principles of digital image processing and geometric morphometry, the morphometry of early and late eggs was characterized from several variables obtained from standardized photos, in order to later compare both types of eggs per species. This approach made it possible to evaluate the potential of larids eggs to reflect laying asynchrony, in addition to reducing the manipulation for recording morphometric variables.

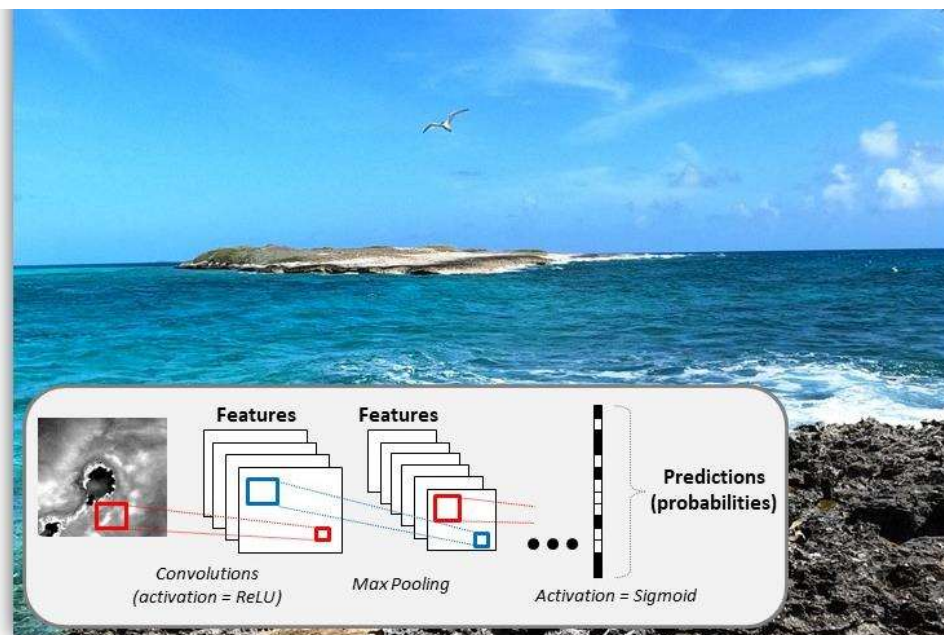
#### 4. Assess the prioritized areas for the conservation of larid breeding colonies in Cuba based on current and future development plans

The conservation of seabirds in Cuba and the Caribbean is a challenge. The main threats to breeding colonies referred to by Bradley & Norton (2009) are summarized in the effects of climate change and anthropogenic activity. Added to this is the weak (and often ineffective) coverage of MPAs in areas of importance to Caribbean seabirds. The uncertainty about the coverage degree offered by the Cuban MPAs system to the breeding areas (including both nesting and foraging zones) of the larids and the continuous need to update conservation policies require novel tools that support decision-making. Besides, conservation approaches in Cuba, and the Caribbean in general, have to consider the effects of two of the region's key socioeconomic activities: fisheries and marine-coastal tourism. Therefore, the identification of priority areas for the conservation of breeding seabirds in countries like Cuba must be based on the principle of accumulation of impacts. Thus, it is possible to improve the efficiency of the management and conservation of protected areas of importance for these birds, and promote the development of sustainable nature tourism; both actions considered as priorities for the region (Bradley & Norton, 2009).

Chapter 7 addresses this objective from the perspective of conservation based on human disturbance accumulation. In this chapter, were implemented systematic reserve site selection algorithms to identify priority conservation areas for the breeding habitats of larids in Cuba considering four of the more important human pressures: fishing, wind farms, coastal tourism and nightlight pollution. The global cost function used to this is a weighted sum of these human pressures. Several conservation scenarios were tested by setting three protection targets for the considered conservation features (*e.g.* number of colonies, breeding habitat suitability), as well as different relative weights of the human pressures in the global cost function. A future conservation scenario was also modeled taking into account the wind farms development plan of Cuba. Modeled areas were compared with the existing marine protected areas to highlight shortages and conservation needs under the current development plans in Cuba.

## Chapter 2:

### Machine and deep learning approaches to understand and predict habitat suitability for seabird breeding



#### Associated publication

Garcia-Quintas A., Roy A., Barbraud C., Demarcq H., Denis D. & Lanco Bertrand S. (*In Rev.*) Machine and deep learning approaches to understand and predict habitat suitability for seabird breeding.

## **2.1 Introduction**

The quality of environment in breeding habitat may greatly affect animal fitness (Danchin *et al.*, 1998). Thus, individuals are under strong selective pressures to select optimal breeding habitats (Orians & Wittenberger, 1991; Piper, 2011). This complex selection process involves environmental conditions over a large range of spatial scales and rely on a hierarchical and sequential decision making by animals (Block & Brennan, 1993). In seabirds, individuals gather information on habitat quality (geographical, physical, biological conditions; Doligez *et al.*, 2002) over a range of spatial scales through prospective movements before breeding (Kristan III, 2006; Ponchon *et al.*, 2013).

Several factors have been suggested for explaining how seabirds chose a place to breed: geographical features of the nesting area (area, spatial isolation) (Greer *et al.*, 1988; Orians & Wittenberger, 1991); vegetation characteristics (coverage, height, density) (Muzaffar *et al.*, 2015; Raynor *et al.*, 2012); climate variability (temperature, rainfall, wind) (Córdoba-Córdoba *et al.*, 2010; Muzaffar *et al.*, 2015); and socio-ecological factors (competition, territoriality, predation pressure, fidelity to the breeding site, group cohesion, information exchange between individuals, colony recruitment, previous breeding experience) (Córdoba-Córdoba *et al.*, 2010; García Borboroglu & Yorio, 2007; Greer *et al.*, 1988). More recently, the development of the use of biologging electronic devices provided information on the type of marine habitats seabirds use to forage during the breeding period (Neumann *et al.*, 2018; Wakefield *et al.*, 2011). A range of oceanographic conditions surrounding the nesting sites may also be assessed by seabirds when selecting a place to nest: water masses characteristics (temperature, salinity), bathymetry and productivity-related variables (chlorophyll-*a* concentration, distance to food sources, prey availability and abundance). In particular, water mass properties and zooplankton abundance have been shown as important factors for this selection process in boobies and auklets (Oppel *et al.*, 2015; Sorensen *et al.*, 2009).

Existing studies on breeding habitat selection by seabirds are mostly focusing either on terrestrial habitats, where nests and colonies are installed, or on the surrounding marine areas, that birds use to forage during the breeding (*e.g.* García Borboroglu & Yorio, 2007; Raynor *et al.*, 2012). Also, most of these studies focused on a single spatial scale of analysis and were often species or colony specific. More integrative (over land and seascapes), multi-specific and multi-scale approaches should improve our understanding of the breeding habitat selection process by seabirds. In addition to these existing limitations, seabird habitat selection in the tropics is much less understood than that of temperate and polar species. In tropical waters, primary productivity is generally low and seasonally stable compared to the cooler waters of polar and temperate regions (Hockey & Wilson, 2003; Jaquemet *et al.*, 2008). One might therefore expect key factors for habitat selection to differ between tropical, temperate or polar seabirds, and one could hypothesize that tropical seabirds are comparatively more influenced by terrestrial than by marine features.

Furthermore, many tropical regions lack a full and regular inventory of seabirds' breeding sites due to economical and logistical constrains, as well as the scarcity of qualified human resources. For instance, Laridae (gulls, terns and skimmers; Winkler *et al.*, 2020) in Cuba are the most

abundant seabird group with 25 species recorded (Navarro, 2021), 36% of them breeding in the archipelago (Jiménez *et al.*, 2009). However, information on their colonies is presently very limited: scarce records of sites, species, number of breeding pairs, and basic habitat features and breeding parameters (*e.g.* Acosta *et al.*, 2022; Jiménez *et al.*, 2009). In particular, the most important environmental variables affecting breeding habitat selection remain poorly known. In order to prioritize the areas to be monitored, an important prerequisite is to predict potential breeding sites as well as to identify the main drivers of breeding habitat selection at the scale of the entire archipelago. Considering both terrestrial and marine areas should provide a more realistic and eco-functional approach to predict tropical seabirds' breeding sites.

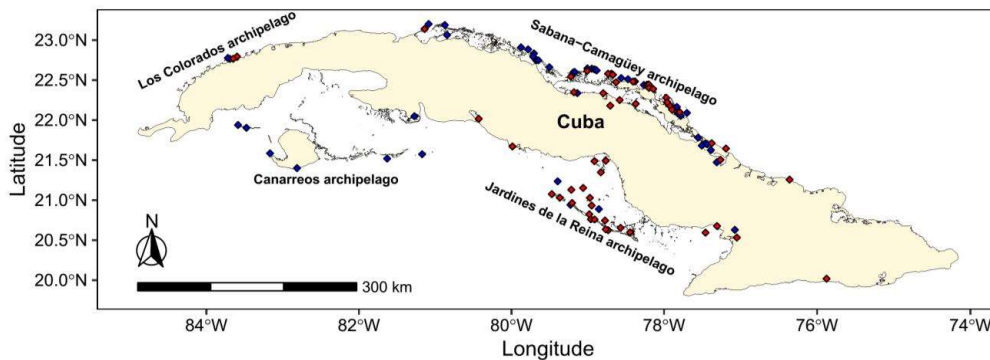
Machine learning is a family of statistical tools that aims to learn statistical relationships from data (Fincham *et al.*, 2020; Olier *et al.*, 2021). Among the most popular models are the neural networks (such as Convolutional Neural Networks (CNN)), and Random Forest (RF). CNNs have become a state-of-the-art approach in the field of computer vision and remote sensing (Ghanbari *et al.*, 2021; Ma *et al.*, 2019). CNNs are composed of multiple layers of processing units which can learn from complex features and represent data with a high level of abstraction at multiple scales. They are known for their outstanding ability to segment and classify images within end-to-end learning framework, *i.e.* without requiring any preliminary feature engineering (Fincham *et al.*, 2020; Kattenborn *et al.*, 2021; Ma *et al.*, 2019). RF (Breiman, 2001) is highlighted for its robustness to heterogeneous predictors, its high accuracy (Ma *et al.*, 2019) and its ability to provide a contribution level or importance of each covariate. CNNs usually outperform RFs for classification and prediction purposes (Kattenborn *et al.*, 2021; Mahdianpari *et al.*, 2018). Yet, an important advantage of RFs over CNNs is their more explicit understanding of the associations between the response variable and its covariates. In the remote sensing research area, CNNs have been identified as potentially attracting for predicting habitat suitability for animals such as birds (*e.g.* Chilson *et al.*, 2019; Su *et al.* 2018). “A picture is worth a thousand words” and a satellite image represents an excellent example of that due to its stack of spectral bands with high potential for habitat description. Su *et al.* (2018) used CNNs (and Support Vector Machine) with satellite images to model the habitat suitability for a migratory geese species. Others, as Chilson *et al.* (2019) and Wang *et al.* (2021), identified birds' habitat elements using radar data and photographic images respectively. Deneu *et al.* (2021) used CNNs to improve species distribution modeling by capturing complex spatial structures of the environment.

Considering the main strengths of CNN (high performance for prediction) and RF (assessing of ecological hypotheses through the covariates contribution), the complementary use of both methods could increase our understanding of the patterns and processes involved in habitat selection and be helpful for developing effective management and conservation strategies. Here, we predict the suitability of macrohabitat for the breeding of Laridae in Cuba (using CNN) and investigate the ecological variables driving their habitat selection (using RF) from satellite data. More precisely we 1) predict the breeding macrohabitat suitability of Laridae at the scale of the entire Cuba archipelago using CNN, and 2) assess the selection of the breeding macrohabitat by these seabirds considering the contribution of landscape and seascape covariates, at different spatial scales, using RFs.

## 2.2 Materials and Methods

### 2.2.1 Study area

This study focuses on the marine coastal ecosystems of the Cuban archipelago (Fig. 2.1). Cuba is the largest Caribbean island (length = 1256.2 km, maximal width = 191 km) and includes four insular groups (Los Colorados, Sabana-Camagüey, Canarreos and Jardines de la Reina) featuring > 1600 cays (small, low-elevation, sandy islands on the surface of the coral reef) and islets with large variation in relief, geology and landscapes. Climate is tropical hot and seasonally wet with marine influence and semi-continental traits (www.insmet.cu). Annual mean temperature varies between 24°C in the plains of the main island and >34°C at the eastern coasts. Mean relative humidity in the island is high ( $\approx 82-90\%$ ) and mean annual precipitation  $\approx 1375$  mm. Daily weather variations are more important between November-April while the weather is more stable during May-October due to the influence of a North Atlantic anticyclone (www.insmet.cu). The mean sea surface temperature over the continental shelf varies from  $\sim 23^\circ\text{C}$  to  $28^\circ\text{C}$  in January and from  $\sim 29^\circ\text{C}$  to  $32^\circ\text{C}$  in September, from North to South, with the largest spatial gradients at the vicinity of the shelf break. The mean chlorophyll-a varies from  $\sim 0.5$  to  $>10$   $\text{mg}\cdot\text{m}^{-3}$  with the largest values observed between the coast and the northern islands as well as in the Southwest region, with moderate seasonal variations.



**Figure 2.1.** Map of the study area and the sites used to train and validate the modelling of the breeding macrohabitat selection patterns of nine Laridae species. Blue diamonds = breeding sites, red diamonds = non-breeding sites.

### 2.2.2 Breeding and available sites

We compiled and filtered (deletion of duplicates, erroneous and imprecise data about species identification, location of colonies and date of breeding) all available informations on observed breeding sites of Laridae (*i.e.* cay, islet or coastal site) from scientific publications, books, thesis, project reports and unpublished data. A database was built with the names and spatial coordinates of the 49 reported breeding sites (Fig. 2.1), years of observation, breeding species and information sources (Annex 1). Observed breeding species of Laridae were laughing gull *Leucophaeus atricilla* (LAGU), brown noddy *Anous stolidus* (BRNO), sooty tern *Onychoprion fuscatus* (SOTE), bridled tern *Onychoprion anaethetus* (BRTE), least tern *Sternula antillarum*



(LETE), gull-billed tern *Gelochelidon nilotica* (GBTE), roseate tern *Sterna dougallii* (ROST), royal tern *Thalasseus maximus* (ROYT) and sandwich tern *Thalasseus sandvicensis* (SATE). Breeding records of common tern *Sterna hirundo* were treated as ROST due to the misidentification of these species' colonies (Navarro, 2021; Nisbet, 2020). Additionally, we selected (non-randomly) 52 sites distributed along the coast of Cuba where none of the nine species was observed breeding in 2020 (Fig. 2.1, Annex 1). These non-breeding sites represented the potential macrohabitat available. Both terrestrial and marine features surrounding the observed breeding sites were considered for predicting suitable breeding macrohabitats.

### **2.2.3 Prediction of breeding macrohabitat suitability**

#### **2.2.3.1 Data acquisition and formatting based on satellite images**

For each breeding site available we extracted satellite imagery of Landsat 5 and 7 from EOS Data Analytics platform. The date of the image was matched to the year of the breeding colony presence record, and to 2020 for non-breeding sites. Several images were associated to each site (depending on availability) to ensure a good representation of the natural variability during the breeding period (May to August) and to reduce the influence of clouds in some images. In some cases, we incorporated images of both months of April and September (climatology similar to the May-August period) when none was available from May to August of the current year. In total, we selected 136 satellite images describing the conditions of the study sites (Annex 2).

We then resized the Landsat images into scenes (9.0 x 9.0 km square areas centered on the sites) and standardized them through the “Dark Subtraction” (based on the bands minimum digital number) to apply atmospheric scattering corrections to the imagery data and “SLC Gap-Filled” correction for Landsat 7 imagery since 31 May 2003. In the end, GeoTIFF files (299 x 299 pixels, 30 m-spatial resolution) were created for all channels, except panchromatic and thermal because these do not match between Landsat satellites. The definition of scene size followed a balanced criterion: sufficiently large image size that included land and sea components, and sufficiently small to minimize the inclusion of other breeding and available sites in the same image scene (which would affect the prediction quality). We organized the data into two datasets considering the quality of scene images related with cloud cover (Annex 3) to control for cloud-related confounding effects. We randomly mixed the images database of both types of sites (*i.e.* with and without breeding colonies) and then split them into two groups containing 70% (training) and 30% (validation) of the data (Annex 3) for the building and selection of the best CNN.

Satellite images from 2021 at 12 breeding and 52 non-breeding sites (verified as such that year) were used as test dataset to assess the predictive performance of the CNN. For predicting breeding macrohabitat suitability, we applied the same preprocessing to Landsat 7 images of 2021 (Annex 2) that covered the entire Cuban archipelago. A mosaic was built with these images, masking mainland to retain only the marine-coastal ecosystems up to the insular shelf. Images with open water only or predominance of land of the main two islands (Cuba and

Juventud) were excluded since they were irrelevant to Laridae breeding (Jimenez *et al.*, 2009). Finally, this mosaic image was gridded into 793 scenes (63805.5 km<sup>2</sup>) with the same format and structure than train and validation datasets. Satellite images were processed using the ENVI 4.7 (ITT VIS Inc) software.

### **2.2.3.2 CNN implementation**

A CNN architecture is typically composed by multiple layers of processing units where two main processes occur: convolution and pooling. During convolutions several filters are applied to extract relevant features of data that will be used for calculating the matches in the testing phase. Pooling operations capture large images and reduces the parameters to preserve important information. Kattenborn *et al.* (2021) and Krishna & Kalluri (2019) offer more details about architectures, parameters and functions of CNNs. Here, we use a CNN with three consecutive layers of convolutions and max pooling, followed by a dense network. Finally, the last layer consists in a sigmoid activation so that the output of the network is a value between 0 and 1. This CNN aims therefore to ingest an image of 299 x 299 pixels with the selected channels (Annex 3) as input and to output the probability of the described habitat to be suitable for breeding seabirds.

Parameters were finally estimated using an Adam optimizer and minimizing a “Sparse categorical crossentropy” loss. In order to prevent overfitting, we also added a L2 regularizer, a Deep Learning technique to get better generalization and predictive properties (Kussul *et al.*, 2017). Finally, models were trained using the ‘training dataset’, and selected when minimizing accuracy score over the ‘validation dataset’. This analysis was implemented with the keras R package (v. 2.6.1) (Kalinowski *et al.*, 2021).

We performed this training procedure for distinct parameters and the best CNN (better performance and lowest loss in validation and test datasets) was used to predict the breeding macrohabitat suitability using the satellite images of 2021 along all marine-coastal ecosystems of the archipelago. The most frequently reported metrics, Overall Accuracy, Precision, Recall and F1-score (see confusion matrix, Annex 4) were used to assess CNN performance. All analysis was implemented in R 4.1.1 (R Core Team, 2021).

## **2.2.4 Assessing the breeding macrohabitat selection pattern**

### **2.2.4.1 Physical and geographical covariates**

Because of the absence of information on the foraging ranges of Cuban seabirds during their breeding period, we did a bibliographic compilation of all information available on the same species observed elsewhere during breeding, from polar to tropical zones. From this review we estimated the potential maximum foraging ranges during breeding for each studied species (Annex 5). Then, we defined three spatial scales (radius of 10, 50 and 100 km from the breeding site) approximately corresponding to the estimated foraging ranges of our study species, and computed several oceanographic characteristics at each spatial scale.

Twelve potentially important features for the establishment of Laridae breeding colonies, described through 18 metrics, were considered at the defined spatial scales (Table 2.1): 11 of them described the conditions of the nesting landscape, and seven of them described the conditions of the surrounding seascape. The variables were measured at the date of the colony observation, and in 2020 for the non-breeding sites.

Using the Landviewer product of the EOS Data Analytics platform (<https://eos.com>), we calculated the Normalized Difference Water (Gao, 1996) and Vegetation (Rouse *et al.*, 1973) Indexes (NDWI and NDVI respectively) from satellite images of the Landsat series. Dates of images ranged between May and August, matching the breeding season of Laridae in Cuba (Jimenez *et al.*, 2009). Both spectral indices vary between -1 and 1 with higher numbers corresponding to higher humidity (NDWI) or green vegetation (NDVI). Based on the NDWI we then calculated the drought emerged areas (NDWI range = -1 to 0.2) and the percentage of non-flooding cover (NDWI range = -1 to 0). The NDVI allowed to quantify the total (NDVI range = 0.2 to 1) moderate and dense vegetation covers (NDVI range = 0.4 to 1). Thus, the area, non-flooding zone cover and vegetal covers of each nesting site were computed from the satellites images. The perimeter was calculated after vectorization of the imagery scenes.

**Table 2.1.** Potentially important variables for Laridae breeding macrohabitat selection (breeding site, *i.e.* cay, islet or coastal site) in Cuba.

Feature	Variable	Unit	Ecological meaning
Site extent	Area	km <sup>2</sup>	Available space for nests establishment
Site perimeter	Perimeter	km	Indicator of the availability of potential coastal zones for breeding
Site shape	Shape index based on perimeter/area ratio	-	Related to geographical features ( <i>e.g.</i> peninsulas) that could be important for breeding
Isolation degree	Minimum distance from the colony to the nearest cay/islet	km	Indicator of accessibility for predators and other disturbance sources
	Minimum distance from the colony to the nearest main island (Cuba or Isla de la Juventud) of the archipelago	km	Indicator of accessibility for predators and high disturbance sources (higher risk)
	Cays/islets number within 10, 50 and 100 km of the colony	-	Indicator of the number of potential sources (at different spatial scales) of predators, alien species and other disturbances that could affect the colonies
Terrain	Non-flooding zone cover	%	Suitability of the locality for colony establishment based on flooding risk

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Vegetation	Vegetal cover <sub>total</sub>	%	Surface occupied by plants (species-specific suitability for breeding, Burger & Gochfeld, 1981; Raynor <i>et al.</i> , 2012)
	Vegetal cover <sub>moderate+dense</sub>	%	Surface occupied by moderate to dense vegetation that could affect the establishment of colonies (some Laridae tend to avoid high vegetation cover while others are attracted, Bukacinska & Bukacinsky, 1993; Burger & Gochfeld, 1986)
Oceanographic	Sea surface temperature within 10, 50 and 100 km radius of the colony	°C	Reflects thermal conditions that influence primary productivity and prey availability at different foraging ranges
Bathymetric	Minimum distance to the 200-m isobath	km	Indicates the limit of the insular shelf in Cuba and therefore is a proxy for suitable foraging areas for most Laridae (Schreiber & Burger, 2002).
Phytoplanktonic biomass	Chlorophyll <i>a</i> concentration at sea surface within 10, 50 and 100 km radius of the colony	mg m <sup>-3</sup>	Proxy for phytoplanktonic biomass, primary productivity and prey availability at different foraging ranges

We calculated the index of shape complexity for islets and cays (Hu *et al.*, 2011) as  $SI = P / [2 * (\pi * A)^{1/2}]$  where SI = shape index, P = perimeter and A = area of the site. A SI value of 1 indicates an islet or cay with a perfect circular shape and SI increases as the shape becomes more irregular and complex. Isolation variables (minimum distances to Cuba/Isla de la Juventud (IJ) and to nearest cay, and cays/islets number at the three spatial scales) were estimated using Google Earth Pro 7.3.3 software. Minimum distances to the 200-m isobath were measured using a bathymetric shapefile of the exclusive economic zone of Cuba (using information both from GEBCO and Cuban research agencies databases).

Sea surface temperature (SST) and surface chlorophyll *a* concentration (Chl *a*) around the sites were obtained at a spatial resolution of 1 km from level-2 MODIS-Aqua satellite data (<https://oceancolor.gsfc.nasa.gov/data/aqua/>) after sampling and spatial reprojection of the data. For both variables we averaged the monthly values between May and August of the year corresponding to the last register of each breeding colony and for 2020 for available sites. Nevertheless, due to the absence of logistical support for a systematic monitoring of these variables before 2002, and given the small interannual variability of both variables in Cuba, data for breeding colonies observed in that period were estimated from the mean of 2002-2021 period for the same months (Annex 6). A summary of the satellite images used for the study is provided in Annex 2.

The eldest colony record, at Rincón del Guanál (Annex 1), was excluded from the study as we could not obtain the same variables from Landsat 4 satellite (fewer bands than Landsat 5 and 7). Breeding macrohabitat was characterized considering both mixed and monospecific colonies.

#### **2.2.4.2 RF implementation and contribution of variables**

Variables were compared among sites using Mann-Whitney U tests considering significance at  $p < 0.01$ . Breeding macrohabitat selection was analyzed through random classification forests (RFs) models considering the measured variables at three spatial scales. Similar to CNN, we mixed and splitted the data to create the training and validation datasets (70 vs 30% proportions) for the building and selection of the best RF. The same training and validation datasets were used in all RFs to compare their classification performances. We implemented three RFs, one that processed physical-geographical variables registered within a radius of 100 km from the breeding colony (RF\_100), a second within a 50 km radius (RF\_50) and a third one within a 10 km radius (RF\_10). For each RF type we used the 10 best runs in order to get an average and variance of model performance.

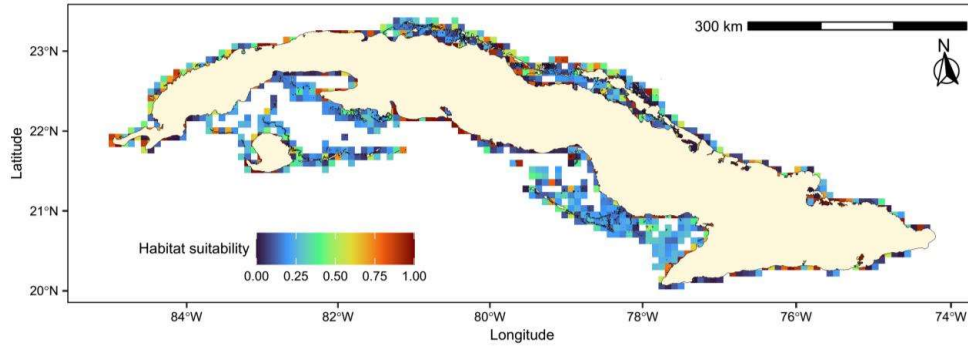
Same performance metrics than CNN (Annex 4) were used to assess the training, validation and test of RFs. Variables contributions were calculated from the mean decreasing Gini index (values are directly proportional to variable importance) derived from the RF with better performance. The randomForest R package (v. 4.6–14) (Breiman *et al.*, 2018) was used to this analysis.

### **2.3 Results**

#### **2.3.1 Prediction of macrohabitats breeding suitability**

In general, the performance of CNN exceeded significantly that of RF\_50 and RF\_100, with indicators values  $\geq 80.0\%$  for the validation datasets (Table 2.2, Tables S6-S7). Image quality (according to cloud cover) had no significant consequence on the classification power of CNNs (F1-score validation = 85.7 and 84.6% for CNNs that used all and best images, respectively; Annex 3). We thus worked with the architecture that used all images. Based on the test dataset, the CNN exhibited good performance test indicators with accuracy = 79.7%, precision = 91.5%, recall = 82.7% and F1-score = 86.9%.

When used for predicting over the entire Cuba archipelago, the CNN estimated 32 184, 12 069, 6 598 and 12 954 km<sup>2</sup> of suitable habitat for breeding within 0-0.25, 0.26-0.50, 0.51-0.75 and 0.76-1 probability ranges, respectively (Fig. 2.2). Thus, the probability ranges  $>0.50$  and  $>0.75$  covered 30.6% and 20.3% of the predicted area, respectively. The best areas (high suitability scores) tended to be concentrated in three general types of ecosystems: 1) remote cays/reef islets of all subarchipelagos (Fig. 2.1, with Jardines de la Reina archipelago under-represented), 2) coastal zones with sand, rocks or interior lagoons and 3) interior of bays, gulfs and swamps that contained small islets and sand banks (Fig. 2.2). The southern region of Cuba had less suitable breeding macrohabitats than the northern region (Fig. 2.2).



**Figure 2.2.** CNN prediction of macrohabitat suitability for the breeding of Laridae in Cuba, for the 2021 breeding season, using Landsat images.

### 2.3.2 Breeding macrohabitat selection and importance of covariates

The general statistics (median, quartiles) of most covariates were quite similar between breeding and non-breeding sites (Fig. 2.3). Only SST at the three spatial scales and Chl *a* at 50 and 100 km radii exhibited significant differences: SST was lower and Chl *a* higher at breeding sites (Fig. 2.3). Additionally, breeding sites tended to have a smaller number of cays/islets within 10 km compared to non-breeding sites ( $p = 0.01$ , Fig. 2.3). Performance metrics for RF\_50 (200 trees, four variables by split) and RF\_100 (300 trees, four variables by split) were very similar and outperformed RF\_10 (150 trees, three variables by split) (Table 2.2, Tables S6-S7). For RF\_100, SST had the highest contribution to discriminate breeding from non-breeding sites (Fig. 2.4). A second group of covariates with lower contribution included isolation-related variables (number cays/islets within 10 and 50 km from colonies) and Chl *a* within 100 and 50 km radius (Fig. 2.4). Remaining variables exhibited relatively low contributions and non-flooding area cover had the lowest importance (Fig. 2.4).

**Table 2.2.** Training and validation performance (in %) of a convolutional neural network (CNN) and three random forest (RF) models used to respectively predict breeding site suitability and assess breeding site (macrohabitat) selection by Laridae in Cuba. RF\_10, RF\_50 and RF\_100 indicate models that used physical-geographical variables within 10, 50 and 100 km radius from localities, respectively; CNN = model that used Landsat images with 9 x 9 km square areas. Statistics indicate the mean ( $\pm$  standard deviation) of the best 10 runs for each RF.

Model type	Training accuracy	Training F1-score	By image				By site			
			Validation accuracy	Validation precision	Validation recall	Validation F1-score	Validation accuracy	Validation precision	Validation recall	Validation F1-score
CNN	98.4	98.7	75.7	75.5	76.9	76.2	86.7	80.0	92.3	85.7
RF_10	72.0 $\pm$ 2.5	71.2 $\pm$ 2.3	-	-	-	-	70.0 $\pm$ 1.6	67.4 $\pm$ 2.0	69.3 $\pm$ 3.4	68.3 $\pm$ 1.9
RF_50	81.7 $\pm$ 2.4	80.7 $\pm$ 2.4	-	-	-	-	77.3 $\pm$ 2.1	77.8 $\pm$ 3.4	72.1 $\pm$ 2.3	74.8 $\pm$ 2.0
RF_100	85.1 $\pm$ 1.1	84.5 $\pm$ 1.4	-	-	-	-	76.7 $\pm$ 0 <sup>a</sup>	76.9 $\pm$ 0 <sup>a</sup>	71.4 $\pm$ 0 <sup>a</sup>	74.1 $\pm$ 0 <sup>a</sup>

<sup>a</sup> There was no variability in the indicator.

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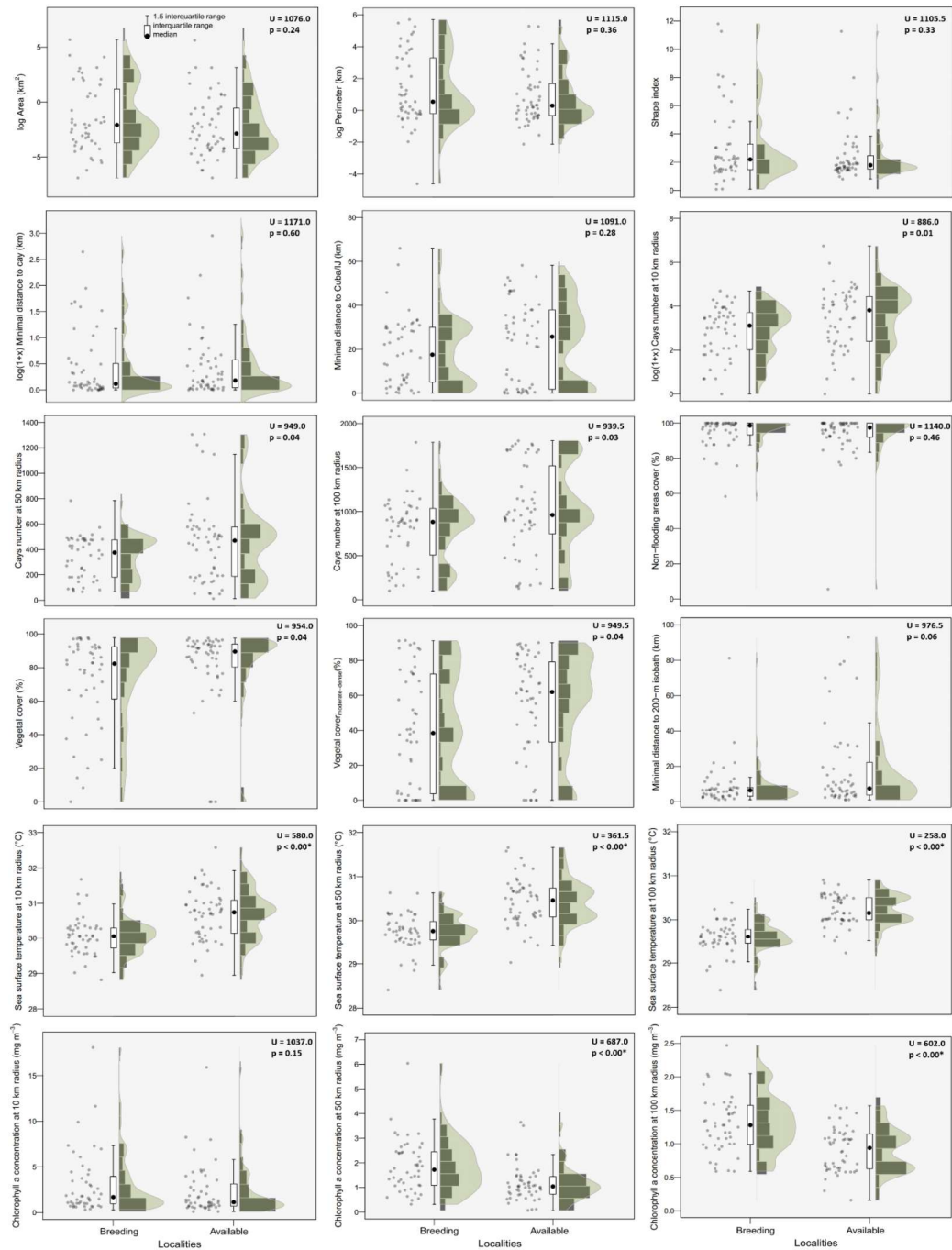
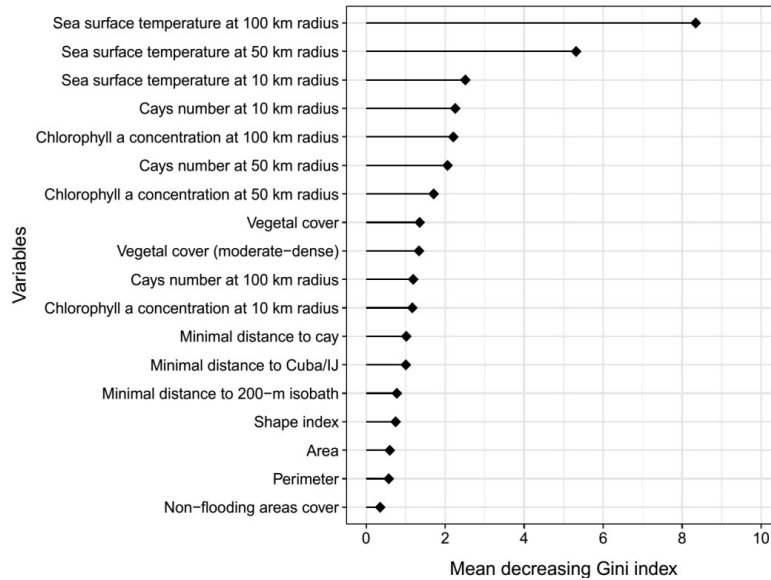


Figure 2.3. Comparison of 18 physical-geographical variables corresponding to 48 breeding and 52 non-breeding sites (available macrohabitats) for Laridae in Cuba. Some variables were log-transformed for visualization purpose exclusively. \*= Significant differences.



**Figure 2.4.** Contribution of marine and terrestrial environmental features to the breeding macrohabitat selection pattern of Laridae in Cuba based on random classification forests model (corresponding to the spatial scale of 100 km radius from breeding colonies, but includes the nested scales of 10 and 50 km radius).

## 2.4 Discussion

### 2.4.1 Prediction of breeding macrohabitat suitability

Based on CNNs we provided a map of macrohabitats suitability over the whole Cuban archipelago for the year 2021. Predictions were based on physical-geographical suitability of marine-coastal ecosystems and it does not imply *per se* the existence of breeding colonies at areas with higher habitat suitability. However, these areas represent the localization of sites with favorable conditions for breeding in 2021 and thus constitute alternatives or additional breeding sites for Laridae around Cuba.

The most suitable breeding sites (probability range >0.50) for Laridae exhibited a scattered general distribution along the coasts of Cuba, although a slightly higher concentration of sites occurred in the northern marine-coastal ecosystems. Nevertheless, areas of Los Colorados, Canarreos and Sabana-Camagüey archipelagos showed higher number of favorable breeding sites acting as potential hotspots for Laridae reproduction (Figs. 2.1 & 2.5). These predictions are relatively consistent with current field knowledge in these areas, and with the location of historical persistent breeding colonies.

In particular, breeding habitats for Laridae such as beaches, rocky platforms and sand banks in distant or difficult-access cays and islets were often true positive predictions. Two of the most scientifically studied regions, the Sabana-Camagüey and Jardines de la Reina archipelagos, had



respectively high and low predicted breeding habitat suitability depicted by CNN, a point confirmed by field observations (Figs. 2.1 & 2.2). Nevertheless, some predicted areas seemed irrelevant for breeding because of the presence of extensive anthropogenic infrastructures (cities, towns, industries) that cause disturbance.

On the other hand, main false negatives of the predictions were located at Mono Grande, Cinco Leguas, Felipe de Barlovento and Las Salinas breeding sites (Annex 1). Prediction scenes (grid cells) containing these breeding sites were not highly different (from a visual interpretation) from the training sites. Then, this suggests the importance of incorporating oceanographic (*e.g.* SST, Chl *a*) or ecological variables (*e.g.* prey availability-related) into the CNN to improve its prediction quality. It is important to point out that the habitat suitability diversity predicted by the model (that addressed all Cuban Laridae) could result from the different species-specific breeding habitats requirements; especially LETE that has a high dynamic and opportunistic behavior to select its breeding sites (this species may change its nesting sites between consecutive breeding seasons depending on the availability of isolated sand bodies). For this reason, even if CNN obtained relevant predictive performance metrics, the prediction map (Fig. 2.2) should be interpreted carefully, and further studies would be required to improve its accuracy. However, the good global quality of the model highlights its potential for application to other species and regions of the world.

#### **2.4.2 Breeding macrohabitat selection pattern**

Simplistic approaches to the study of breeding habitat selection have been criticized decades ago (*e.g.* Burger & Shisler, 1978) as the environment of many animals, such as seabirds, consists in heterogeneous composition of habitat characteristics along several spatial and temporal scales (Danchin *et al.*, 1998). Here, we found that breeding macrohabitat selection by Laridae in Cuba could be partly explained through seascape and landscape features of the breeding sites.

Overall, breeding site (macrohabitat) selection by Laridae was mainly explained by lower SST values within 100 and 50 km from colonies. Thus, we show that SST at larger scales played an important role in Cuban Laridae habitat selection, despite its relative seasonal stability throughout tropical waters (Hockey & Wilson, 2003; Jaquemet *et al.*, 2008). The greater contribution of larger spatial scales for SST probably reflects the role of oceanographic conditions (*e.g.* thermal fronts) at relatively large distances from breeding habitats, coinciding with the foraging range of most species which often exceeds 30 km from colonies (Annex 5). Chl *a* at the same spatial scales was also important, although to a lesser extent, for breeding site selection, highlighting the role of marine productivity for breeding. However, it should be noted that Chl *a* is an index of phytoplanktonic biomass that does not match exactly in space with the maximum of forage fish abundance (*e.g.* Zavalaga *et al.*, 2010).

SST (indirectly) and Chl *a* could be considered as proxies of marine productivity and food availability, and hence key factors for breeding habitat selection by seabirds (Vilchis *et al.*, 2006). However, mismatching patterns between both variables may occur (*e.g.* Zavalaga *et al.*, 2010). In several regions of the world these variables have been shown as having important

effects on seabirds foraging, demography and population dynamics, with generally cooler SST favoring higher Chl *a*, and hence the foraging and breeding success of seabirds (Barbraud *et al.*, 2012; Carroll *et al.*, 2015). The selective pattern of breeding macrohabitat found for Laridae in Cuba is consistent with this general pattern, although the effect of Chl *a* appears lesser than for SST (Annex 6).

Similar to previous studies (*e.g.* Burger & Gochfeld, 1981; 1986; Greer *et al.*, 1988), areas with moderate to dense vegetation cover were avoided by Laridae for breeding (Fig. 2.3). For seabirds, high cover and dense vegetation cover usually constitutes a barrier to breeding as it limits the visibility and social communication between neighbors at colonies, and hence, may increase predation risk (Bukacinska & Bukacinsky, 1993; Raynor *et al.*, 2012).

### **2.4.3 Complementarity of CNN and RF approaches**

According to our results, prediction of habitat suitability can be successfully obtained by processing satellite images with CNN exclusively. This constitutes a significant advance for habitat ecology studies and expands the applications and perspectives of image analysis via deep learning approaches. Deep architecture of CNNs conveys a high computation cost (Kattenborn *et al.*, 2021; Yuan *et al.*, 2020) but, at the same time its versatility provides a great generalization capacity with a broad applicability in the remote sensing field (Kattenborn *et al.*, 2021; Ma *et al.*, 2019; Mahdianpari *et al.*, 2018). Scene classification with an emphasis on land cover, vegetation and crop types appears as one of the most common applications of CNNs (*e.g.* Kattenborn *et al.*, 2021; Kussul *et al.*, 2017; Mahdianpari *et al.*, 2018). However, these classifications are based on relatively easily distinguishable element classes (*e.g.* water, bare soil, marsh, fen, forest, grassland, paddy rice) and animal habitat selection is a more complex phenomenon.

Our CNN had relatively good performance and predicted the breeding habitat suitability using spectral data of terrestrial and oceanographic elements. After visual inspection of the image mosaic of 2021, the more suitable predicted areas included heterogeneous covers such as sands, marshes, bare soils, terrestrial vegetation and mangroves, and waters with contrasting depths. Yet, our ecological understanding here is limited as we have no explicit indication on the metrics CNNs finally used to maximize prediction quality. Some techniques exist in order to get insight into the metrics automatically extracted by the CNN, such as layer-wise backpropagation or saliency maps. It is however an active field of research, and using these approaches is beyond the scope of this paper. Based on RFs results and statistical analysis, we could yet hypothesize that important features such as vegetation, number of cays/islets but also ocean color (related to Chl *a*) were captured through Landsat spectral data. Additional analysis could help to identify directly from CNNs' layers the main features used to disentangle breeding from non-breeding localities. The CNN performance might be probably increased including SST information at the radius of 100 km (according to the main results of RF) and being trained over larger datasets.

This study illustrates the benefits obtained from a complementary analysis of CNN and RF. Here, RF can be seen as an explicative tool relying on features directly related to our *a priori*

ecological hypotheses, while CNN can act as an evaluative tool in order to assess the relevance of habitat spectral features, as well as an efficient predictive tool producing large scale prediction of habitat suitability in a convenient manner. Moreover, prediction of breeding habitat suitability with CNN should also be systematically updated considering the changing dynamics of marine ecosystems and seabird colonies. Finally, we recommend the exploration of building CNNs that use both spectral and relevant ecological data (identified by RF), to produce finer predictions supported ecologically.

#### **2.4.4 Management and conservation implications from the complementary approach**

The scattered distribution of suitable breeding sites in Cuba offers to Laridae a wide variety of options for colony's establishment, what may allow to dampen the effects of climatic change and anthropogenic pressures. It may also provide flexibility for management agencies as it offers a large number of alternative sites for Laridae conservation in Cuba. Also, possibilities of legal protection of some important breeding colonies (*e.g.* predicted hotspots) increases because of a low risk of spatial overlapping of breeding sites with places of social-economic interests.

From a practical point of view, we recommend a field validation of effective presence of colonies in sites predicted to be highly suitable. This could be done through field surveys at these places constituting a proper way to optimize logistical and economical resources for conservation purposes. Then, confirmed breeding sites could be considered to update the Marine Protected Areas coverage in Cuba, improve the governmental strategy of adaptation to climate change, detect negative effects from natural and anthropogenic causes (McGowan *et al.*, 2013; Perrow *et al.*, 2015) and realize a sustainable use of the marine-coastal ecosystems by humans (tourism, fisheries, industry). An effective conservation of seabirds should be based on species' distribution along space including both colonies establishment places and surrounding waters (Oppel *et al.*, 2018). More precisely, according to the complementary approach CNN-RF, the conservation and management actions for Laridae breeding macrohabitats in Cuba should include areas of the predicted breeding hotspots. Also, oceanic characteristics (SST and Chl *a*) at mesoscale (50-100 km) around cays as well as the coverage degree of dense and moderate vegetation should be considered in future management plans.

### Chapter 3:

## Breeding microhabitat patterns among sympatric tropical larids



#### Associated publication

Garcia-Quintas A., Denis D., Barbraud C. & Lanco Bertrand S. (2023) Breeding microhabitat patterns among sympatric tropical larids. *Marine Ornithology* 51: 97–107.



### **3.1 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 (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).

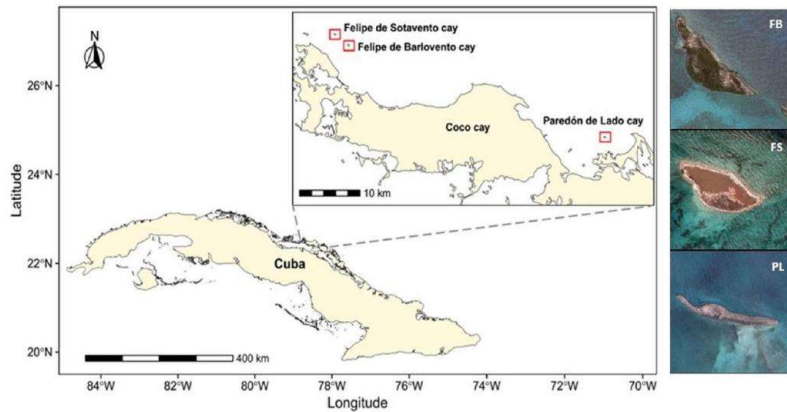
In the West Indies, Cuba is an important seabird breeding region (Bradley & Norton 2009). Laridae (gulls, terns, and skimmers) are the most common type of seabirds in Cuba, with 25 species registered but only nine of which breed within the archipelago (Jiménez *et al.* 2009, Navarro 2021). Ecological 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. 3.1). 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, Garcia-Quintas *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 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.

### 3.2 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. 3.1). 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<sup>-1</sup> prevail year round (Meteorological Station 78339 of the Coastal Ecosystem Research Center, Cayo Coco, Ciego de Ávila, Cuba).



**Figure 3.1.** 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.

These very small cays (< 0.1 km<sup>2</sup>) are at low elevation and have sandy and rocky substrata with sparse vegetation. Plant cover is composed of sandy and rocky coastal vegetation with stands 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).

### **3.2.1 Data collection**

We characterized the nesting sites of five larid species on FB, FS, and PL during the 2021 breeding season (Annex 7A). 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 3.1). 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  $\pm 1$  mm), and horizontal vegetation cover was estimated using a plastic tube with visual fields divided into four (Wallace et al. 1996). NDWI values at nesting sites (previously georeferenced using a handheld GPS unit with a precision of  $\pm 3$  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 (Annex 7A). Environmental variables at the available sites were recorded during 04–06 May 2021 (the pre-laying period) to minimize disturbance at the colonies.

**Table 3.1.** Ecological components measured to assess reproductive microhabitat selection (nesting site) by five species of Larids in three northern cays of Cuba during the 2021 breeding season.

Factors	Variables	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	Minimum distance to cay edge (quantitative)	m	Indicates the potential vulnerability of nesting sites to sea surges
Vegetation	Horizontal vegetation cover (quantitative)	%	Related to the visibility level of the nesting site to predators, to microclimatic conditions, and to potential aggression interactions between neighbors mediated by nest visibility
	Minimum distance to vegetation patch (quantitative)	m	Associated with the use of that resource for the nesting site safety
	Dominant plant species (qualitative)	-	Allows the detection of plant-Laridae associations for nesting if they exist
Exposition level	Horizontal non-vegetation cover (quantitative)	%	Cover originated by any non-vegetal component such as rock and dead wood. Indicates the visibility level of the nesting site to predation and its direct exposition to the sun and rainfall
	Minimum distance to open area (quantitative)	m	Represents a measure of the nesting site shelter (access level) and escape facility of adults facing threats

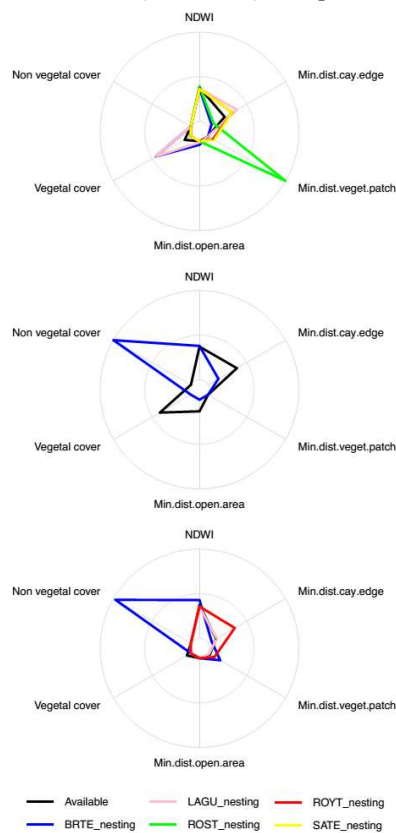
### 3.2.2 Data analysis

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.



### 3.3 Results

Spatial distribution of the larid breeding colonies showed a general tendency toward segregation (Annex 7B). 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 3.2, Figs. 3.2–3.4). 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. 3.2). For this species, overall differences among nesting and available sites were weak (Table 3.3) and mainly explained by the dominant plant species, distance to cay edge, and ground wetness (via NDWI), independent of the study cay (Fig. 3.5).



**Figure 3.2.** 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.area = 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 sandvicencis*.

**Table 3.2.** Quantitative variables describing the breeding microhabitat of five species of larids and available sites in three central-northern cays in Cuba.

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

Table 3.2 (continued)

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

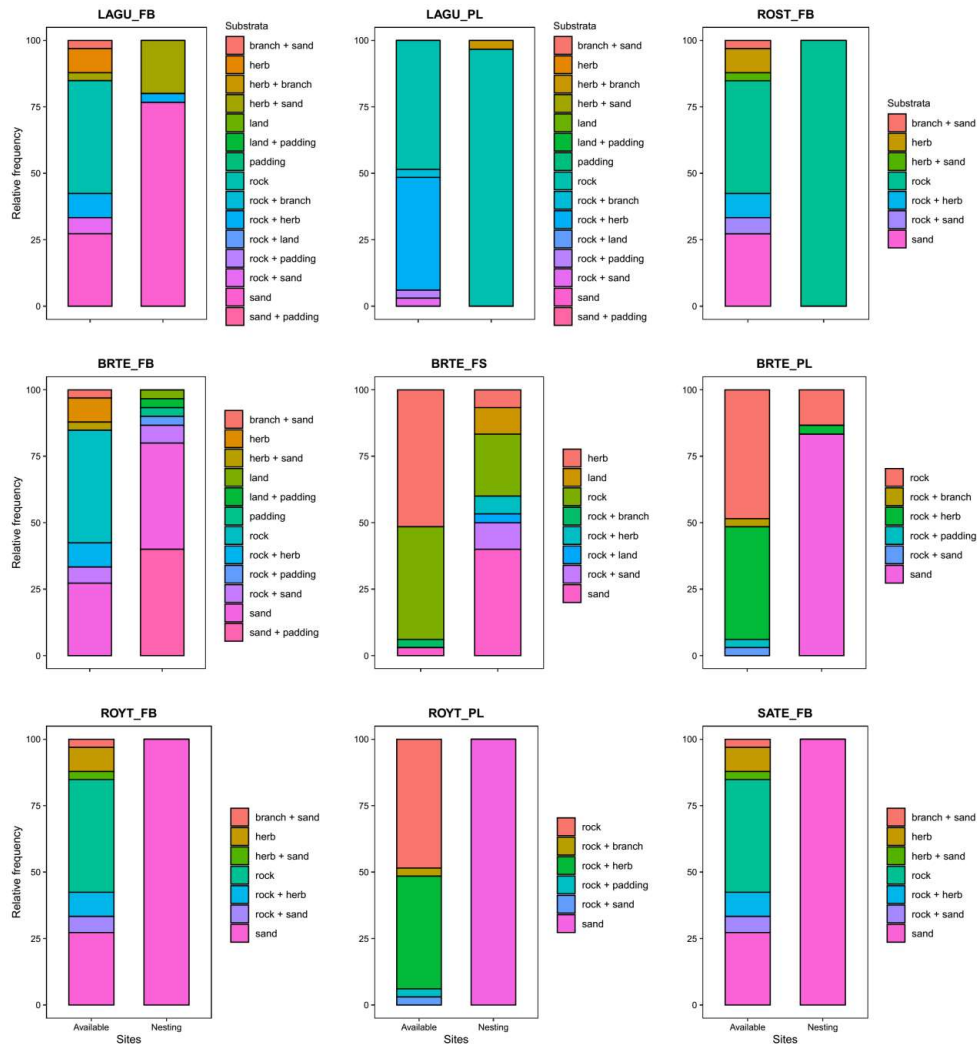
<sup>a</sup> Values are median (quartiles). Distance units are in meters and percentages in %.

<sup>b</sup> 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.

<sup>c</sup> 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.

A very consistent nesting-site selection pattern was found for BRTE (Table 3.3): nesting sites were located on sand, near to cay edges (*i.e.*, the median distance of nesting sites was within the first quartile of distance on available sites), associated with button mangrove, and protected by high non-vegetation cover (mainly by rock; Table 3.2, Figs. 3.2–3.4). The selection pattern was similar among the three studied cays, despite their different landscapes (Fig. 3.2). 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. 3.5).

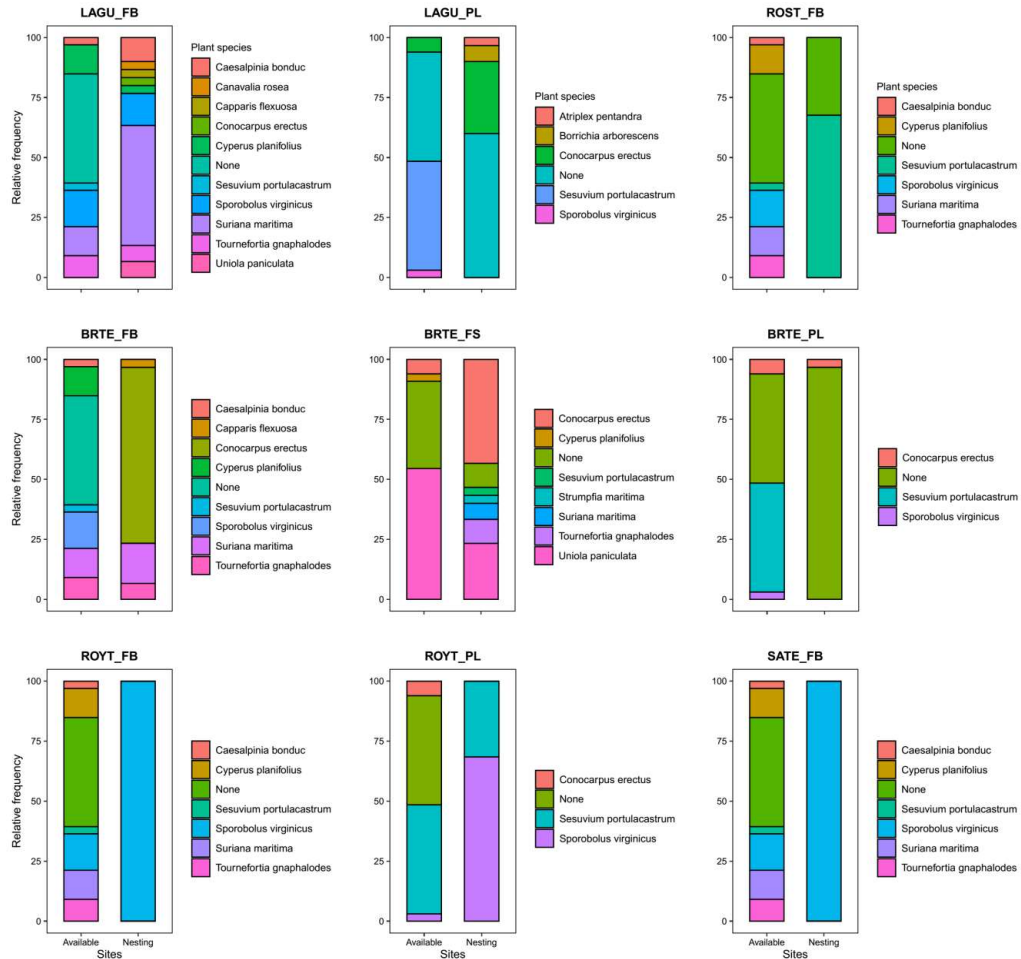
The highly gregarious species ROST, ROYT, and SATE exhibited clear selection patterns (Table 3.3) that differed among species. Nesting-site selection was easy to distinguish with respect to available sites on the cays due to the narrow ranges of values for some variables (Table 3.2, Figs. 3.3–3.4). Breeding microhabitat for ROST was marked by a high distance to vegetation patches, closeness to cay edge, and location above rocky substratum without vegetation cover (Table 3.2, Figs. 3.2–3.4). Minimal distances to vegetation patches and to cay edges were the most important covariates for ROST (Fig. 3.5).



**Figure 3.3.** 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.

Similarly, ROYT and SATE exhibited clear nesting selection patterns that were similar among cays (Table 3.3). 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 3.2, Figs. 3.2–3.4). 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. 3.5). 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. 3.5).



**Figure 3.4.** 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.

### **3.4 Discussion**

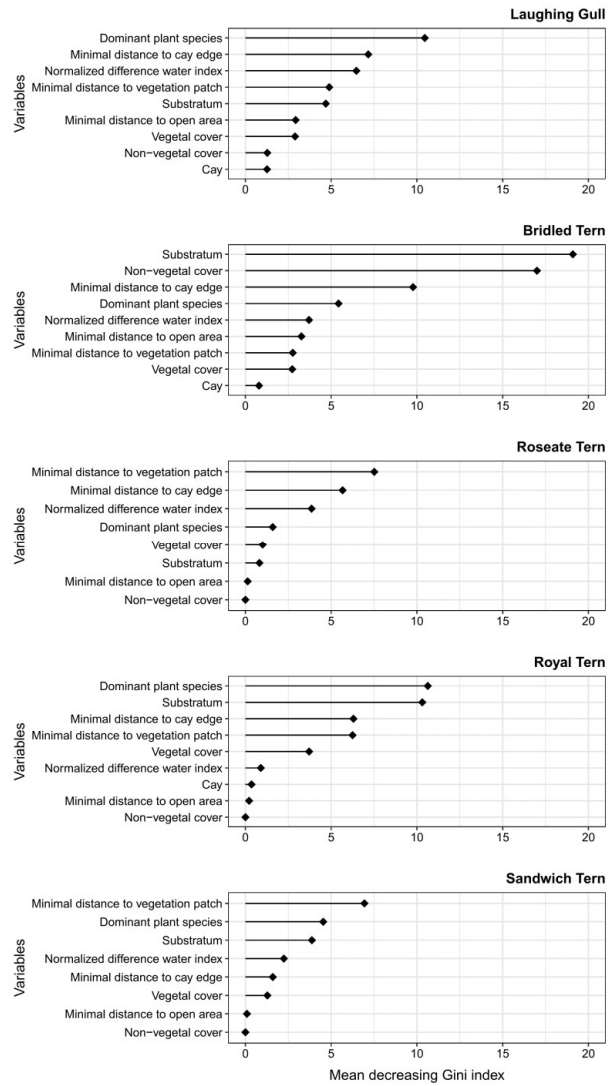
Each of five larid species in the study exhibited contrasting patterns of microhabitat selection, revealing differences in their ecological plasticity. In this sense, LAGU could be considered to be a generalist compared to other larid species. Although social interactions such as nesting-site defense 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.



**Figure 3.5.** 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*.

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 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.

**Table 3.3.** 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<sup>a</sup>.

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	90.32	94.92
Roseate Tern <i>Sterna dougallii</i>	50	2	0	0	100	100	100	100
Royal Tern <i>Thalasseus maximus</i>	50	3	0	0	100	100	100	100
Sandwich Tern <i>Thalasseus sandvicensis</i>	50	2	0	0	100	100	100	100

<sup>a</sup> Performance indicators (Overall Accuracy, Precision, Recall, and F1-scores) are in %.

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 (Bukacińska & Bukacińska 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



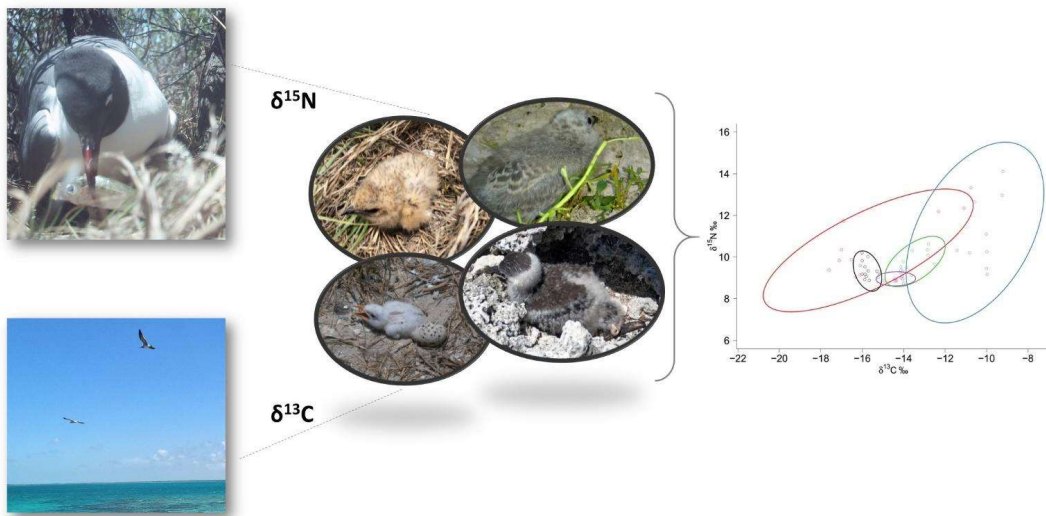
substratum stabilization (herbs) to avoid the risk of eggs rolling and breaking.

Finally, the minimal distance to cay edges represented an important variable for all species except SATE, but with different patterns for each species (Figs. 3.2 & 3.5). 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.

## Chapter 4:

### Multidimensional plasticity of the trophic niche in tropical breeding Laridae



#### Associated publication

Garcia-Quintas A., Bustamante P., Barbraud C., Lorrain A., Denis D. & Lanco Bertrand S. (*In Rev.*) Multidimensional plasticity of the trophic niche in tropical breeding Laridae.



#### **4.1 Introduction**

Most seabird populations display large seasonal changes in foraging and prey consumption patterns. The larger contrast in foraging strategies occur between the non-breeding and breeding periods when seabirds change from a “spatially free” (Ashmole 1963, Labbé *et al.* 2013, Lisnizer & Yorio 2019) to a “central-place” (Ashmole 1963, Gatto *et al.* 2019, Lorentsen *et al.* 2019) foraging strategy. The latter limits the spatial extent breeding seabirds may explore due to the need of regular return to colonies for chick-rearing (Paredes *et al.* 2015, Lamb *et al.* 2017). This leads to changes in the diet compared to the non-breeding season (Barrett *et al.* 2007, Jaquemet *et al.* 2008). Also, the type of prey may differ between adults and chicks at the same period, and between periods (*e.g.* pre-laying and chick-rearing) and years for a same adult (Barrett *et al.* 2007, Jaeger *et al.* 2017).

Those differences in foraging and feeding behaviors may lead to intra and interspecific segregation patterns of the trophic niches (Surman & Wooller 2003, Bolton *et al.* 2019, Gatto *et al.* 2019), what allows reducing the competition level for trophic resources (Oppel *et al.* 2015, Ramos *et al.* 2020). Studies on diet and feeding strategies of seabirds are key to understand their ecology, to detect changes in their behaviors and variations in the state of marine trophic networks (Bost & Le Maho 1993, Barrett *et al.* 2007, Gaglio 2017). The strong predator-prey association exhibited by many seabirds make them good bioindicators of oceanic productivity (Bost & Le Maho 1993) and seasonal or inter-annual changes in food availability (Gaglio *et al.* 2018). As such, used as sentinels of marine ecosystems changes, seabirds may contribute to the development of management plans, marine spatial planning and the design of marine protected areas architectures (Barrett *et al.* 2007, Soanes *et al.* 2016).

Stable isotope analysis is one of the most widely used biochemical method for studying the trophic ecology and spatial behaviour of birds (*e.g.* Hobson 1990, Cherel *et al.* 2000, Barrett *et al.* 2007, Meier *et al.* 2017, Ausems *et al.* 2020). This technique is based on the natural variation of the proportions of stable isotopes of several chemical elements, where proportions of heavier isotopes experience modifications relative to lighter forms depending on differences in rate of metabolic reactions (Inger & Bearhop 2008, Dunlop 2011). The integrated analysis of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopes allows to infer the trophic networks structure and interactions, including top predators as seabirds (Hobson 1990, Labbé *et al.* 2013, Grecian *et al.* 2015). The  $\delta^{15}\text{N}$  values allow to infer the trophic level and diet variety of organisms due to the gradual and predictable increase that occurs during trophic transfers (Barrett *et al.* 2007, Layman *et al.* 2007, Ramos *et al.* 2020). The  $\delta^{13}\text{C}$  values reflect the foraging areas and prey sources used by species (Barrett *et al.* 2007, Hong *et al.* 2019, Ausems *et al.* 2020), considering the natural isotopic variation of this compound among primary producers with different photosynthetic pathways in the coastal-ocean gradient (Quillfeldt *et al.* 2005, Ramos *et al.* 2020).

Other applications of both stable isotopes on seabirds ecology include the characterization of foraging locations (*e.g.* McGinnis & Emslie 2001, Quillfeldt *et al.* 2005), monitoring of diet changes at short- and long-term time periods (*e.g.* Hong *et al.* 2019), delineation of non-breeding distributions (*e.g.* Thompson *et al.* 2015), assessing sexual segregation in distribution, diet and trophic level (*e.g.* Phillips *et al.* 2011) and identifying migration strategies and molting

areas (e.g. Cherel *et al.* 2000, Polito *et al.* 2017). While having a complete view of the species trophic ecology would require an isotopic baseline of the ecosystem, the sole quantification of predator isotopic ratios allows the basic description, comparison and inferences on their trophic niches (e.g. Catry *et al.* 2008, Labbé *et al.* 2013, Ausems *et al.* 2020).

Newsome *et al.* (2007) conceptualized the isotopic niche where the stable isotope proportions ( $\delta$  values) act as analogous of environmental variables associated to the ecological niche. The isotopic niche summarizes the n-biochemical dimensions into a reduced number of axes (e.g.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) thus constituting a proxy of the trophic niche (Grecian *et al.* 2015). The analysis of the isotopic niche breadth of organisms, populations and communities helps to detect segregation or overlapping patterns within and among species, and understand the associated ecological implications (Layman *et al.* 2007, Jackson *et al.* 2011, Ausems *et al.* 2020). Nevertheless, Jackson *et al.* (2011) pointed that, independently of their high correlation, the trophic and isotopic niches are not the same and should not be confounded.

Most of the studies on trophic ecology of breeding seabirds consider polar and temperate regions, highlighting the shortage of works in tropical ecosystems (Weimerskirch 2007). Some characteristics of tropical marine environments (less productivity and seasonal variability respect to higher latitudes, highly variables, patchy and unpredictable feeding resources) lead to specific patterns of foraging and prey consumption by tropical seabirds (Jaquemet *et al.* 2008, Opper *et al.* 2015). The stable isotopes approach can help to clarify underlying traits of the trophic interrelation among tropical breeding seabirds that should be more complex than its counterpart in cold water assemblages (Surman & Wooller 2003). More precisely, the isotopic signatures have been used to describe the diet and foraging habits of shearwaters, frigatebirds, boobies, petrels, tropicbirds, gulls and terns during the breeding season at tropical regions of the Pacific, Atlantic and Indian oceans (e.g. Catry *et al.* 2008, Labbé *et al.* 2013, Wiley *et al.* 2019, Ramos *et al.* 2020, Zam *et al.* 2020). However, these studies are still too scarce and many tropical areas remain practically unknown.

West Indies is one of the lesser studied tropical region in relation with the trophic ecology of seabirds (e.g. Soanes *et al.* 2015, 2016, Chatfield-Taylor 2017, Madden & Eggermont 2020). However, this area supports large breeding colonies of 22 seabird species (Bradley & Norton 2009) and Cuba highlights with 14 species and more than 7100 breeding pairs (Jiménez *et al.* 2009). The cays of the north-central part of this country constitute one of the more important breeding centers with a large number of species and breeding pairs, with the Laridae family (gulls, terns and skimmers, Winkler *et al.* 2020) best represented. Nevertheless, the basic elements of the trophic ecology that allow sympatric reproduction of these species in Cuba are still unknown.

This study focuses on the quantification of the intra- and interspecific isotopic niche variation and overlap (based on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values) to infer the species-specific trophic niche plasticity and among sympatric Laridae species in two breeding locations of Cuba. Two periods of the breeding season were considered: pre-laying (niches of adult females) and chick-rearing (niches of chicks) to identify the potential trophic bases that support the successful species coexistence on the breeding areas. Considering the known differences in foraging behavior and diet

characteristics of these species elsewhere (see Dosch 2003, Dunlop & Surman 2012, Robertson *et al.* 2014, Liechty *et al.* 2016), we expect an interspecific isotopic segregation based on the contrasted foraging distances (inshore, offshore) and trophic positions during the breeding season. Our aims are assessing 1) the intraspecific isotopic niche ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) plasticity of Laridae species during different breeding phases at two breeding locations of Cuba, and 2) the interspecific isotopic niche overlap by breeding phase and location. For the study, the local (breeding area) and general (containing both breeding areas) spatial scales were considered based on the potential Laridae foraging radius in Cuba (Annex 5).

## **4.2 Materials and methods**

### **4.2.1 Study areas**

Laridae tissue samples were collected in three cays (Felipe de Barlovento, Felipe de Sotavento and Paredón de Lado) of the Sabana-Camagüey archipelago in the central-north region of Cuba (Fig. 4.2.1). These cays are among the most important breeding area for seabirds in Cuba, in terms of numbers of species and breeding pairs. Felipe de Barlovento hosts the largest number of breeding Laridae species (Jiménez *et al.* 2009, García-Quintas *et al.* 2020).

Seven larids species bred in these cays from May to August 2021. Laughing Gull *Leucophaeus atricilla* and Bridled Tern *Onychoprion anaethetus* nested at the three cays, Brown Noddy *Anous stolidus* nested in Felipe de Barlovento and Felipe de Sotavento, Sooty Tern *Onychoprion fuscatus* and Royal Tern *Thalasseus maximus* bred in Felipe de Barlovento and Paredón de Lado, while Roseate Tern *Sterna dougallii* and Sandwich Tern *Thalasseus sandvicensis* nested in Felipe de Barlovento. Brown Noddy had a very low representation (two nests only) and hence was discarded from this study.

### **4.2.2 Tissue sampling and stable isotope analysis**

During the 2021 breeding season (May to August), down and body feathers were collected from chicks of Laughing Gull, Sooty Tern, Bridled Tern, Roseate Tern, Royal Tern and Sandwich Tern along studied cays according to the colony's composition (see Annex 8A). Both types of samples were pulled (small handful for down, 5 or 6 body feathers) from the back of chicks during the growth phase (few days post-hatching to pre-fledgling) and stored into labeled plastic bags until analysis. Down samples recorded the characteristics of foraging areas and prey consumed by mothers (adult females) during the pre-laying phase (a few days before egg laying) while the body feathers reflected the food provided by the parents to the chicks during their rearing (Ausems *et al.* 2020). The birds sampled were ringed for individual identification and to avoid the risk of pseudo-replication.

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 h at 45°C and cut into small fragments with stainless steel scissors. Approximately 0.3 mg of down and body feather homogenates were encapsulated in tin cups. Their stable isotope values were subsequently determined by a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyzer (Thermo Scientific Flash 2000) at La Rochelle

University. Stable isotope values are reported following the  $\delta$  notation and expressed as ‰ according to the equation:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 100$ , where X is  $^{13}\text{C}$  or  $^{15}\text{N}$ , R is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ , and Rstandard is the ratio of international references Vienna PeeDee Belemnite for carbon and atmospheric N<sub>2</sub> (AIR) for nitrogen. Replicate measurements of internal laboratory standards (USGS-61 and USGS-62) indicated measurement errors <0.10 ‰ and <0.15 ‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively.

#### **4.2.3 Data analysis**

As Felipe de Barlovento and Felipe de Sotavento cays are very close in space (Fig. 4.2.1), they were gathered and two breeding areas were considered for the data analysis: Felipes and Paredón de Lado (hereafter FBA and PBA, respectively). Sooty Tern were discarded for comparison analysis because of insufficient data to cover both breeding areas.

Intraspecific isotopic variation during the breeding season was assessed following two approaches: temporal (prelaying vs chick-rearing phases through down vs feather tissues) and spatial (FBA vs PBA). Wilcoxon-Mann-Whitney tests were used to compare the isotope values among down and feathers at each location and in all locations, as well as by tissue, between breeding areas for species that nested at both places (Laughing Gull, Bridled Tern and Royal Tern). Interspecific comparison of isotope values was done through the Kruskal-Wallis test at pre-laying (all combinations of down isotopes) and chick-rearing phases (all combinations of feather isotopes) at each location and all locations together. Pairwise Wilcoxon Rank Sum tests (based on “BH” correction method, Benjamini & Hochberg 1995) were used as post-hoc tests to investigate paired differences for significant factors. Statistical significance was considered for  $p < 0.05$ .

Isotopic niches breadth and overlap of  $\delta^{15}\text{N}$  vs  $\delta^{13}\text{C}$  of the species at each breeding phase and spatial scale were calculated by the Stable Isotope Bayesian Ellipses method via R-package SIBER (Jackson *et al.* 2011). This method quantifies the isotopic d-space from data using Bayesian inference based on the metric of multivariate standard ellipses. The ellipses represent the core of the isotopic niches and are computed from the variance and covariance of the bivariate data matrix. This approach corrects for the effects of small samples by generating standard ellipses areas (SEAc) that facilitate comparisons between spaces and the overlap of core isotopic niches (Jackson *et al.* 2011). Thus, SEAc were the metric used to estimate the isotopic niche space while the degree of overlap was calculated using the maxLikOverlap command with ellipses fitted to 95% of data. The calculation of SEAc (excluding Sooty Tern) was based on the smallest sample size (standardization) of all categories included in each comparative analysis. Overlaps <30%, 30-60% and >60% were considered ecologically low, moderate and high respectively (Schwartz-Narbonne *et al.* 2019). All data analysis was performed in R 4.1.1 (R Core Team 2021).

## **4.3 Results**

### **4.3.1 Intraspecific isotopic niche variations among tissues (temporal approach)**

In general, differences in time (through down vs feathers comparison) of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  by species were higher in  $\delta^{15}\text{N}$  for Laughing Gull, Royal Tern and Sandwich Tern (Fig. 4.1A, see Annex 8A). Only Bridled Tern presented significant differences for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in FBA ( $W = 39.5$ ,  $p = 0.03$  for  $\delta^{15}\text{N}$  and  $W = 3.0$ ,  $p = 0.03$  for  $\delta^{13}\text{C}$ , Fig. 4.1A, see Annex 8B) and for  $\delta^{13}\text{C}$  at PBA ( $W = 27.0$ ,  $p < 0.01$ , Fig. 4.1A, see Annex 8B) and all locations together ( $W = 53.5$ ,  $p < 0.01$ , see Annex 8B). For Bridled Tern the isotopic ratios of feathers were higher than those of down in most cases (Fig. 4.1A, see Annex 8A).

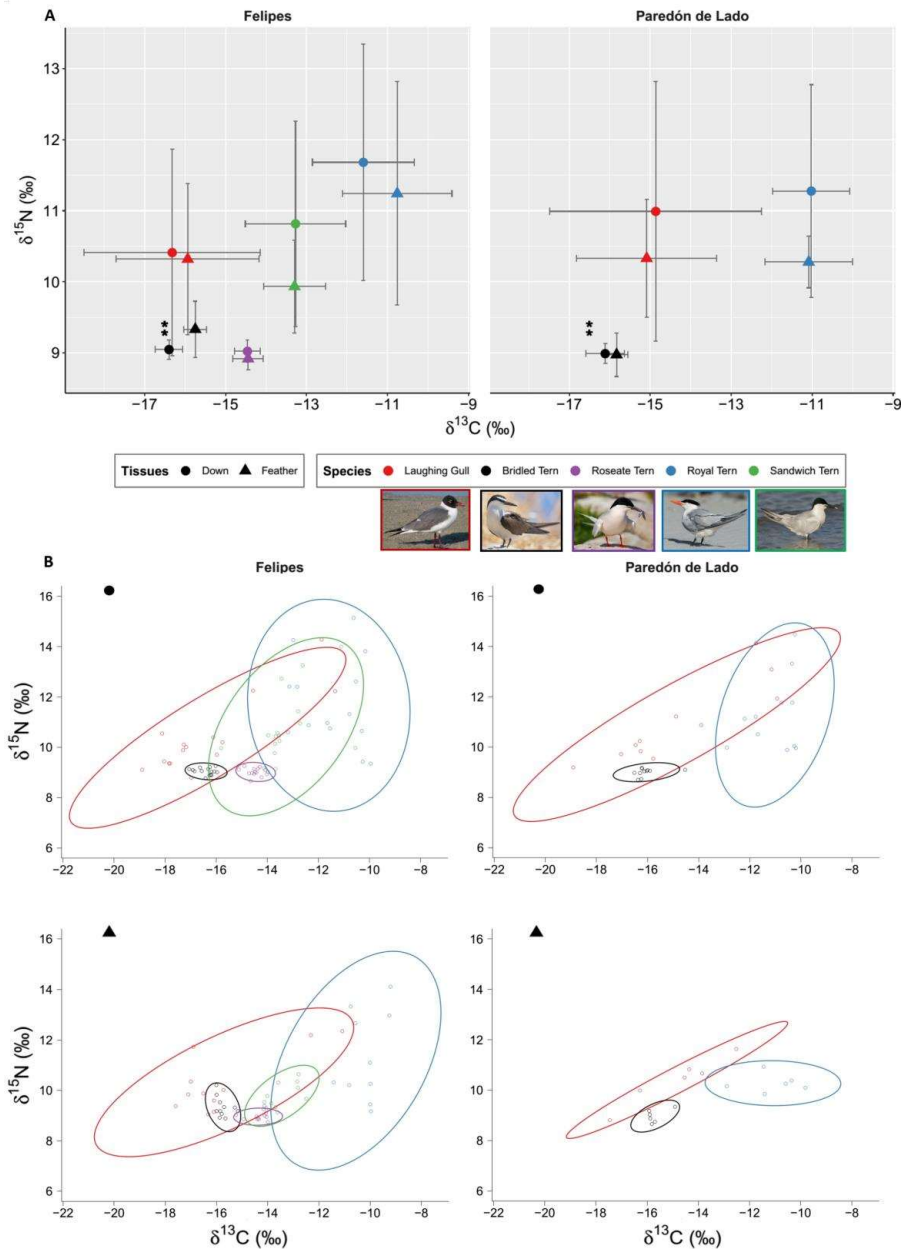
SEAc of Laughing Gull feathers were smaller than those of down for both isotopes in all breeding areas, especially in PBA (Fig. 4.1B). SEAc of Royal Tern was larger for down than for feathers in FBA and especially in PBA (Fig. 4.1B). For Sandwich Tern in FBA, SEAc were much smaller (both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  axes) for feathers than for down (Fig. 4.1B). SEAc of Roseate Tern was highly similar for both tissues in FBA (Fig. 4.1B). SEAc of Bridled Tern feathers was larger than down in FBA with a higher range of  $\delta^{15}\text{N}$  and lesser range of  $\delta^{13}\text{C}$  (Fig. 4.1B). In PBA, SEAc of Bridled Tern was relatively similar between tissues exhibiting discrete reduction in  $\delta^{13}\text{C}$  and increase in  $\delta^{15}\text{N}$  from down to feather (Fig. 4.1B).

### **4.3.2 Intraspecific isotopic niche variations among breeding areas (spatial approach)**

Among breeding areas,  $\delta^{15}\text{N}$  values for Bridled Tern feathers were the only ones showing significant differences ( $W = 125.0$ ,  $p = 0.03$ , see Annex 8C), with higher values in FBA compared to PBA (Fig. 4.1A, see Annex 8A). SEAc of Laughing Gull down in PBA was larger than in FBA with higher values for both isotopes, especially  $\delta^{13}\text{C}$  (Fig. 4.1B). Nevertheless, SEAc of Laughing Gull feathers in PBA was smaller than in FBA for both isotopic ratios (Fig. 4.1B). SEAc of Royal Tern in PBA was smaller than in FBA for both tissues and considering both isotopes, the range of  $\delta^{15}\text{N}$  from feathers at PBA being particularly small (Fig. 4.1B). SEAc of Bridled Tern down in PBA was larger than in FBA mostly due to the  $\delta^{13}\text{C}$  range (Fig. 4.1B). For feathers, this species showed similar SEAc at both areas but with different isotopic characteristics (higher  $\delta^{15}\text{N}$  and smaller  $\delta^{13}\text{C}$  ranges in FBA than PBA, Fig. 4.1B).

### **4.3.3 Interspecific isotopic variation and niche overlap**

Significant differences among species isotope values were found for chick down and feathers in FBA, in PBA and on the general scale (Table 4.1). Most pairwise comparisons of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values among species based on chick down exhibited significant differences at all spatial scales, and only the Royal Tern-Sandwich Tern combination on the general scale did not show significant difference for both isotopes (Fig. 4.1, see Annex 8D). Similarly, there was a predominance of significant pairwise differences for both isotopic ratios from chick feathers, except for the Laughing Gull-Sandwich Tern comparison at global scale (Fig. 4.1, see Annex 8E).



**Figure 4.1.** A: Comparisons of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values (mean  $\pm$  SD) from two chicks' tissues of five Laridae species at two breeding areas (Felipes FBA and Paredón de Lado PBA), central-north of Cuba, during the 2021 breeding season. Asterisk = intraspecific significant differences among tissues by area (color = matched with the corresponded species, quantity = number of isotopic ratios significantly different). B: Bayesian standard ellipses for corrected sample sizes representing the isotopic niches (‰,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of the same species by tissue and area.



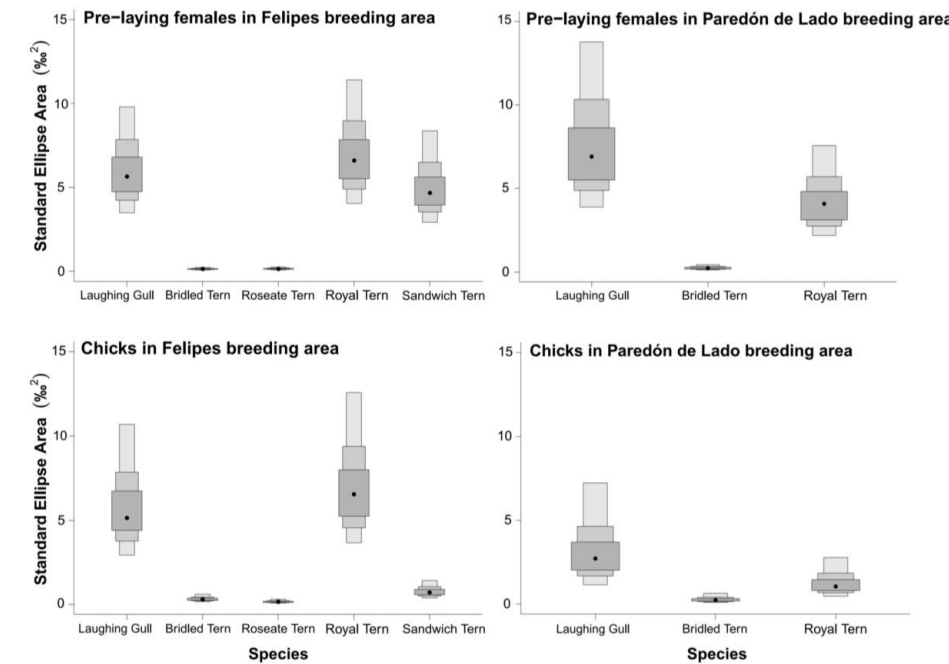
Considering SEAc in global, there were two different groups of species: species with small and weakly variable isotopic niches (Bridled Tern and Roseate Tern) and species with large and highly variable isotopic niches (Laughing Gull, Royal Tern and Sandwich Tern) (Fig. 4.1B). These two groups exhibited clear differences in almost all space-time comparisons (Fig. 4.2). There was a general tendency to avoid large overlaps among SEAc of down (40% were moderate and high overlaps) and feathers (30% of overlaps were moderate and high) in FBA. Yet, Roseate Tern was always highly comprised within Sandwich Tern SEAc in FBA (Fig. 4.1B, see Annexes 8F&G). Species with the smallest isotopic niches (Bridled Tern and Roseate Tern) did not overlap (Fig. 4.1B, see Annex 8F). In PBA, 50% of overlap among SEAc was observed for down tissue while almost no overlap was observed for feathers (Fig. 4.1B, see Annexes 8F&G). Bridled Tern and Royal Tern SEAc never overlapped, whatever the tissue and location (Fig. 4.1B, see Annexes 8F&G).

**Table 4.1.** Interspecific overall comparisons through Kruskal-Wallis tests of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from chick down and feathers of five Laridae species from central-north of Cuba during the 2021 breeding season. Significant differences are in bold.

Stable isotopes	Felipes breeding area (FBA)		Paredón breeding area (PBA)		General breeding area	
	Down	Feather	Down	Feather	Down	Feather
$\delta^{15}\text{N}$	K-W = 53.7 df = 4 <b>p &lt; 0.01</b>	K-W = 41.9 df = 4 <b>p &lt; 0.01</b>	K-W = 27.7 df = 2 <b>p = 0.01</b>	K-W = 21.3 df = 2 <b>p = 0.02</b>	K-W = 80.7 df = 4 <b>p &lt; 0.01</b>	K-W = 61.1 df = 4 <b>p = 0.01</b>
	$\delta^{13}\text{C}$	K-W = 55.5 df = 4 <b>p = 0.03</b>	K-W = 56.0 df = 4 <b>p = 0.02</b>	K-W = 19.7 df = 2 <b>p = 0.04</b>	K-W = 15.3 df = 2 <b>p &lt; 0.01</b>	K-W = 75.2 df = 4 <b>p = 0.01</b>

#### 4.4 Discussion

Trophic niche plasticity appears to be an important adaptive mechanism to ensure the reproductive success of sympatrically breeding Laridae in north-central Cuba. The bivariate isotopic niche ( $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$ ) of five Laridae species differed in time (among pre-laying and chick-rearing phases) and space (among breeding areas) showing generalist and specialist trophic species groups. Interspecific trophic segregation could be due to differences in niche width and overlap, as well as species-specific feeding strategies. Patterns of isotopic niche variation indicated two main patterns of trophic plasticity among breeders: niche contraction/expansion and niche displacement along different ranges of trophic position and/or foraging localities. A thorough understanding of the trophic relationships among these seabirds can be achieved by analyzing the isotopic and morphological characteristics of the prey consumed, and also by assessing the isotopic niche patterns of predators and prey at different breeding seasons.



**Figure 4.2.** Density plots of the standard Bayesian ellipses areas based on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values (‰) in chicks down (representing pre-laying females) and feathers (representing chicks) of five Laridae species from two breeding areas, 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.

#### 4.4.1 Intraspecific isotopic niche variations among tissues (temporal approach)

Isotopic niche bi-dimensional reduction of Laughing Gull among breeding phases in both breeding areas reflects variations of feeding behavior (captured prey and foraging locations) of adults during pre-laying (females) and chick-rearing phases (males and females). Thus, the diet of Laughing Gull pre-laying females appears to be more varied and obtained from more diverse foraging locations than that of adults rearing chicks. This isotopic niche contraction over time could reflect the movement restrictions of adults because of the central-place foraging behaviour during the chick-rearing phase, that reduces the variety of captured prey. Similarly, Sebastiano *et al.* (2017) found an isotopic niche (smaller than our findings) bi-dimensional contraction in a Laughing Gull colony of French Guiana between these two periods. Based on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from chicks' down, González-Medina *et al.* (2020) found that Laughing Gull pre-laying females consumed marine prey mainly at the coast of Sinaloa (Mexico) occupying a smaller isotopic niche ( $\text{SEAc} = 3.02\text{‰}$ ) than their conspecific in our studied areas ( $\text{SEAc} = 5.54, 6.54$  and  $5.89\text{‰}$  at FBA, PBA and general area respectively). At the same Laughing Gull colony in Sinaloa,  $\text{SEAc}$  of chick feathers ( $2.52\text{‰}$ ) was smaller and larger than

our findings in FBA (5.90‰) and PBA (1.59‰), respectively. These variations demonstrate the large ecological plasticity of the feeding behavior of this gull species.

The pattern of Royal Tern isotopic niche in PBA, changing among breeding phases, suggests that adults provide specific food items to chicks (likely due to their specific nutritional requirements for growth) at the expense of increased foraging areas with respect to females during the pre-laying phase. Isotopic niche reduction among adults and chicks of Royal Tern occurred in a breeding colony of French Guiana, although with different isotopic ranges (Sebastiano *et al.* 2017). We also showed a remarkable contraction of Sandwich Tern SEAc in FBA from pre-laying females to chick-rearing phases. This pattern of isotopic niche contraction from breeding adults to chicks of Sandwich Tern was found also by Sebastiano *et al.* (2017) in a colony of French Guiana, but with Sandwich Terns occupying smaller niches than in our study. This niche contraction could result from the constraints due to central-place foraging combined with specific food requirements of chicks.

Pre-laying females and chicks of Roseate Tern consumed similar prey from similar foraging locations in FBA. Similar to our findings, Roseate Tern breeding females at the Gulf of Maine acted as dietary specialists with restricted foraging areas (from eggshells  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopes) exhibiting a smaller isotopic niche breadth than the co-occurring breeding species (Bratton *et al.* 2022). Despite its small size, the Bridled Tern isotopic niche exhibited contrasting patterns among breeding phases at both areas. The main variations showed that Bridled Tern chicks had a richer diet obtained from fewer locations than pre-laying females. This could suggest the need to frequently supply more variety of prey to chicks from nearby locations, optimizing seasonal food availability to ensure the suitable prolonged growth and development typical of this species (Hulsman & Langham 1985). In New Caledonia, the growth rate of Bridled Tern chicks was negatively correlated with the adults foraging distances (Villard & Bretagnolle 2010). Coinciding with our results, feeding strategies of adults can change along the breeding season according to their own trophic requirements as well as those of chicks in Laughing Gull (Dosch 2003, Washburn *et al.* 2013, González-Medina *et al.* 2020), Royal Tern and Sandwich Tern (*e.g.* Aygen & Emslie 2006, Marinao *et al.* 2019), and Bridled Tern (*e.g.* Dunlop & Surman 2012, Labbé *et al.* 2013). These variations are less marked in the Roseate Tern (*e.g.* Monticelli *et al.* 2008).

#### **4.4.2 Intraspecific isotopic niche variations among tissues (spatial approach)**

The opposite direction in differences in isotopic niche breadth between breeding areas in pre-laying females of Laughing Gull and Bridled Tern (wider in PBA), and Royal Tern (narrower in PBA) could respond to the local availability or accessibility of prey taking into account the specific food requirements of each species. Successful feeding of adult females during the pre-laying phase is particularly important because they must undergo the so-called "pre-breeding exodus" to obtain enough food to face the subsequent energetic costs of laying and chick-rearing (Jaeger *et al.* 2017, Bratton *et al.* 2022). Apparently, Royal Tern females satisfied their needs in smaller areas in PBA than Laughing Gull and Bridled Tern.

Differences among breeding areas in the isotopic niche of Laughing Gull chicks could be based on the availability and abundance of prey at each area. FBA receives greater disturbance pressures from activities such as fishing and coastal tourism than PBA. This could lead (considering direct disturbances on seabirds and indirect disturbances on the different components of marine food webs) that in FBA Laughing Gull adults need to forage in more places farther away from the colonies to capture prey for the chicks. Then, their chances of capturing more varied prey could increase. There are evidences that perturbations by ship traffic affect the foraging, resting and breeding behavior of seabirds and increase their energetic costs by escape reactions (Afán *et al.* 2019, Lieske *et al.* 2020). Another plausible explanation is that the larger isotopic niche of Laughing Gull chicks in FBA reflects a strategy to reduce intraspecific competition (by increasing the variety of prey and foraging sites) of foraging adults with central-place restrictions to supply the food needs of the larger number of chicks observed in this area relative to PBA. This argument also seems to support isotopic niche differences among Royal Tern chicks considering the contrasting size of breeding colonies among both areas. Despite the similarity of the isotopic niches of Bridled Tern chicks among the breeding areas, different spatial niche patterns were observed indicating the consumption of a greater variety of prey from fewer locations in FBA than PBA. These isotopic variations could be the way to reduce intraspecific competition in species with a small niche such as Bridled Tern, which had the highest number of chicks in FBA.

#### **4.4.3 Interspecific isotopic niche variation and overlap**

Normally, species with large and highly variable isotopic niches constitute trophic generalists, whereas species with small and weakly variable isotopic niches are trophic specialists. This was clearly detected in the Laridae breeding communities in this study. Trophic niche partitioning among tropical breeding seabirds appears to be a common phenomenon based on species specificities such as prey characteristics, feeding strategies, and foraging site fidelity (Gorke & Brandl 1986, Chérel *et al.* 2008, Gatto *et al.* 2019). Precisely, the species-specific feeding characteristics could lead to a better understanding of the isotopic niche characteristics (breadth and overlap) of the Laridae in this work.

Laughing Gull constitutes the main ecological generalist and opportunistic Laridae species at the studied colonies. As most of breeding gulls' species, Laughing Gull can exploit several foraging habitats (open seawater, coasts, estuaries, open grassland, agriculture, urbanized coasts) consuming a broad variety of items from marine (*e.g.* fishes, crabs, shrimps, bivalves) and terrestrial (*e.g.* earthworms, snails, insects, fruits, plant materials) origins, as well as anthropogenic foods (*e.g.* bread, chicken, vegetables, garbage) (Burger 1988, Dosch 2003, Washburn *et al.* 2013). Additionally, Laughing Gull could act as predator of eggs and chicks of terns (Raynor *et al.* 2012). It forages through the pick-up technic during daylight and nights (Dosch 2003).

Royal Tern and Sandwich Tern are mainly diurnal foragers specialized on a diet based on a variety of fishes, some invertebrates and demersal prey indicating the use of discards from local fishing activities (Perrow *et al.* 2011, Liechty *et al.* 2016, Gatto *et al.* 2019). Both species nest in sympatry frequently exploiting broad foraging areas from riverine estuaries to open ocean

but nearshore (Shealer 1996, McGinnis & Emslie 2001, Gatto *et al.* 2019). Depending on the characteristics of the ecosystem where they reproduce, trophic niche segregation among the two species may be supported by the different proportions and sizes of prey consumed or by the different use of their foraging areas (*e.g.* McGinnis & Emslie 2001, Liechty *et al.* 2016, Gatto *et al.* 2019).

As all *Sterna* spp., Roseate Tern is a small tern that forages mainly by snatching food from the sea surface or by plunge-diving up to 1 m in depth at relatively short foraging ranges (inshore waters) although larger distances have been reported (Shealer 1996, Robertson *et al.* 2014). Its feeding strategy tends to be based on an association with the presence of predatory fish that facilitates the capture of low-diverse types of very small fish (Surman & Wooller 2003, Robertson *et al.* 2014), including in the West Indies (Shealer 1996). Bridled Tern belongs to the “contact-dipping” guild of dark-plumaged tropical terns and forages on floating Sargassum spp. and macro-algae reefs in oligotrophic waters with low salinity and productivity (Dunlop & Surman 2012, Labbé 2017). This species is a near-offshore forager with a diversified diet based on small fishes and invertebrates (sometimes including insects) (Kohno & Kishimoto 1991, Dunlop & Surman 2012, Moser & Lee 2012).

Overall at the interspecific level, a partial trophic niche overlap among pre-laying females was observed in the studied breeding areas. Differences among the isotopic niche width (from down tissue) of generalist vs specialist species indicate the trophic niche partitioning in the communities of pre-laying females in both breeding areas. Regardless of the width and degree of SEAc overlap, a gradient pattern among pre-laying females taking into account  $\delta^{13}\text{C}$  values can be detected. In FBA from far to near shore, the species appear to forage in the sequence Laughing Gull-Bridled Tern-Roseate Tern-Sandwich Tern-Royal Tern while the Laughing Gull-Bridled Tern-Royal Tern sequence was consistent in PBA. With respect to  $\delta^{15}\text{N}$  values, the most evident niche differentiation was among the groups Bridled Tern-Roseate Tern (trophic specialist) and Laughing Gull-Sandwich Tern-Royal Tern (trophic generalist), coinciding with their specific food requirements.

Moreover, despite moderate to high overlap among SEAc of pre-laying females in each area (mainly in the ecologically complex FBA, which harbors more species that breed together), there was at least one significant isotopic difference among each pair of species. These findings support the existence of segregation mechanisms of trophic niches (based on trophic position and/or foraging locations) among species breeding in sympatry. Trophic niche partitioning among females with moderate and high SEAc overlaps could be supported from adjustments of their feeding strategies, a frequent behavior of breeding seabirds to avoid competition by food and hence reduce the trophic niches overlap (Phillips *et al.* 2011, Washburn *et al.* 2013, Labbé 2017, Clay *et al.* 2019). Our results were consistent with Chereil *et al.* (2008) and Sebastiano *et al.* (2017) in breeding colonies of tropical seabirds, including Laridae species.

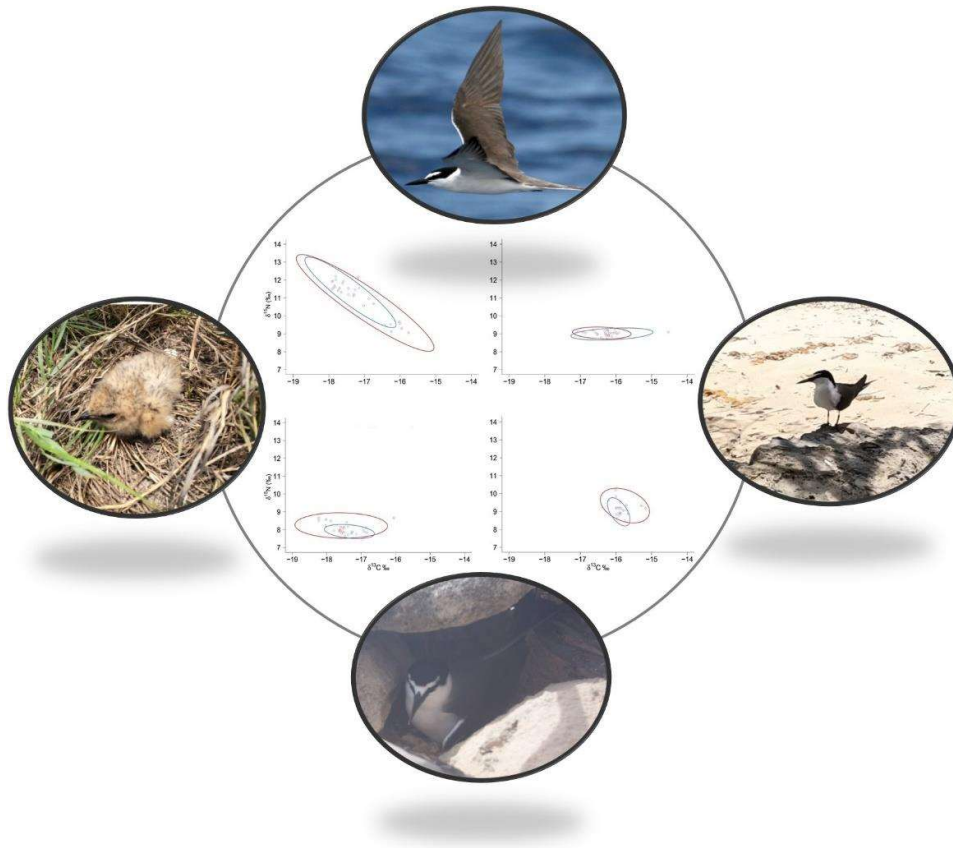
The overall reduction in the high overlap among SEAc from chick feathers in both breeding areas suggests that species tended to maximize their trophic segregation mechanisms during the chick provisioning phase. This could contribute to reduce competition by the available food in partially common foraging locations (due to central-place foraging at this phase) guarantying

the successful growing and development of more chicks. Trophic niche variation among pre-laying and chick-rearing phases seems to be expected if one takes into account the influence of nestling development and feeding needs on the feeding behavior of adults (Dosch 2003). In PBA, the pairwise Laughing Gull-Bridled Tern showed segregation in their prey mainly, Laughing Gull-Royal Tern through their foraging locations (Royal Tern foraged nearer shore than Laughing Gull), and Bridled Tern-Royal Tern had trophic niches fully segregated for trophic position and foraging location. In addition, the near-perfect niche segregation among breeding species could be due to the ease of access to abundant prey in a relatively low disturbed area, such as PBA.

The chick-rearing phase in the FBA was probably the most complex scenario for the interaction of trophic niches among species. Besides the increase of common feeding locations due to central-place foraging restrictions, prey distribution in FBA could be largely dispersed due to observed human disturbances. Furthermore, the number of species breeding together in this area should result in a high net demand for food by the chicks. The FBA Laridae appeared to adopt different strategies to reduce moderate and high trophic niche overlaps, according to the characteristics of SEAc. Chicks of Laughing Gull and Royal Tern kept the trophic generalist behavior (broad SEAc) consuming a great prey variety obtained from several locations, although Royal Tern chicks tended to consume more coastal prey than pre-laying females (higher  $\delta^{13}\text{C}$  values in Royal Tern SEAc). The SEAc of Sandwich Tern chicks represented an intermediate level (clearly lower than Laughing Gull and Royal Tern but slightly higher than Bridled Tern and Roseate Tern), showing high overlap with trophic generalist species and low overlap with Roseate Tern. Differing with previous pre-laying phase, there were some overlaps (but low) among the chicks SEAc of specialist Bridled Tern and Roseate Tern. However, the variation (with respect to pre-laying females) in the isotopic niche pattern of the former could be interpreted as a response (niche displacement) to reduce the overlap of its trophic niche with the (practically stable) Roseate Tern. Apparent stresses from niche overlap among the Sandwich Tern-Roseate Tern-Bridled Tern group may be diminished by their contrasting feeding strategies. Similar to pre-laying females, there was at least one isotope differing among each pairwise of chick species, especially for  $\delta^{13}\text{C}$ . Thus, some segregation at foraging area and/or trophic position was hidden behind the overall overlap among the chicks' isotopic niches of studied species.

## Chapter 5:

### Annual plasticity of the trophic niche of Bridled Tern (*Onychoprion anaethetus*) in Cuba



#### Associated publication

Garcia-Quintas A., Barbraud C., Bustamante P., Lorrain A., Denis D. & Lanco Bertrand S. (In Rev.) Annual plasticity of the trophic niche of Bridled Tern (*Onychoprion anaethetus*) in Cuba.



## 5.1 Introduction

Bridled Tern *Onychoprion anaethetus* (BRTE) 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 & Rodriguez, 1996; Tayefeh *et al.*, 2014). This species usually forages on floating groups of *Sargassum* and macroalgae 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 fish 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 breeding and non-breeding seasons (Labbé *et al.*, 2013; Tayefeh *et al.*, 2017).

Despite being an abundant (worldwide population being estimated between ~600 000 - 1 500 000 mature individuals) and cosmopolitan species in the tropics and subtropics (Villard & Bretagnolle, 2010; Tayefeh *et al.*, 2017), the ecology of BRTE is poorly known (Hulsman & Langham, 1985; Bretagnolle & Benoit, 1997). Most studies on this species have focused on the description of new breeding locations, molting patterns, diet, feeding and brood-attendance behaviour (*e.g.* Diamond, 1976; Kohno & Kishimoto, 1991; Komar & Rodriguez, 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 on the trophic ecology of BRTE 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  $\delta^{15}\text{N}$  as a proxy of the trophic position and  $\delta^{13}\text{C}$  as a proxy of the feeding location) of BRTE in breeding colonies in the Seychelles archipelago (Catry *et al.*, 2008) and in 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 (Newsome *et al.*, 2007), a concept of increasing application that integrates isotopic ratios as a proxy for the species trophic niche (Grecian *et al.*, 2015). This approach has recently been applied to the BRTE colonies in Cuba (Chapter 4).

Within the BRTE's wide distribution range, the Caribbean is virtually an enigma in terms of feeding ecology. However, several breeding colonies of BRTE are established in this region with important population sizes (~8909 - 10368 breeding pairs) (Bradley & Norton, 2009), which are probably underestimated due a lack of spatial and temporal coverage of breeding surveys. This region is thus essential to BRTE while important conservation values (biodiversity hotspots, Important Bird Areas, Ramsar sites) are insufficiently covered by Marine Protected Areas and significant anthropogenic disturbances (*e.g.* from fisheries, tourism) occur. Thus, the study of the BRTE's trophic niche in Caribbean areas could contribute



to the management and conservation of the species, based on the evaluation of threats to its foraging areas and its habituation ability to human disturbance.

The stable isotope approach could serve as a starting point for assessing BRTE's 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). Analyzing the seasonal variability of the isotopic niche can help to characterize biogeographic or connectivity patterns, crucial aspects for the conservation of highly migratory species (Newsome *et al.*, 2007) such as BRTE. To our knowledge, only one study addressed the isotopic niche of this species in the Caribbean in two breeding areas of North Central Cuba (*i.e.* Chapter 4). In those areas, BRTE occupied a small and relatively plastic isotopic niche ( $\delta^{15}\text{N}$  vs  $\delta^{13}\text{C}$ ) between the pre-laying and chick-rearing phases of the breeding season compared to other Laridae species. However, the year-round characterization of its isotopic niche remains unknown, although it could be important for the management and conservation of BRTE in the Caribbean basin by contributing to the detection of critical stages where the niche is restricted.

In this study, stable isotope analysis of different tissues was used to estimate the spatio-temporal variability of the BRTE 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 BRTE 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 BRTE isotopic niche breadth to occur between the non-breeding phase and the other periods, as they represent times with contrasting foraging strategies (opportunistic vs central-place foraging, Dunlop & Surman, 2012; Labbé *et al.*, 2013). As well, the lowest variation in  $\delta^{13}\text{C}$  (suggesting the smallest foraging range) should occur during chick-rearing due to restrictions on adult movements to meet the feeding and protection needs of the chicks.

## **5.2 Materials and methods**

### **5.2.1 Study areas and sampling**

Sampling of BRTE tissues took place in Felipe de Barlovento, Felipe de Sotavento and Paredón de Lado cays, belonging to the Sabana-Camagüey archipelago, North central Cuba (Fig. 5.2.1). These cays are one of the more important breeding area for seabirds in Cuba, both in terms of number of individuals and number of species (Jiménez *et al.*, 2009). BRTE is a summer resident in Cuba (Garrido & Kirkconnell, 2011) that normally establishes breeding colonies on all three cays according to Jiménez *et al.* (2009) and field observations. Tropical climate of this region shows a mean annual temperature of  $26.3 \pm 0.4^\circ\text{C}$ , an average monthly precipitation of  $88.5 \pm 18.1\text{mm}$  and average annual wind speed of  $14.5 \pm 2.2\text{km}\cdot\text{h}^{-1}$  (easterlies mainly). Specifically, during the breeding season of BRTE in Cuba (May to August, Garrido & Kirkconnell, 2011) temperature values are  $28.0 \pm 1.0^\circ\text{C}$  and precipitations average  $109.2 \pm 83.1\text{mm}$  (Meteorological Station 78339, Centro de Investigaciones de Ecosistemas Costeros, Cayo Coco).

During the 2021 breeding season we collected body feathers and blood of adults, and down and body feathers of chicks of BRTE in all three study cays. Adults were captured directly on or in the vicinity their nests using a handle net during the incubation phase. Feather (5-6 per individual) were pulled from the back of incubating adults and stored in labeled plastic bags until analysis. Blood samples (0.6mL) were collected in heparinized capillary tubes after tarsal vein puncture with a needle. Blood samples were stored in Eppendorfs with 90% ethanol due to the impossibility of keeping them frozen in the field. This procedure does not significantly alter the subsequent isotope analysis in seabird tissue samples (Catry *et al.*, 2008). BRTE undergo an annual molt prior to the breeding season (*i.e.* during non-breeding period) (Bridge *et al.*, 2007). Thus, feathers and blood samples reflected the characteristics of the foraging locations and prey consumed by BRTE adults during the non-breeding and incubation phases, respectively.

Sampling of down (small handful) and feathers from chicks followed the same procedure as for adults, and was performed respectively after hatching and at different times during chick growth until fledgling. 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 the parents to the chicks during the rearing phase (Ausems *et al.*, 2020). All sampled birds were ringed for individual identification and to avoid problems of pseudo-replication.

### **5.2.2 Stable isotope analysis**

Stable isotope ratios were measured in body feathers samples, which reflect the feeding ecology at the time of their synthesis (Cherel *et al.*, 2000) and in down samples, which represents the diet of the mother a few days before egg laying (Ausems *et al.*, 2020). They were also measured in blood samples, which integrate dietary information over the 3–4 weeks prior to sampling (Hobson & Clark, 1992; Bearhop *et al.*, 2002). Prior to the analyses, blood samples were oven dried at 50°C during 24h and grounded to get 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 h 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  $\delta$  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  $^{13}\text{C}$  or  $^{15}\text{N}$ , R is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ , and  $R_{standard}$  is the ratio of international references Vienna PeeDee Belemnite for carbon and atmospheric  $\text{N}_2$  (AIR) for nitrogen. Replicate measurements of internal laboratory standards (USGS-61 and USGS-62) indicate measurement errors < 0.10‰ and < 0.15‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively.

### **5.2.3 Data analysis**

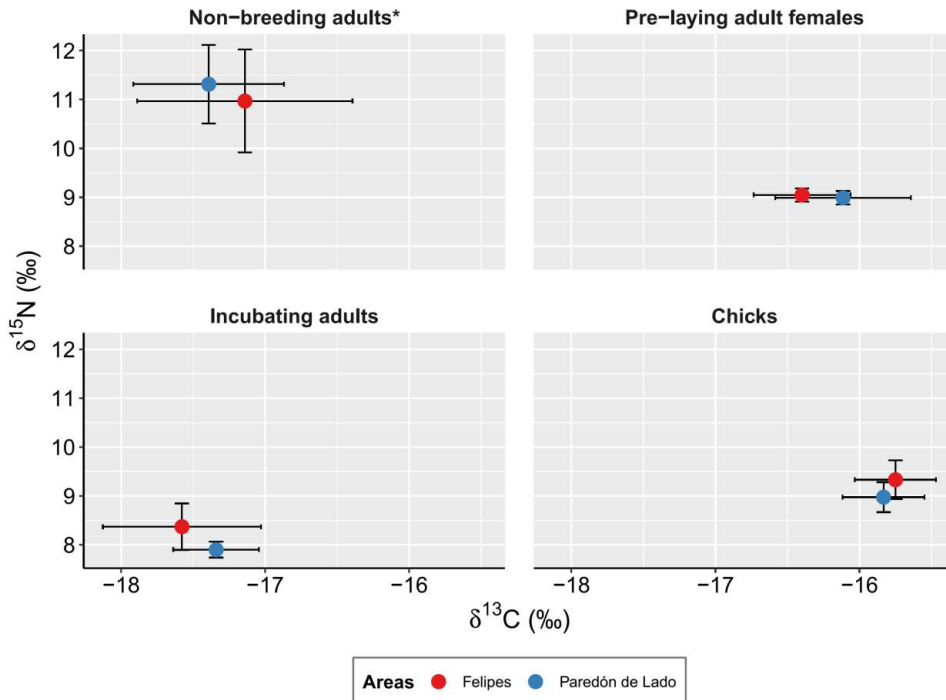
Due to the proximity of the Felipe de Barlovento and Felipe de Sotavento cays (Fig. 5.2.1), only two breeding areas were considered for data analysis: Felipes and Paredón de Lado (hereafter FBA and PBA, respectively). The isotopic proportions were compared among breeding areas (FBA and PBA) for each tissue by Wilcoxon-Mann-Whitney tests (because the assumptions for parametric tests were not met). This allowed to evaluate the spatial variability of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  at different phases of the BRTE annual cycle. For adult feathers, the individual-area association was preserved for the purpose of following the annual cycle by groups of birds, yet the foraging areas of BRTE during non-breeding phase are outside Cuba, unknown and possibly the same for the two colonies. Significance was considered for  $p < 0.05$ .

The isotopic niches breadth of  $\delta^{15}\text{N}$  vs  $\delta^{13}\text{C}$  of BRTE at each phase (from each tissue) were 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 ellipses areas (SEAc) that facilitate comparisons among spaces of core isotopic niches (Jackson *et al.*, 2011). SEAc was the metric used to estimate the isotopic niche space with ellipses fitted to 95% of data. All data analyses were performed with R 4.1.1 (R Core Team, 2021).

### **5.3 Results**

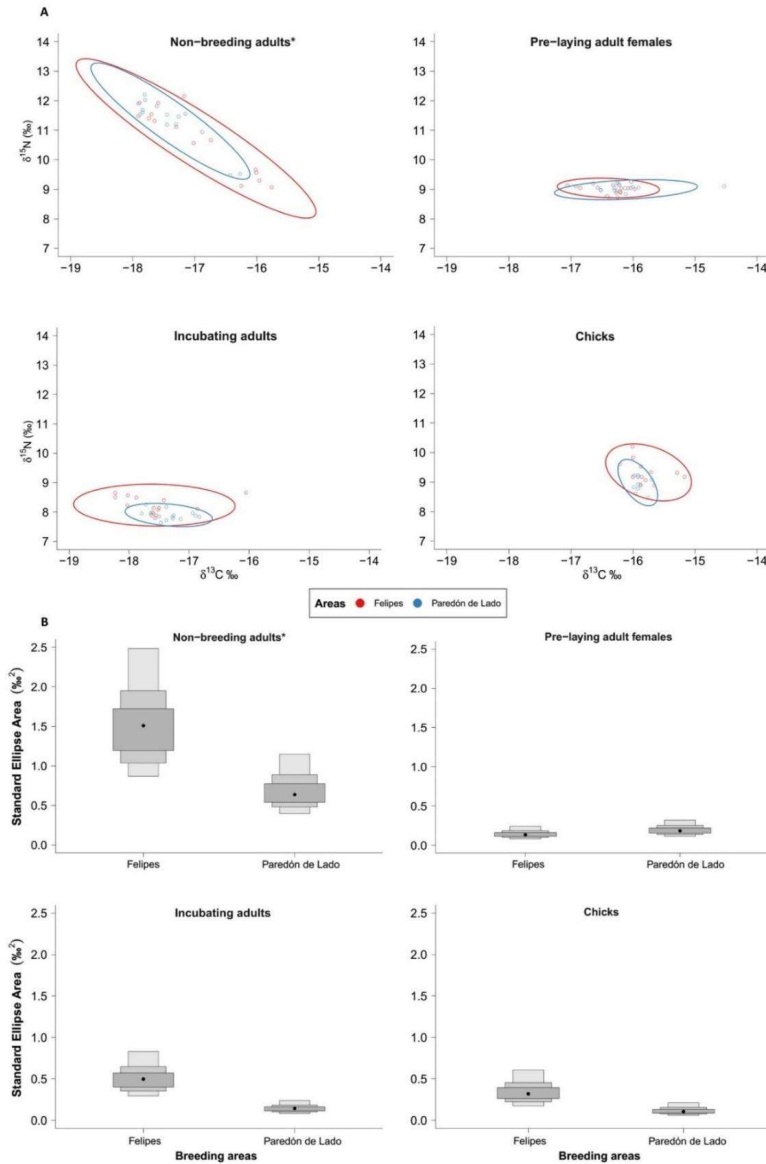
Considering all tissues, the largest  $\delta^{13}\text{C}$  variability was observed in feathers (in individuals from both breeding areas) and blood (in FBA only) of adults (Fig. 5.1; Annex 9). The variability of  $\delta^{15}\text{N}$  was highest for the feathers of adults from the two areas (Fig. 5.1; Annex 9). Among breeding areas, blood  $\delta^{13}\text{C}$  in PBA was significantly larger than in FBA ( $W = 62.5$ ,  $p = 0.04$ ; Fig. 5.1), while the opposite was found for blood  $\delta^{15}\text{N}$  ( $W = 189.0$ ,  $p < 0.01$ ; Fig. 5.1). Also, the  $\delta^{15}\text{N}$  of chick feathers in FBA was significantly larger than in PBA ( $W = 125.0$ ,  $p = 0.03$ ; Fig. 5.1).

The isotopic niche of non-breeding adults (from feathers) associated to FBA was bi-dimensionally larger than that of those associated to PBA (Fig. 5.2). During the pre-laying phase (from down), the isotopic niche of adult females in PBA was slightly larger than in FBA based on the  $\delta^{13}\text{C}$  range (Fig. 5.2). The isotopic niches of incubating adults (from blood) and chicks (from feathers) in FBA were broader than in PBA taking into account both isotopes (Fig. 5.2).



**Figure 5.1.** Relationship (means  $\pm$  SD) between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of feathers (from non-breeding adults and chicks), blood (from incubating adults) and down (from chicks but representing to pre-laying adult females) of Bridled Tern *Onychoprion anaethetus* from two breeding areas (North Central Cuba), during the 2021 breeding season. \* = 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.

Annual variation in BRTE isotopic niche breadth was contrasted between the non-breeding (from adult feathers) and breeding (pre-laying, incubation and chick rearing; from down, blood and chick feathers respectively) phases, being larger in the non-breeding period (Fig. 5.2). However, there were different patterns of niche variation (considering all tissues) among individuals associated to each breeding area. BRTE at FBA showed a contraction of the isotopic niche from adult feathers (proxies of the non-breeding phase) to down (proxies of pre-laying phase) (Fig. 5.2). Afterwards, an expansion of the niche toward the incubation phase (blood-based) occurred, which was relatively similar to the isotopic niche of the chicks (from their feathers) (Fig. 5.2). BRTE at PBA also experienced a significant reduction of the isotopic niche from non-breeding adults to pre-laying females, and then kept niches with similar breadth during the remaining reproductive phases (Fig. 5.2).



**Figure 5.2.** A) Bayesian standard ellipses for corrected sample sizes representing the isotopic niches (‰,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of Bridled Terns *Onychoprion anaethetus* (from feathers of non-breeding adults, blood of incubating adults, and chick down – representing to pre-laying adult females – and feathers) from two breeding areas in North Central Cuba during the 2021 breeding season. B) Density plots of the Bayesian standard ellipses areas by each phase of Bridled Terns annual cycle. Black dots represent their mode, shaded boxes represent 50, 75 and 95% credible intervals from dark to light grey, respectively. \* = 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.

#### **5.4 Discussion**

Compared to other species, BRTE occupies a small isotopic niche ( $\delta^{15}\text{N}$  vs  $\delta^{13}\text{C}$ ) during the breeding phases indicating a reduced trophic niche based on specialized diet and foraging locations (e.g. Catry *et al.*, 2008; Dunlop, 2011; Labbé *et al.*, 2013; Chapter 4). Although the isotopic values of blood and down/feathers cannot be directly compared due to different fractionation factors, the breadth of their isotopic niches can be compared (Jackson *et al.*, 2011). Similar to Labbé *et al.* (2013), we found that the largest isotopic variability and broadest niches occurred in adults during the non-breeding phase. This reflects a more varied diet (from large  $\delta^{15}\text{N}$  ranges) of adults likely foraging in oligotrophic tropical waters before the breeding season. Although the exact wintering areas of BRTE breeding at Cuba are unknown, it can be hypothesized that all adults sampled in this study use common foraging areas, as the SEAc at the two locations were perfectly nested (coinciding  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  ranges) during the non-breeding phase. Isotopic values recorded in adult feathers in this study are consistent with those reported by Dunlop (2011) from primary feathers of BRTE adults wintering in the Sulawesi Sea (western Pacific), while breeding in western Australia. These isotopic values were lower for  $\delta^{13}\text{C}$  than those corresponding to feathers from BRTE adults in colonies in the Seychelles (Catry *et al.*, 2008) and Western Australia (Labbé *et al.*, 2013). Our  $\delta^{15}\text{N}$  results were smaller than those of adults from the Seychelles 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 BRTE wintering areas around the world and cannot be discussed further without knowledge of isotopic baselines (e.g. Graham *et al.*, 2010).

Isotopic information derived from down reflected a high specialization in prey by pre-laying adult females. It appears that females select specific food items during the presumed "pre-breeding exodus", which could be important for obtaining appropriate energy reserves to face the requirements of ovogenesis and reproductive period (Jaeger *et al.*, 2017; Bratton *et al.*, 2022). The extent of foraging locations underpinned the main variation in the isotopic niches of pre-laying females among breeding areas. These inter-area variations could be due to the accessibility of the specific prey needed by pre-laying females, possibly easier to obtain in FBA than in PBA. This could explain the smaller isotopic niche and lower range of  $\delta^{13}\text{C}$  values of pre-laying BRTE females in FBA than in PBA.

The differences in the level of human disturbance among breeding areas could explain the significant differences among the isotopic niches of incubating adults. Many anthropogenic activities such as commercial and tourist shipping can impact seabirds by causing behavioral alterations due to commercial and tourist ship traffic (increased energy expenditure due to flight reactions) (Anderson *et al.*, 2018; Afán *et al.*, 2019; Lieske *et al.*, 2020). Central-place foraging starts from laying onwards, and adults alternate incubation and feeding activities (Hulsman & Langham, 1985). Movement restrictions during foraging may vary depending on the accessibility of food in response to human disturbance. Thus, it could be expected that adults in the highly disturbed FBA would need to forage in more locations and consume a greater variety of prey (presumably widely dispersed) than in PBA to satisfy their energetic requirements. This also appeared to occur during the chick-rearing period, especially in the types of consumed prey (significant differences in  $\delta^{15}\text{N}$  among breeding areas) as foraging

restrictions tend to increase due to the frequent need to return to the colony to care for the chicks (e.g. Hulsman & Langham, 1985; Garavanta & Wooller, 2000). Also, local foraging conditions (e.g. oceanography, climatology, marine productivity, human pressures) may produce differences in BRTE isotope ratios among distant breeding sites. The isotopic differences between the feathers of the chicks and those registered by Dunlop (2011) and Labbé *et al.* (2013) in chick feathers from western Australia (lower  $\delta^{15}\text{N}$  and higher  $\delta^{13}\text{C}$  in those of this study) can be due to different isotopic baseline between regions.

Some important variations in the breadth of the BRTE isotopic niche among the phases of its annual cycle were detected. The most remarkable occurred from the non-breeding to the pre-laying phases (within the breeding season), characterized by a niche contraction for both isotopes. This indicates a reduction in the variety of prey consumed as well as in the extent of foraging locations by pre-laying females, which could result from a shift from opportunistic foraging (during the non-breeding phase) to a specialized foraging (primarily on prey types) to cope with the energetic costs of reproduction. Afterwards, the niche breadth remained small throughout the phases corresponding to the breeding season (pre-laying, incubation and chick-rearing), although with different patterns of variation according to the breeding area. This suggests that the breadth of the BRTE trophic niche varied according to prey (usually linked to floating patches of algae and plants) accessibility in the breeding area, and potentially according to other factors such as the size of the breeding population (directly proportional to food demand), marine productivity and the degree of human disturbance. On the other hand, the constraints due to central-place foraging during the chick-rearing may explain the change in the isotopic niche geometry (SEAc wider in the  $\delta^{15}\text{N}$  range and narrower in the  $\delta^{13}\text{C}$  range) during this breeding phase. This implies that the chicks' trophic niches were based on the consumption of more types of prey provided from locations closer to the colonies (e.g. Hulsman & Langham, 1985).

The slightly broader isotopic niches ( $\delta^{15}\text{N}$  mainly) of adult blood and nestling feathers suggest some variation in incubating adults and chicks diet, respectively. The latter is in agreement with the findings of Labbé *et al.*, (2013) in a BRTE colony on Penguin Island, Western Australia, although following a protocol based exclusively on feather sampling. Diet variation among breeding phases is common in BRTE (Dunlop & Surman, 2012; Labbé *et al.*, 2013) and its detection from metabolically inert tissues (down and feathers) is not affected by the reproductive status of individuals (Labbé *et al.*, 2013). Coinciding with the results of Dunlop (2011) and Labbé *et al.* (2013), the  $\delta^{13}\text{C}$  values of chick feathers were higher than those of chick down, meaning that the food consumed by chicks came from feeding areas closer to shore (carbon-enriched areas due to the contribution of benthic habitats) than the prey consumed by pre-laying females (Cherel & Hobson, 2007).

The trophic ecology of BRTE remains insufficiently studied. However, this species can, from 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 BRTE-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

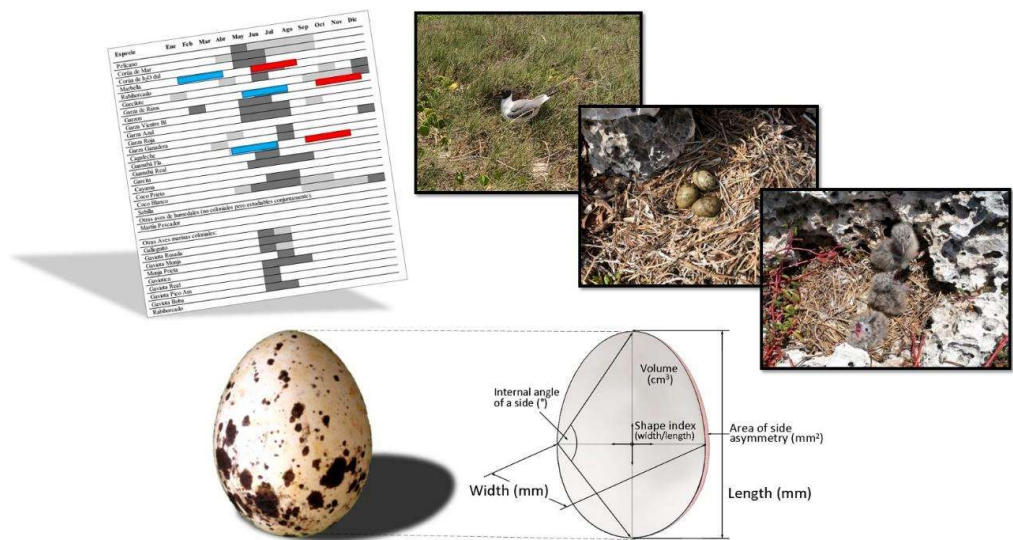
Chapter 5: Trophic niche plasticity of Bridled Tern

of health risks associated with socioeconomic activities (industry, fishing, tourism) carried out in coastal and marine areas of this region. In addition, long-term monitoring of the annual plasticity of the BRTE trophic niche could contribute, together with indicators of breeding success, to detect 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). The consumption of specific prey and the reduction of foraging range highlight the pre-laying and chick-rearing phases as stages of high vulnerability within the annual cycle of BRTE in Cuba.



**Chapter 6:**

**Breeding phenology and egg morphometry in a tropical Laridae community**



Associated publication  
 Garcia-Quintas A., Denis D., Barbraud C. & Lanco Bertrand S. (*In Prep.*) Breeding phenology and egg morphometry in a tropical Laridae community.



## **6.1 Introduction**

The ecology of tropical seabirds is in general poorly known, including their breeding phenology (e.g. Passuni *et al.*, 2016; Surman *et al.*, 2012). Nevertheless those tropical species are displaying very different breeding patterns (synchrony, asynchrony, seasonality, periodic breeding, episodic breeding, aseasonal breeding), contrary to temperate or polar seabird species which generally breed seasonally and synchronously (Hamer *et al.*, 2002). Knowledge of breeding phenology is essential to understand seabird ecology as it is a potentially highly variable life-history trait that impact breeding success and population dynamics (Lindén, 2018; Quintero *et al.*, 2014; Reed *et al.*, 2009). Indeed, the timing of breeding is crucial for breeding success since it is closely related with local environmental conditions and prey abundance (Brandl *et al.*, 2019; Englert Duursma *et al.*, 2018; Reed *et al.*, 2009), although it also has a hereditary component (Dobson *et al.*, 2017; Moiron *et al.*, 2020). Breeding phenology influences clutch size, chick growth, and probabilities of predation, all potentially affecting breeding success.

Variations in laying phenology among females may also influence egg features (Bridge *et al.*, 2007; Reed *et al.*, 1999; Zhang *et al.*, 2015). Generally, eggs produced early in the breeding season (early eggs) have larger size (Fernández & Reboreda, 2008), volume (Gronstol, 1997) and better internal composition (Bridge *et al.*, 2007) than those laid later (late eggs). These differences reflect the physiological state and level of maternal investment in eggs production (Boersma & Rebstock, 2010; Reed *et al.*, 1999), resulting from hereditary characters, prey availability, age and experience of females (Denis, 2014; Fernández & Reboreda, 2008; Ramírez-Arrieta *et al.*, 2021). In consequence, except in a few cases (e.g. Massaro & Davis, 2004), early eggs have higher probabilities of success compared to late eggs due to temporal matching with optimal environmental conditions (climatic and trophic), and because they are laid by females with better physical conditions that produce chicks with higher growth rates and survival (Cram *et al.*, 2019; Reed *et al.*, 1999; Zhang *et al.*, 2015).

Cuba is a tropical archipelago that hosts a large seabird community (Bradley & Norton, 2009) where the Laridae family (gulls, terns and skimmers) is the best represented group (Jiménez *et al.*, 2009; Navarro, 2021). Nevertheless, breeding phenology of this seabird family is practically unknown in the archipelago and in tropical areas more generally. In addition although laying phenology and its relationship with egg characteristics and chick survival has been documented in several Laridae species (Williams, 1994), it also remains poorly known in tropical areas. Therefore, the aims of this study are to (1) characterize the breeding phenology of Laridae species in Cuba and (2) assess whether egg morphometry varies as a function of laying phenology for these species.

## **6.2 Materials and methods**

### **6.2.1 Study sites**

The study was conducted in three cays of the Sabana-Camagüey archipelago in the central-north region of Cuba (Fig. 3.1). Climatological data, obtained from the Meteorological Station

78339 (located at the Coastal Ecosystem Research Center, Cayo Coco), indicate that the climate is tropical, showing a moderate and stable thermal regime with annual averages of temperature and precipitation accumulation of 26.3 °C and 88.5 mm, respectively. Easterlies prevail along the year with an average annual wind speed of 14.5 km.h<sup>-1</sup>. The average temperature between May and August (core breeding season of most seabirds in Cuba, Garrido & Kirkconnell, 2011) is 28.0 °C and precipitations average 109.2 mm.

Field studies were conducted at Felipe de Barlovento (FB), Felipe de Sotavento (FS), and Paredón de Lado (PL) cays, all < 0.1 km<sup>2</sup> (Fig. 3.1) and covered with sandy-rocky substratum with little vegetation. Mosaics of sandy and rocky coastal vegetation and mangroves (composed by *Conocarpus erectus* exclusively) are the main plant formations (González-Leiva & González-Pérez 2021), although an extended grassland dominated by *Uniola paniculata* occurs in FS. Plant richness is low (28 species) without significant seasonal variations, while species numbers by cay are 19 (FS), 17 (FB), and nine (PL) (González-Leiva & González-Pérez 2021). These cays constitute one of the most important breeding locality for seabirds in Cuba.

### **6.2.2 Fieldwork**

Weekly surveys between May and August 2021 were undertaken in each study cay to monitor the phenology of breeding colonies of Laridae. Surveys were performed between 09:00 am and 10:00 am to minimize the disturbance in colonies. During surveys, we recorded the presence of adults, nests, eggs, chicks or fledglings. Additionally, we counted the number of eggs per nest by species through a longitudinal 2 m-wide linear transect in FB to detect the time of the laying peak (defined as two consecutive surveys with a stable egg number). The transect was implemented in FB since this cay supports the larger breeding species richness of Laridae.

Once laying started, seven camera traps (WCB-00116 – BirdCam Pro) were settled near established colonies at the three cays in order to obtain more detailed information about the reproductive phenology of Laridae (e.g. duration of hatching and chick rearing). Cameras were installed at 0.5 m from the nesting sites, although for dense colonies this distance was increased to 1 m. Each camera was programmed to take a photo (resolution = 2592 x 1944 pixels, off flash) after 10 s of any activation of the motion sensor (low sensitivity). We placed one camera per nest for loosely colonial species, while for highly gregarious species one camera included several nests within the observation field. The locations of the cameras were changed weekly to another nesting site without repetitions until chicks left the nests. This allowed accounting for the phenological variability between breeding pairs during camera sampling. Data from camera traps and weekly surveys were used to estimate the duration of the phenological events.

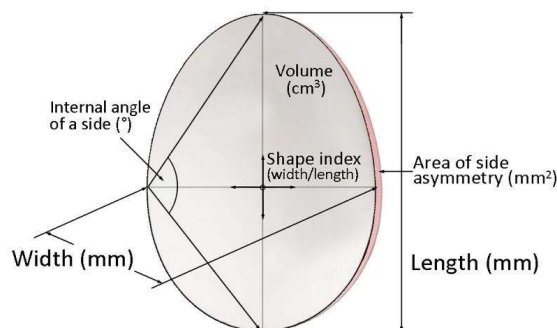
To describe the breeding phenology of Laridae we considered seven periods that we observed during the study: (1) Courtship, the period including any type of adult interaction to constitute a pair or to attempt copulation; (2) Copulation; (3) Laying, the period extending from the first egg observation to a stable number of eggs; (4) Incubation from the first egg to the absence of eggs (apparently failed or abandoned eggs were excluded); (5) Hatching, the period between first chick observation to the absence of eggs (apparently failed or abandoned eggs were excluded); (6) Rearing, the period of parental care from hatching of the first egg to all chicks

became fledglings; (7) Fledgling, the period extending from the first fledgling observation to the end of the monitoring period.

### 6.2.3 Acquiring and processing egg photos

We selected two groups of eggs respectively corresponding to the beginning and the end of the laying period for those species that exhibited asynchronous laying. Each egg found in a nest was photographed with a mobile camera (resolution = 8 megapixels) according to a standardized procedure (Ramírez–Arrieta *et al.*, 2021). Each egg was set on a red bristol paper with a millimetric scale, fixed in a position that allowed to see one full side of the egg, and a photo was taken in a perpendicular position relative to the main egg axes. We paid attention to have a homogeneous lighting over the surface on which photos were taken to avoid interference during posterior digital processing.

Egg images were processed with the Ovometrik application (Ramírez-Arrieta *et al.*, 2021) implemented in R 4.1.1 (R Core Team, 2021). Images were binarized, the pixel units were transformed to millimeters with the reference scale, the coordinates of the egg contour were extracted using the Claude (2008) algorithm, and a series of morphometric variables were automatically calculated. Six variables were selected (Fig. 6.1) including Length (mm), Width (mm) and Volume ( $\text{cm}^3$ ), and three variables that described the egg shape: Area of lateral asymmetry ( $\text{cm}^2$ ), Shape index (width/length) and Internal angle of a side ( $^\circ$ ). The volume was estimated by the allometric formula described by Hoyt (1979).



**Figure 6.1.** Morphometric variables used to characterize the eggs morphology of tropical Laridae.

### 6.2.4 Data analysis

Associations among egg morphometric variables by species were assessed through Pearson's correlation tests. Clutches were classified as early and late, according to laying date for species with two distinct laying periods within the breeding season. Comparison of egg characteristics among early and late clutches was performed through Wilcoxon-Mann-Whitney tests to assess the potential effects of laying phenology on morphometry of eggs. The *post hoc* statistical

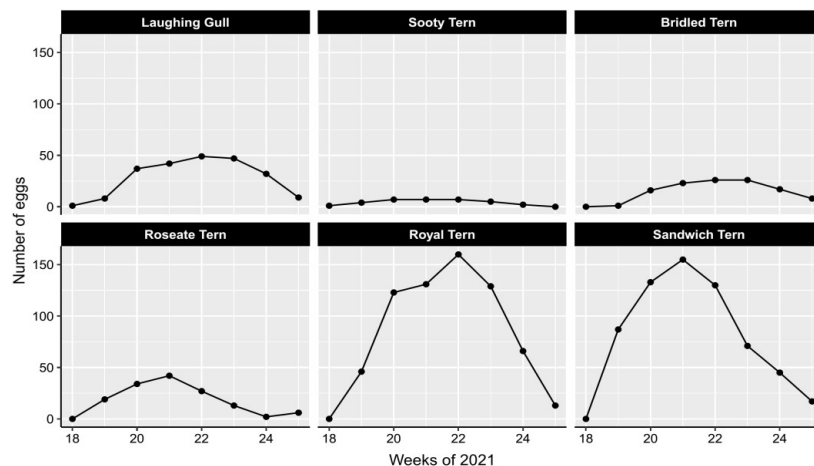
power was computed. Outliers were discarded in all analysis and significance was considered for  $p < 0.05$ . Correlations and comparisons were carried out in R 4.1.1 (R Core Team, 2021) whereas statistical power was computed in the G\*Power 3.1.9.4 software (Faul *et al.*, 2007).

### 6.3 Results

Seven Laridae species nested in the study sites. These were Laughing Gull *Leucophaeus atricilla* (LAGU) in FB and PL, Brown Noddy *Anous stolidus* (BRNO) in FB and FS, Sooty Tern *Onychoprion fuscatus* (SOTE) 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 *Thalasseus sandvicensis* (SATE) in FB. BRNO had only two nests that were directly monitored.

#### 6.3.1 Breeding phenology

According to transect surveys the peak of laying for all breeding species occurred between weeks 20 and 22, corresponding to 17 May – 6 June (Fig. 6.2). Sampling with camera traps included nesting sites of five species where the effectiveness (*i.e.* the proportion of useable photos) of registered photos exceeded 70% (Table 6.1).



**Figure 6.2.** Weekly egg counts of six Laridae species along a longitudinal transect in Felipe de Barlovento cay, central-north of Cuba, during the 2021 breeding season.

SOTE, ROST and SATE exhibited a high level of breeding synchrony as they all reached the laying peak three weeks after the onset of laying (Fig. 6.2). BRTE and ROYT lasted four weeks to reach laying peak (Fig. 6.2). LAGU had a staggered laying that took five weeks to reach peak (Fig. 6.2), so its breeding phenology was the least synchronous with respect to the other species. In general, there was a high temporal coincidence between the phenological periods of the breeding species (Fig. 6.3). The main differences occurred between the relative duration of the incubation, hatching and rearing periods. LAGU, BRTE, ROST, ROYT, and SATE exhibited

two separated laying periods producing chicks in both, but ROST failed producing chicks at the second laying period (Fig. 6.3).

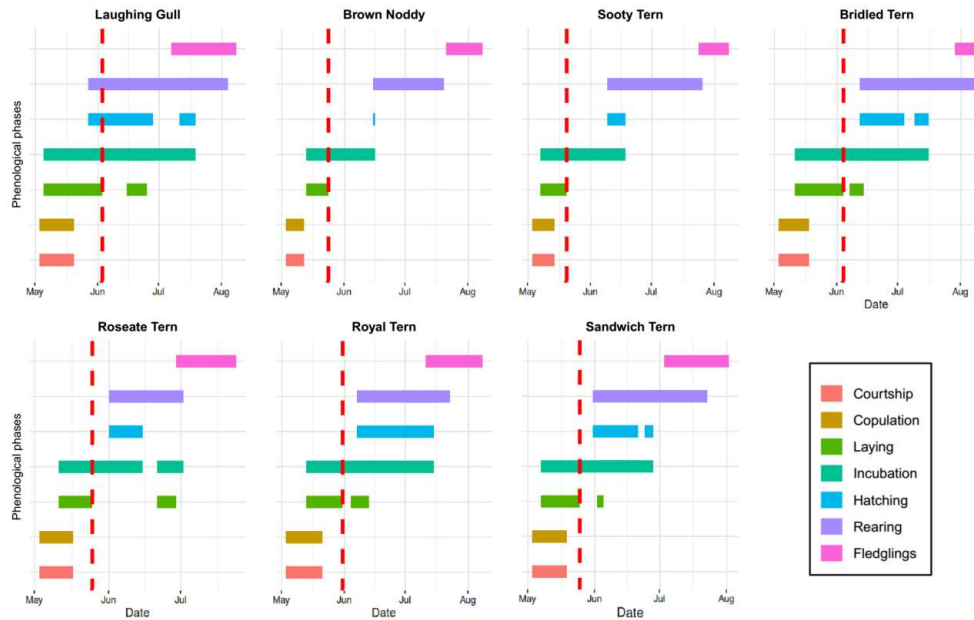
**Table 6.1.** Characteristics of sampling nesting sites of Laridae species in three cays of central-north of Cuba during the 2021 breeding season using camera traps.

Monitored species	Cay	Duration of the monitoring (days)	Number of monitored nests	Number of recorded photos	Number of usable photos
Laughing Gull	Felipe de Barlovento	27	4	9937	9240 (93.0 %)
	Felipe de Sotavento	8	2	1276	944 (74.0 %)
	Paredón de Lado	8	2	1032	990 (95.9 %)
<b>Total</b>		<b>29 (without duplicates)</b>	<b>8</b>	<b>12245</b>	<b>11174 (91.3 %)</b>
Brown Noddy	Felipe de Sotavento	72	1	994	847 (85.2%)
	<b>Total</b>	<b>72</b>	<b>1</b>	<b>994</b>	<b>847 (85.2%)</b>
Bridled Tern	Felipe de Sotavento	47	6	4026	3090 (76.8 %)
	Paredón de Lado	6	1	6441	4632 (71.9 %)
	<b>Total</b>	<b>47 (without duplicates)</b>	<b>7</b>	<b>10467</b>	<b>7722 (73.8 %)</b>
Royal Tern	Felipe de Barlovento	18	ca.10	2690	2449 (91.0 %)
	Paredón de Lado	27	13	4118	3924 (95.3 %)
	<b>Total</b>	<b>36 (without duplicates)</b>	<b>ca.23</b>	<b>6808</b>	<b>6373 (93.6 %)</b>
Sandwich Tern	Felipe de Barlovento	23	ca.18	9169	8833 (96.3 %)
	<b>Total</b>	<b>23</b>	<b>ca.18</b>	<b>9169</b>	<b>8833 (96.3 %)</b>

### 6.3.2 Morphometric characteristics of early and late eggs

Early and late eggs could only be measured for LAGU, BRTE, ROST and ROYT. BRTE eggs presented the largest number of significant correlations among their morphometric variables (Annex 10). Length-width, length-volume and width-volume combinations were positively and highly ( $p < 0.001$ ) correlated in all species (Annex 10). The length- and internal angle were positively correlated in LAGU ( $p < 0.05$ ) and BRTE ( $p < 0.001$ ) eggs, as well as the asymmetry area and internal angle in BRTE eggs ( $p < 0.05$ ) (Annex 10). Negative correlations ( $p < 0.05$ ) were also found between the shape index and internal angle for BRTE and ROST eggs, and between width and internal angle of ROST and ROYT eggs (Annex 10).

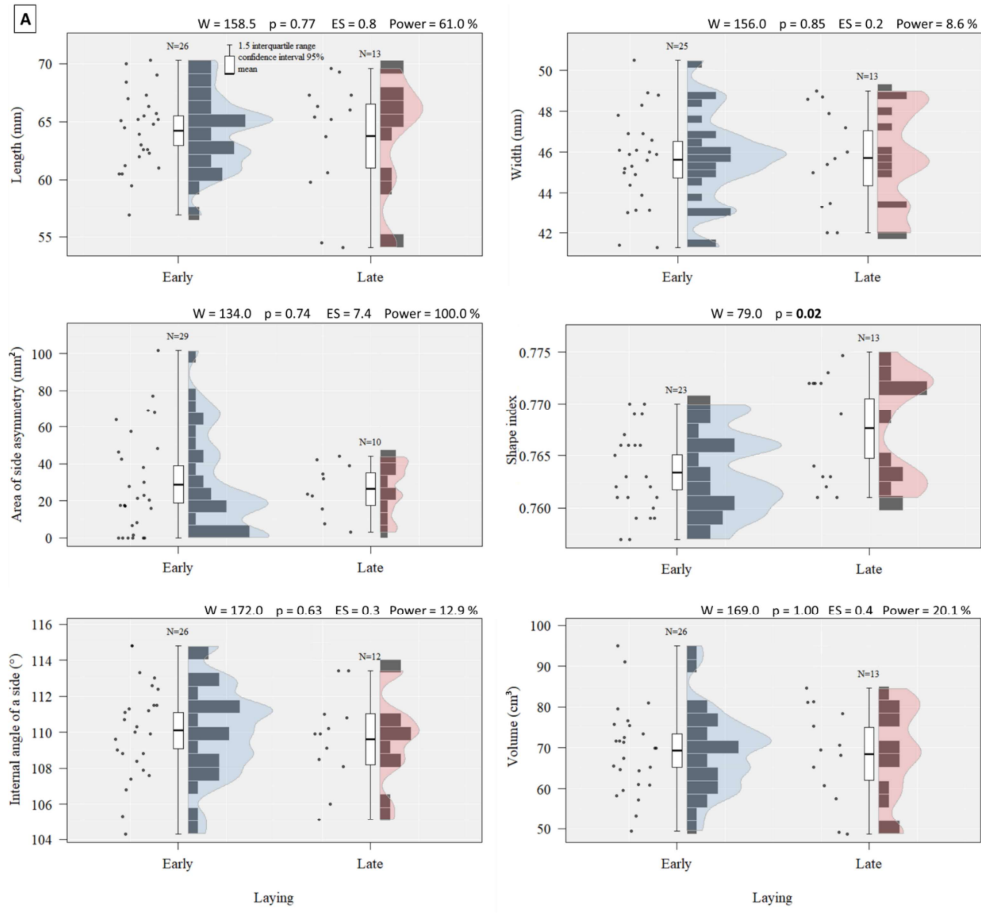
*Chapter 6: Breeding phenology and egg morphometry of larids*



**Figure 6.3** Breeding phenology of seven Laridae species in three cays of central-north of Cuba during the 2021 breeding season. Dashes red lines indicate the laying peak.

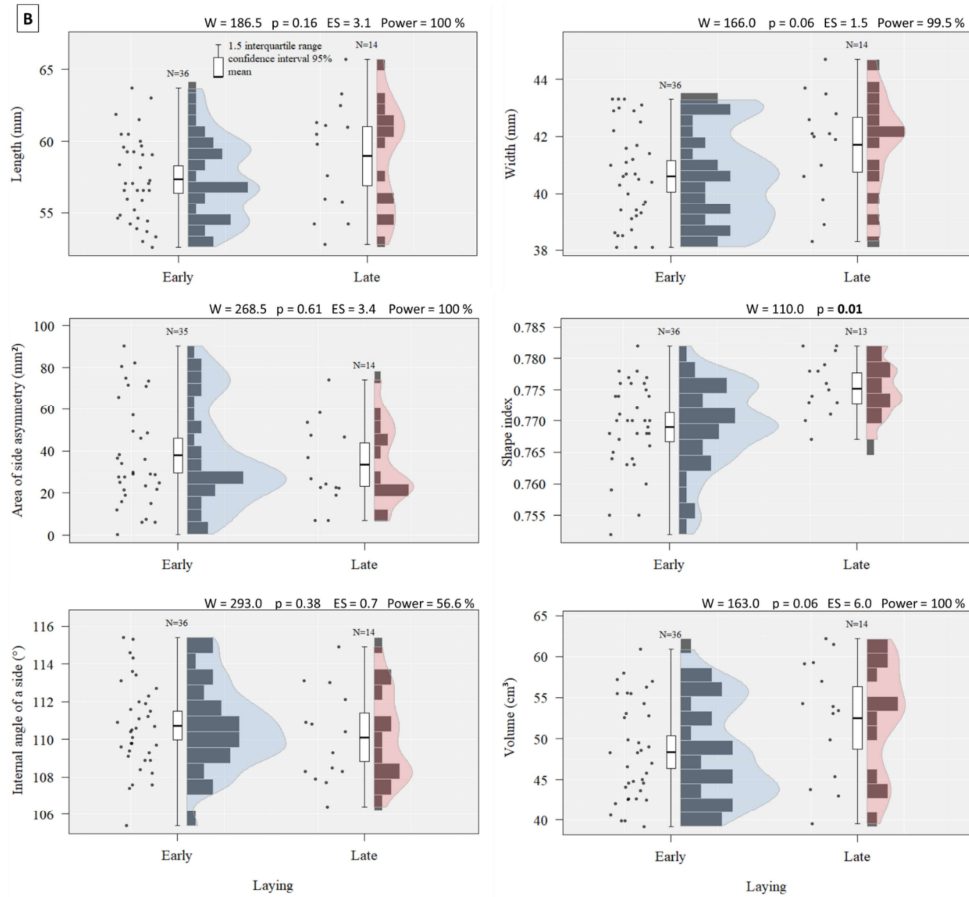
In general, few significant differences were found in the morphometry of early eggs with respect to late eggs of the studied species. Only late eggs of LAGU and BRTE were more rounded (higher shape index) than early eggs (Fig. 6.4 A & B). No significant difference was found in the length, width, area of side asymmetry and volume of BRTE eggs; or in the length, area of side asymmetry, internal angle and volume of ROST eggs (Fig. 6.4 B & C). There was also no difference in the length, area of asymmetry and internal angle among ROYT eggs; or in the area of lateral asymmetry of LAGU eggs (Fig. 6.4 A & D). For the remaining compared variables there was not enough statistical power (< 80 %) to support the apparent similarities found (Fig. 6.4).

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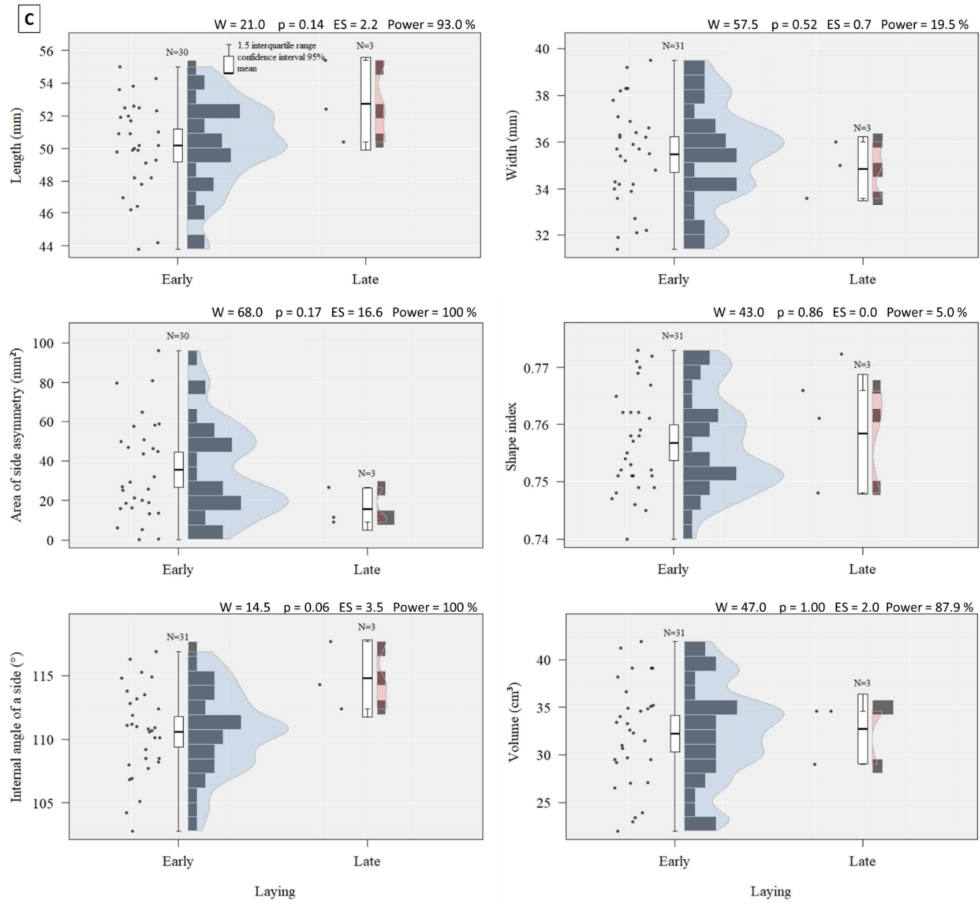




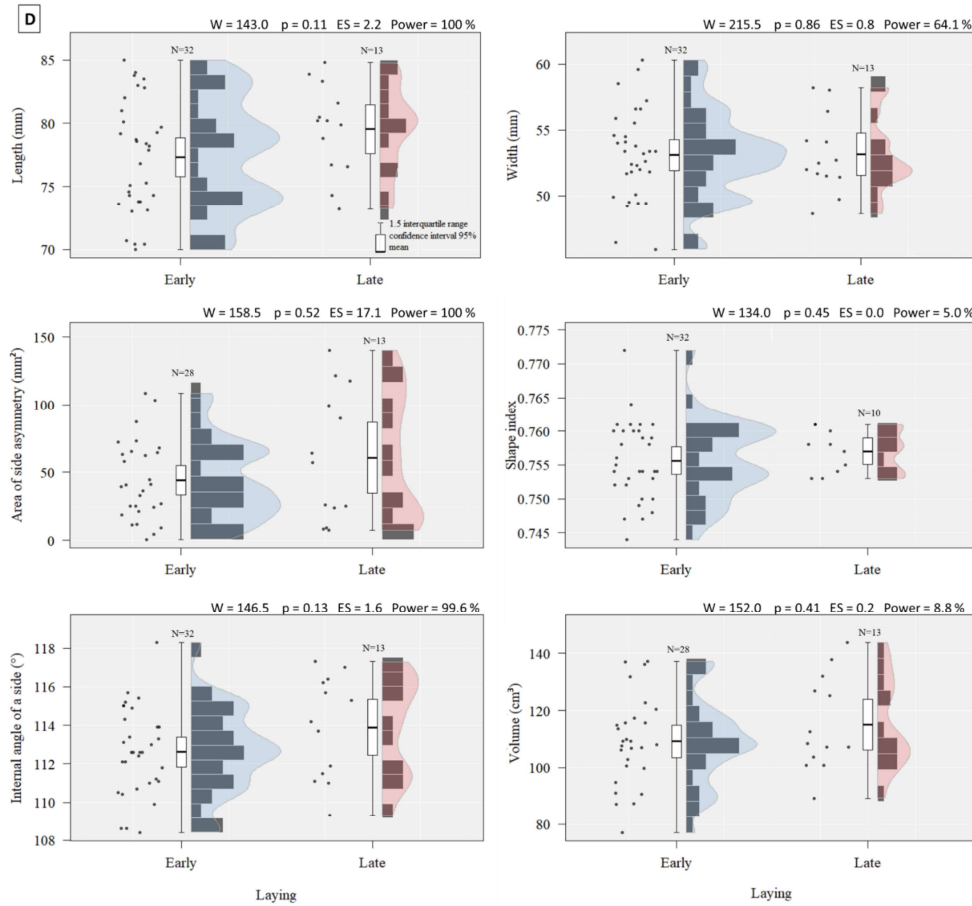
*Chapter 6: Breeding phenology and egg morphometry of larids*



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**Figure 6.4.** Comparing the morphometry of early and late eggs of four Laridae species during the 2021 breeding season at three northern-central cays of Cuba. Significance ( $p < 0.05$ ) is indicated in bold. ES = Effect size. A = Laughing Gull (*Leucophaeus atricilla*), B = Bridled Tern (*Onychoprion anaethetus*), C = Roseate Tern (*Sterna dougallii*), D = Royal Tern (*Thalasseus maximus*).

### 6.4 Discussion

Breeding phenology is a crucial component on the reproductive ecology of seabirds due to its influence on individual fitness, reproductive success, and population dynamics (Black *et al.*, 2018; Dunn & Møller, 2014). Moreover, inter-annual phenological changes in seabirds breeding phenology can reflect changes in weather and food webs of marine ecosystems (Hindell *et al.*, 2012). This work offers a more comprehensive characterization of Laridae breeding phenology in Cuba, highlighting the relative breeding synchrony between species. Although limited, previous studies (*e.g.* Garrido and Kirkconnell, 2011; Rodríguez *et al.*, 2003) suggested that the reproduction of Laridae in Cuba generally occurs between May and August.

## Chapter 6: Breeding phenology and egg morphometry of Laridae

Results from these earlier studies and ours indicate that Laridae breeding phenology in Cuba is seasonal and relatively synchronous. However, inter annual breeding phenology should be studied during consecutive years to assess whether synchronous breeding occurs annually.

This seasonal and synchronic character of the Laridae breeding phenology could be due to several factors linked to the characteristics of Cuba's climate. The breeding period of these birds is framed within the rainy season in Cuba (May-October), characterized by little daily variation in meteorological conditions with an influence of the North Atlantic Anticyclone ([www.insmet.cu](http://www.insmet.cu)). The most drastic changes are caused by disturbances of the tropical atmospheric circulation such as easterly waves and tropical cyclones. This seasonal weather pattern contrasts with the low rainy season (November-April) during which abrupt daily weather changes predominate due to the influence of frontal systems, of the continental anticyclone and of extratropical low pressure centers ([www.insmet.cu](http://www.insmet.cu)).

Seabirds may adjust their breeding phenology depending on signals they pick up from local weather (Surman *et al.*, 2012b). In our study area, stable weather conditions during the rainy season likely cause predominance of calm sea surface waters, which may facilitate prey capture by surface dipping and shallow diving by species such as gulls and terns. Prey availability and abundance could also be higher during this season. In tropical regions, rainfall abundance is often associated with food availability for birds (Quintero *et al.*, 2014), which could explain the reproduction of Laridae within the rainy season in Cuba. Rainfall could increase runoff to the sea, which is likely to increase nutrient inputs to marine food webs.

On the other hand, the frequent occurrence of rainfall has an impact on vegetation cover, favoring the appearance of annual plants and increasing leaf cover in general. Thus, during the rainy season, vegetation cover increases in the cays with colonies of Laridae. As high vegetation cover and the presence of certain plant species are important variables for the selection of the breeding microhabitat for most of these seabirds (Garcia-Quintas *et al.*, 2023), this could be another contributing factor to the seasonal and synchronous breeding phenology of Laridae in Cuba. Finally, the residence status of the species may also be determinant in this regard. BRNO, SOTE, BRTE, ROST and SATE are essentially summer residents (Garrido & Kirkconnell, 2011), and must synchronise their breeding during their stay in Cuba to ensure that their offspring are able to fly south at the end of the season. LAGU and ROYT are permanent residents (Garrido & Kirkconnell, 2011) that could breed with the other species by taking advantage of the climatic conditions aforementioned and the advantages of collective nesting (*e.g.* increased brood monitoring and exchange of information on optimal foraging areas).

Despite the relative synchrony and seasonality in laying, five out of seven studied species had two distinct laying periods. In general, the first laying period lasted longer than the second laying period. This appears consistent with the advantages of early nesting within the breeding season (*e.g.* Dobson *et al.*, 2017; Dunn & Møller, 2014; Moiron *et al.*, 2020; Sydeman & Emslie, 1992). The short duration of the second laying period and limited number of breeding individuals could come from uncompetitive females unable to occupy nesting sites early in the season, females in a second breeding attempt due to failed early laying and/or young/inexperienced females.

Only the shape index reflected significant differences between early and late eggs of LAGU and BRTE. Egg shape is an important life history trait in birds (Ramírez–Arrieta *et al.*, 2021) due to its adaptive value regarding nesting site characteristics, heat conservation, incubation efficiency, egg structural strength, and gasses exchanges (Chowdhury *et al.*, 2020; Denis & Olavarrieta, 2011; Ramírez–Arrieta *et al.*, 2021). Denis (2014) and Ramírez–Arrieta *et al.* (2021) found that egg shape has a strong genetic basis and is related to species body mass, internal anatomy of the oviduct and laying date. The more rounded shape in the late eggs of LAGU and BRTE could result from a less flexible oviduct of these females (perhaps younger than the first ones). It could also maximize the heat conservation and shell resistance (Denis, 2014) as a strategy to increase hatching success when antipredator protection by grouping-effect is reduced compared to early layings. However, rounded eggs have a higher risk of falling from the nest. Both LAGU and BRTE are species that use the largest variety of nesting substrates in the study cays, so the shape of their eggs may be key to reduce the risk of accidents due to the terrain characteristics (García-Quintas *et al.*, 2023). Normally, the elongated shape of the eggs (more pronounced in the early ones) contributes to their stability in the nest reducing the probability of falling (Denis, 2014). Among species, the most elongated eggs were those from ROYT. This possibly decreases the risk of the eggs rolling off the nesting site (by strong winds, pushed by neighboring seabirds) since both species lay directly on the substrate, in fully open areas and very dense colonies (García-Quintas *et al.*, 2023). On the contrary, the more rounded eggs in BRTE could match with the fact that this species forms more spatially dispersed colonies and lays also on bare substrates, but in sites highly protected by different cover types (García-Quintas *et al.*, 2023). Finally, the shape of LAGU eggs does not appear to result from selective pressures to maximize hatching success since this is the only species that builds nests as such, maximizing clutch protection and eliminating the likelihood of egg rolling.

Early and late tern eggs (BRTE, ROST and ROYT) were highly similar considering that several of the morphometric variables measured did not differ, while LAGU eggs did not differ only regarding the area of lateral asymmetry. However, in the latter it was impossible to detect reliable patterns of oologic variation given the low statistical power in the comparison of most variables. In general, intra-seasonal variations in egg morphometry have been little studied but Parsons (1976) found that early eggs of Herring Gull (*Larus argentatus*) were larger than the later ones. Nevertheless, the little differentiation found between early and late eggs of terns in this work could be due to the climatic and oceanographic conditions of the study region. Tropical waters of Cuba exhibit a low intra-seasonal variation of sea surface temperature and Chlorophyll *a* concentration, considered as proxies of marine productivity (Vilchis *et al.*, 2006). Hence, this could result in enough food resources during the breeding season allowing early and late breeders to produce similar egg morphometry. However, the impossibility to evaluate the differences between some of the measured variables (due to low statistical power) clearly indicates the need to increase sample sizes (especially of late clutches, Fig. 6.4) and to extend spatially and temporally this experiment to obtain accurate inferences.

Among species, linear dimensions and volumes reflected that the smallest eggs corresponded to ROST and BRTE, while LAGU and ROYT produced the largest eggs. This matches directly with the body (and probably oviduct) size of these species. However, LAGU is larger than

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ROYT but its eggs were smaller. This may be because LAGU produced larger clutches (1-3 eggs), so females had to share their energy reserves to produce the structural components of several eggs, while ROYT females produced a single egg.

Based on our findings, the morphological similarity among early and late clutches for species that showed two distinct laying periods prevent using egg morphometry as a proxy of intra-seasonal laying asynchrony of Laridae in Cuba. Some eggs morphometric variables such as the shape index could be used to distinguish early from late clutches in species such as LAGU and BRTE. Because of the great natural variability in oological morphology between bird clutches (Nedomová & Buchar, 2014; Ricklefs *et al.*, 1978) we recommend spatial and temporal replication of this study to assess morphological variation in tropical seabird eggs based on laying phenology.

## Chapter 7:

### Prioritization of conservation areas of breeding Laridae in Cuba under current and future development plans



#### Associated publication

Garcia-Quintas A., Brunel A., Barbraud C., Denis D., Omer J. & Lanco Bertrand S. (*In Prep.*)  
Prioritization of conservation areas of breeding Laridae in Cuba under current and future development plans.



## **7.1 Introduction**

Seabirds constitute one of the most threatened groups of birds in the world, with a deteriorating conservation status in recent decades (Croxall *et al.*, 2012; Dias *et al.*, 2019) together with insufficient levels of effective conservation in many marine protected areas -MPAs- (Lescroël *et al.*, 2016; Opper *et al.*, 2018; Yorio, 2009). The alarming degree of threats to seabirds results from a synergy of disturbances with natural and anthropogenic origins. Nisbet (2000) and Dias *et al.* (2019) defined “disturbance or threat” as any human activity or another factor that produces some effect on birds. Human disturbances can affect, directly or indirectly, the survival and breeding of seabirds. More precisely 75% of the four major threats worldwide over these animals (invasive alien species, bycatch, climate change or severe weather and overfishing) derive from human activities (Anderson *et al.*, 2018; Dias *et al.*, 2019; Mitchell *et al.*, 2020). However, the effects of disturbances are not always significant and the vulnerability is species-specific (Beale and Monaghan, 2004; Becker *et al.*, 2016).

The Laridae family as a whole (gulls, terns, and skimmers) has a good conservation status (<25% of threatened species) relatively to other groups of seabirds (Croxall *et al.*, 2012; Dias *et al.*, 2019). Nevertheless, these species usually forage and breed in habitats highly disturbed by human activities leading to a potential disruption of the seabird colonies. In the Caribbean for example, coastal zones are submitted to an increasing exploitation by commercial, touristic and recreational interests that provoke significant and growing disturbances to breeding seabirds (among which a large share of Laridae) (Croxall *et al.*, 2012; Mejías *et al.*, 2020; Norton, 2009). In Cuba in particular, the increase of coastal tourism activities and the introduction of alien species are serious threats for the reproduction of seabirds (Jiménez *et al.*, 2009).

On one hand, breeding ecology of Laridae in Cuba is practically unknown despite the existence of a large number of breeding colonies. The possible impacts of human activities on the foraging and breeding success of these birds have not been studied neither. Jiménez *et al.* (2009) highlighted the need to identify and quantify the factors affecting the survival of seabird adults and chicks to improve their management and conservation in Cuba. This could contribute to preserve key ecosystem services (*e.g.* regulation of prey populations, fertilization of the substrate through production of guano) and biodiversity in general (Jones *et al.*, 2008), and to characterize the distribution of contaminants in the marine environment if using seabirds as sentinels (Gilmour *et al.*, 2019).

On the other hand, the Caribbean region as a whole, and Cuba in particular (48% of this region's emerging lands), has among the lowest surface of protected areas in the world. Moreover, the gradual opening of Cuba to foreign investment could trigger a genuine explosion of human activities in the coming years. The current MPAs of this country were established mostly based on strictly marine species (*e.g.* fishes, coral reefs, turtles, mammals) or noteworthy cay landscapes. The inclusion of seabirds as a conservation target is limited to few places hosting breeding colonies and their adjacent waters at short distances. Thus, the lack of inclusion of a functional ecological approach to breeding sites of seabirds (combining nesting and foraging



areas) appears to be an important shortcoming of the current MPAs to reach an effective conservation of the Cuban natural legacy.

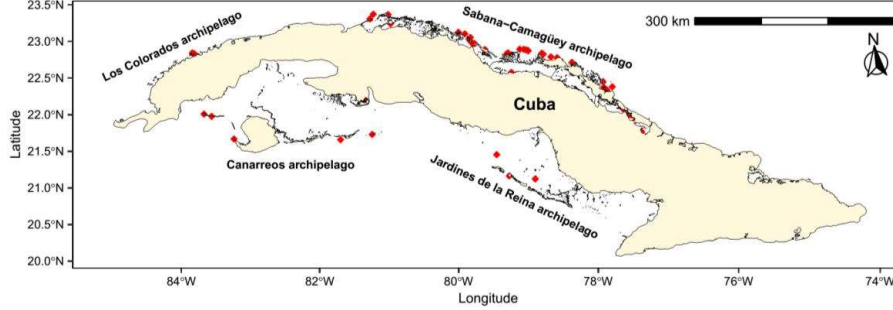
The design of MPAs is a process requiring consensus among stakeholders and negotiations are fed with cross-disciplinary and spatially explicit data (*e.g.* ecological, economic, legal, social; Brunel and Lanco Bertrand, 2023). In this decision-making framework, decision support tools are useful to avoid *ad-hoc* and opaque conservation choices (Pressey, 1994; Pressey and Tully, 1994). In particular, the reserve site selection problem is commonly addressed mathematically using an integer programming framework (Cocks and Baird, 1989; Margules and Pressey, 2000). The reserve site selection problem is expressed as an optimisation problem under constraints. The solution of this problem is the least-cost reserve that meets predefined conservation targets. The recent emergence of efficient exact optimisation solvers (Beyer *et al.*, 2016; Hanson *et al.*, 2019; Schuster *et al.*, 2020) allows to quickly solve real-world instances in practice. Such methods are implemented in common decision support tools (*e.g.* PrioritizR (Hanson *et al.*, 2022)).

In this study, we implemented systematic reserve site selection algorithms to identify areas to prioritize for the conservation of the Laridae colonies in Cuba, considering four of the most important human disturbances in the country: fishing, wind farms, coastal tourism and nightlight pollution. Several conservation scenarios were tested by setting different protection targets of the considered conservation features (*e.g.* number of colonies, threatened species, breeding habitat suitability), as well as different weights assigned to the human activities. A future conservation scenario was also modelled taking into account the wind turbine development plan of Cuba. Finally, the priority conservation areas identified by the model were compared with the current national system of MPAs to highlight shortages and conservation needs in the face of the existing human disturbances in Cuba. Then our aims are 1) to identify priority areas for the conservation of breeding habitats of Laridae in Cuba considering several scenarios with current and future human disturbances, and 2) to compare the coverage of the proposed conservation areas with the current MPAs system of the country.

## **7.2 Material and methods**

### **7.2.1 Study area**

This study focuses on the coastal ecosystems of the Cuban archipelago (Fig. 7.1). Cuba is the largest Caribbean Island (length = 1256 km, maximal width = 191 km) and includes four insular groups (Los Colorados, Sabana-Camagüey, Canarreos and Jardines de la Reina) featuring > 1600 cays (small, low-elevation, sandy islands on the surface of coral reef) and islets displaying large variability in terms of relief, geology and landscapes.



**Figure 7.1.** Study region: breeding habitats of Laridae (red diamonds = locations of recorded colonies) in Cuba.

### 7.2.2 Systematic reserve site selection model

In a reserve site selection problem, the study area is discretized into a set  $J$  of *planning units* within which a set  $I$  of *conservation features* are distributed. A planning unit is one pixel of the gridded study area. A conservation feature is a biotic or abiotic entity considered in the conservation scope (*e.g.* species, habitats, evolutionary process, cultural traditions.). The amount of a conservation feature  $i \in I$  within the planning unit  $j \in J$  is denoted  $a_{ij}$ . Each planning unit has a cost  $c_j$ . The cost represents the socio-economic cost from a manager perspective when human activities are removed from the planning unit. One then seeks to find the least-cost collection of planning units covering sufficient levels of each conservation feature. The coverage of the conservation feature  $i$  is considered sufficient if it exceeds a user-defined target  $t_i$ .

The decision is about whether to include the planning unit in the reserve. Consequently, we associate the decision variables  $x_j$  with each planning unit  $j$ :  $x_j = 1$  if a planning unit  $j$  belongs to the reserve and  $x_j = 0$  otherwise. Since a small perimeter involves a compact reserve, the reserve perimeter is included in the objective function. The perimeter is computed as the total length of the boundaries between reserved and non-reserved planning units. To model this, the length of the shared boundary between planning units  $j_1$  and  $j_2$  is denoted  $b_{j_1 j_2}$ . A multiplier, denoted  $\beta$ , is used within the objective function to reflect the importance of compactness relatively to the total cost of the site selection. The bigger the  $\beta$  multiplier, the more spatially aggregated the computed reserve. Mathematically speaking, the general problem of reserve site selection is expressed as the following combinatorial optimisation problem  $P_0$ :

$$P_0 : \begin{cases} \min_x & \sum_{j \in J} c_j x_j + \beta \sum_{j_1 \in J} \sum_{j_2 \in J} b_{j_1 j_2} x_{j_1} (1 - x_{j_2}) \\ \text{s.t.} & \sum_{j \in J} a_{ij} x_j \geq t_i & \forall i \in I \\ & x_j \in \{0, 1\} & \forall j \in J \end{cases}$$

In this work, we used the Cbc solver to get the exact solution of this optimisation problem. Cbc is a free and open-source solver (Forrest *et al.*, 2018) from the COIN-OR project (Lougee-Heimer, 2003). The code, developed in Julia language (Bezanson *et al.*, 2015, 2012) using the

JuMP optimisation library (Dunning *et al.*, 2017), is available on the GitHub repository <https://github.com/AdrienBrunel>. For more details, see Brunel *et al.* 2021 (<https://hal.science/hal-03445922>).

### **7.2.3 Conservation features**

Four conservation features related to the breeding habitats of Laridae were considered in this study: number of breeding sites (CF\_1), number of breeding species (CF\_2), number of threatened breeding species (CF\_3) and suitable breeding habitats in 2021 (CF\_4). Last are estimates of habitat suitability through a Convolutional Neural Network model using Landsat images of Cuba in 2021 (Chapter 1). We used the compiled database in (Annex 1), containing the names and coordinates of the 49 recorded breeding sites (Fig. 7.1), years of observation, breeding species and information sources. Registered breeding species of Laridae were laughing gull *Leucophaeus atricilla* (LAGU), brown noddy *Anous stolidus* (BRNO), sooty tern *Onychoprion fuscatus* (SOTE), bridled tern *Onychoprion anaethetus* (BRTE), least tern *Sterna antillarum* (LETE), gull-billed tern *Gelochelidon nilotica* (GBTE), roseate tern *Sterna dougallii* (ROST), royal tern *Thalasseus maximus* (ROYT) and sandwich tern *Thalasseus sandwicensis* (SATE). Breeding records of common tern *Sterna hirundo* were treated as ROST due to the misidentification of these colonies (Navarro, 2021; Nisbet, 2020).

Breeding sites were defined here as the combination of the terrestrial location used to nest and the surrounding marine areas used to forage (Chapter 1). Because of the absence of information on the foraging ranges of Cuban seabirds during their breeding period, we considered the estimated potential maximum foraging ranges during breeding for each studied species (Annex 5). Finally, we selected a maximum foraging range = 50 km considering it is representative of most of (89%) the study species.

Seabird conservation status for Cuba was obtained from González *et al.* (2012), considering the categories of vulnerable, endangered and critically endangered as representative of threatened species. According this classification, only ROST was classified as vulnerable and hence threatened. Its population declines and its breeding habitat becomes fragmented due to the growing tourism industry development and climate change effects (Blanco, 2012).

### **7.2.4 Anthropogenic activities and cost function**

In a systematic reserve site selection model, costs are assessed from a manager perspective (Brunel and Lanco Bertrand, 2023). In the present case study, costs were represented by human activities having a potential impact on the seabird conservation features. Four main sources of disturbances from human activities on breeding Laridae were identified: fisheries, wind farms, coastal tourism and nightlight pollution. The first three are priority socioeconomic activities for the Cuban government.

Fisheries are one of the most important socioeconomic activities of the country for local food supply and exportations. Cuban marine ecosystems are globally healthy and productive (Roman, 2018), yet they are not exempt of threats such as overfishing and use of destructive

fishing gears (Angulo-Valdes *et al.*, 2022; Giménez *et al.*, 2016). At worldwide level, commercial fisheries constitute one of the most important human disturbance that has produced strong population reductions and mortality of seabirds (Croxall *et al.*, 2012; Mínguez *et al.*, 2003; Mitchell *et al.*, 2020). Directly, commercial fisheries may provoke the mortality of seabirds through incidental bycatch on fishing gear (Afán *et al.*, 2019; Anderson *et al.*, 2018; Mitchell *et al.*, 2020), or may produce local depletions of prey fish becoming a direct competitor of seabirds (*e.g.* Bertrand *et al.*, 2012). Indirectly, the ship traffic may also affect the foraging, resting and breeding behaviors of seabirds and increase their energetic costs by escape reactions (Afán *et al.*, 2019; Lieske *et al.*, 2020; Mínguez *et al.*, 2003). In this study two variables were used as proxies of the fishing activity in Cuba: number of fishing ports (SC\_1) (PAN-Tiburones, 2015, including state and recreative fishing ports) and a semi-quantitative index of fishing derived from reefs areas (SC\_2). The semi-quantitative index is a modification of that established by González-Sansón *et al.* (2009), and ranked six fishing pressure categories taking into account the type of fishing (commercial or subsistence) and the accessibility to the coral reef (Table 7.1).

**Table 7.1.** Definition of six categories of a semi-quantitative index of fishing pressure in Cuba.

<b>Fishing pressure category</b>	<b>Definition</b>
Very low	Reefs which are very far (>30 km) from any urban center. Rare fishing due to effective enforcement of protected areas and fisheries regulations. Catch and release recreational fishing might be allowed.
Low	Reefs which are very far (>30 km) from any urban center. Few commercial vessels (< ~150) fish in these reef areas and target large-size species ( <i>e.g.</i> larger snappers, groupers, jacks).
Medium	Reefs which are very far (>30 km) from any urban center. Commercial vessels (~150 - 300) fish in these reef areas and target large-size species ( <i>e.g.</i> larger snappers, groupers, jacks).
High	Reefs which are very far (>30 km) from any urban center. Many commercial vessels (> ~300) and few live fishing boats fish in these reef areas and target large-size species ( <i>e.g.</i> larger snappers, groupers, jacks).
Very high	Reefs which are far from any urban center but near small coastal villages. Almost no commercial fishing and heavy live fishing pressure mostly with small boats.
Exceedingly high	Reefs which are near the coast in narrow shelf areas adjacent to large urban centers. A very high live fishing effort by people using small rafts, boats, spearguns, gill nets with small mesh size and traps.

The rapid increase of wind farms as renewable energy source constitutes a probable threat to seabirds especially coastal foragers like some of the Laridae species (Dias *et al.*, 2019). Multiple marine wind turbines inside the habitats used by seabirds could provoke direct mortality by collisions and behaviour alterations if birds avoid the wind structures footprint (Dias *et al.*, 2019; Lieske *et al.*, 2019). This could produce disturbances to feeding, roosting and breeding

seabirds including neglecting the broods (Lieske *et al.*, 2019). Although still poorly developed, the energy generation via wind farms already exists in Cuba and represents a national priority to modernize the energy generation matrix. Currently, this country has four small coastal wind farms working, a larger one in construction and 16 other in project (all relatively close to the coastline), representing a growing risk for seabirds. Four variables were defined to represent the disturbances involved by wind farms based on the characteristics of their wind turbines: number of wind turbines (SC\_3) and height (SC\_4), swept areas (SC\_5) and maximum rotation velocity (SC\_6) of the wind turbines ([www.thewindpower.net](http://www.thewindpower.net)). Moreover, the probable location of the projected wind farms (SC\_13) was accounted as a proxy for the future increase of the disturbances.

There are well-documented evidences about the harmful effects of coastal tourism over seabirds' populations. However, the sensitivity of seabirds to human disturbance is species-specific and depends on the disturbance type and intensity (Yorio *et al.*, 2001). Birdwatching is a common ecotourism activity that can produce several disturbances on breeding colonies including the destruction of nests (or their content), nest or offspring desertion by adults, offspring predation due to nest abandonment and reduction of nest densities (Carey, 2009; Velando and Munilla, 2011; Yorio *et al.*, 2001). The rest of tourism activities related to sea involves disturbances to seabirds through recreational marine traffic (leisure and touring boats, cruises) which may alter their behaviours at feeding and roosting areas; as well as a risk of injuries or death of birds by collisions with vessels (Lieske *et al.*, 2020, 2019; Marcella *et al.*, 2017). Tourism plays a pivotal role in the Cuban economy especially based on the activities of sun and beach, nautical activities, sport fishing, recreational diving and ecotourism. We used five variables to quantify the human disturbance by the marine-coastal tourism: number of hotels (SC\_7) and rooms (SC\_8) in coastal touristic poles, number of marinas and diving centers (SC\_9), number of practiced nautical activities (SC\_10) and the estimated number of tourists from May-August (matching with the Laridae breeding season in Cuba) of 2017-2019 (SC\_11) by touristic pole (Oficina Nacional de Estadísticas e Información de Cuba, updated inventory until 2020 of the Ministry of Tourism of Cuba, [www.nauticamarlin.com](http://www.nauticamarlin.com), [www.gaviota-grupo.com](http://www.gaviota-grupo.com)).

Nightlight pollution is a major and growing threat to seabirds, especially for nocturnal species such as petrels, shearwaters and some terns (Dias *et al.*, 2019; Gineste *et al.*, 2017). Artificial lights affecting seabirds are produced by urban centers and others infrastructures (*e.g.* industry, touristic pole, lighthouse) located at the coast and offshore, as well as by marine traffic (*e.g.* fishing fleets, cruise ships) (Gineste *et al.*, 2017; Lieske *et al.*, 2020, 2019). Basically, nightlight pollution can attract and disorient seabirds altering their migration and foraging behaviour, may cause changes in their reproductive physiologies and impact foraging through disruption of the diurnal vertical migration of zooplankton (Lieske *et al.*, 2020, 2019). The light attraction can provoke the direct mortality of adults and fledglings via collisions or secondarily by predation, starvation, hypo- or hyperthermia, and accidents with vehicles when birds remain stunted (Gineste *et al.*, 2017; Lieske *et al.*, 2019). Cuba has several marine and coastal sources of nightlight pollution including cities, small towns, touristic poles, industry zones and the infrastructure associated with marine traffic. We quantified the nightlight pollution of the

country with one variable obtained by teledetection: the median annual nighttime light in 2021 (SC\_12). This variable was taken from the annual 2021 VNL V2.1 image of the Visible Infrared Imaging Radiometer Suite Day/Night Band provided by the Joint Polar-orbiting Satellite System (Elvidge *et al.*, 2021). The image is a GeoTIFF normalized product (it excludes pixels contaminated by clouds, sunlight, moonlight, biomass burning) containing grid-values of radiance ( $\text{nW}/\text{cm}^2/\text{sr}$ ) with a resolution of 15 arc seconds ( $\sim 500\text{m}$  at the Equator), and was downloaded from <https://eogdata.mines.edu/products/vnl/>.

### **7.2.5 Formatting data**

All conservation features and socioeconomic costs were spatially represented. The area considered for each breeding site and breeding species was the disk with radius = 50 km centered at the colony. The suitable breeding habitats were represented in 9.0 x 9.0 km cells (Chapter 1). Spatialization of the semi-quantitative fishing index (values resulting from the median of the years with registers) was done following criteria of Cuban experts. The spatial allocation of hotels and rooms was pooled at touristic poles areas. The areas of influence of marine recreational activities were estimated differently depending if they relied on boat operation or not: sea areas of  $\sim 3$  nm (in latitude) and 8 nm (in longitude) centered on the position of facilities on land without boats operations, and  $\sim 5$  nm (in latitude) and 15 nm (in longitude) else. Only in Jardines de la Reina the latitudinal and longitudinal distances from the dive center were greater ( $\sim 40$  nm) because tourist activities are carried out from live-aboard vessels with wide mobility within that area (there is no dependence on a dive center per se). Data on the estimated number of tourists were represented along the areas of influence of hotels and nautical activities by touristic pole considering the potential use of the customers of all available options. Values of nightlight pollution were represented in pixels of 0.088 x 0.081 degrees from the satellite image.

The spatial resolution of all variables was normalized applying the grid used in the model of breeding habitat suitability of Laridae (Chapter 1). This rectangular grid was composed by 128 x 44 = 5632 squared planning units (PUs) of side = 9.0 km. Then, the range of values of each variable was standardized in three ranks of importance: 1 (low), 2 (medium) and 3 (high) (Annex 11). Finally, we generated a file containing the PUs identifier and their corresponding ranking values for each conservation feature and socio-economic cost.

### **7.2.6 Model parametrization and sensitivity analysis**

For CF\_1, CF\_2 and CF\_4, three protection levels (targets) were considered: 50%, 75% and 90%. CF\_3 was fixed at 90% because it represents threatened species, requiring strict protection. We assigned the same weight to the socioeconomic cost variables originating from the same disturbance source (*e.g.* fishing, tourism, etc). We arbitrarily chose the value of  $\beta = 1.0$  due to its suitability to produce compact reserves relatively to the total cost of site selection in our numerical experiment.

In order to model the prioritized areas for Laridae breeding, 18 scenarios were built combined different weights assigned to the socioeconomic costs with the three fixed targets of the

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conservation features (Table 7.2). Because we consider that fishing and tourism are more invasive than wind farms and nightlight pollution, we assigned higher weights to these socioeconomic costs within the design scenarios (Table 7.2). We also evaluated three scenarios (for each target level) putting the heaviest weight to the cost of the wind farm but including SC\_13 to predict the priority areas taking into account the future pressures from this disturbance. For each scenario, a cartographic layer was produced with the priority areas for the conservation of breeding Laridae in Cuba based on the optimisation approach. Finally, seven scenarios were considered to perform sensitivity analysis on the parameters involved in the reserve site selection model in order to assess their contribution to the final solution (Table 7.2).

**Table 7.2.** Parametrization and performance of the designed scenarios to model the prioritizing conservation areas for Laridae breeding in Cuba taking into account current and future human pressures. Conservation targets = protection degree for the conservation features; Socioeconomic costs = weighting of the human activities; Planning units, Objective and Cost = performance parameters of the modeled reserve solution in arbitrary units.

Conservation targets (%)	Socioeconomic costs	Application	Planning units	Objective	Cost
50/50/90/50	All = 1	Sensitivity analysis	556	453.7	139.7
75/75/90/75	All = 1	Sensitivity analysis	975	696.1	246.1
90/90/90/90	All = 1	Sensitivity analysis	1380	895.1	335.1
50/50/90/50	Fishing = 2 / Others = 1	Sensitivity analysis and modeling from current human plans	557	475.7	161.7
50/50/90/50	Wind farms = 2 / Others = 1	Sensitivity analysis and modeling from current human plans	560	417.6	111.6
50/50/90/50	Coastal tourism = 2 / Others = 1	Sensitivity analysis and modeling from current human plans	558	443.9	127.9
50/50/90/50	Nightlight pollution = 2 / Others = 1	Sensitivity analysis and modeling from current human plans	550	483.5	169.5
50/50/90/50	Fishing = 3 / Coastal tourism = 2 / Others = 1	Modeling from current human plans	556	476.4	162.4
50/50/90/50	Fishing = 2 / Coastal tourism = 3 / Others = 1	Modeling from current human plans	568	453.5	137.5
75/75/90/75	Fishing = 2 / Others = 1	Modeling from current human plans	942	734.7	272.7
75/75/90/75	Wind farms = 2 / Others = 1	Modeling from current human plans	1014	633.4	195.4
75/75/90/75	Coastal tourism = 2 / Others = 1	Modeling from current human plans	1004	674.1	222.1

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75/75/90/75	Nightlight pollution = 2 / Others = 1	Modeling from current human plans	950	749.0	291.0
75/75/90/75	Fishing = 3 / Coastal tourism = 2 / Others = 1	Modeling from current human plans	946	734.7	270.7
75/75/90/75	Fishing = 2 / Coastal tourism = 3 / Others = 1	Modeling from current human plans	1001	691.4	237.4
90/90/90/90	Fishing = 2 / Others = 1	Modeling from current human plans	1317	953.4	373.4
90/90/90/90	Wind farms = 2 / Others = 1	Modeling from current human plans	1419	810.5	262.5
90/90/90/90	Coastal tourism = 2 / Others = 1	Modeling from current human plans	1449	858.5	306.5
90/90/90/90	Nightlight pollution = 2 / Others = 1	Modeling from current human plans	1225	968.5	376.5
90/90/90/90	Fishing = 3 / Coastal tourism = 2 / Others = 1	Modeling from current human plans	1366	948.7	366.7
90/90/90/90	Fishing = 2 / Coastal tourism = 3 / Others = 1	Modeling from current human plans	1479	882.2	328.2
50/50/90/50	Wind farms = 2 / Others = 1	Modeling from future human plans	561	406.6	100.6
75/75/90/75	Wind farms = 2 / Others = 1	Modeling from future human plans	1029	613.5	175.5
90/90/90/90	Wind farms = 2 / Others = 1	Modeling from future human plans	1447	782.9	236.9

**7.2.7 Comparison between the modelled priority conservation areas and current Cuban MPAs**

According to the Centro Nacional de Áreas Protegidas de Cuba, in 2022 the Cuban National System of Protected Areas was composed of 119 MPAs, among which 65 included marine and/or coastal areas (Annex 12). These MPAs are subject to eight management categories, from maximal to minimal protection level: Natural Reserve, National Park, Ecological Reserve, Highlighted Natural Element, Managed Floristic Reserve, Fauna Refuge, Protected Natural Landscape and Protected Area of Managed Resources (Centro Nacional de Áreas Protegidas, 2013). For those MPAs including terrestrial areas, we retained only their marine components (Annex 12). Then the current MPAs geographic layer was overlapped with the layers of the modelled conservation areas of each scenario for the breeding Laridae to compute the difference. The cartographic processing and data manipulation were done using QGIS 3.10.2 (Development Team, 2020) and R 4.1.1 (R Core Team 2021) via RStudio (RStudio Team 2021).



### **7.3 Results**

#### **7.3.1 Conservation areas of breeding Laridae under current and future human disturbance**

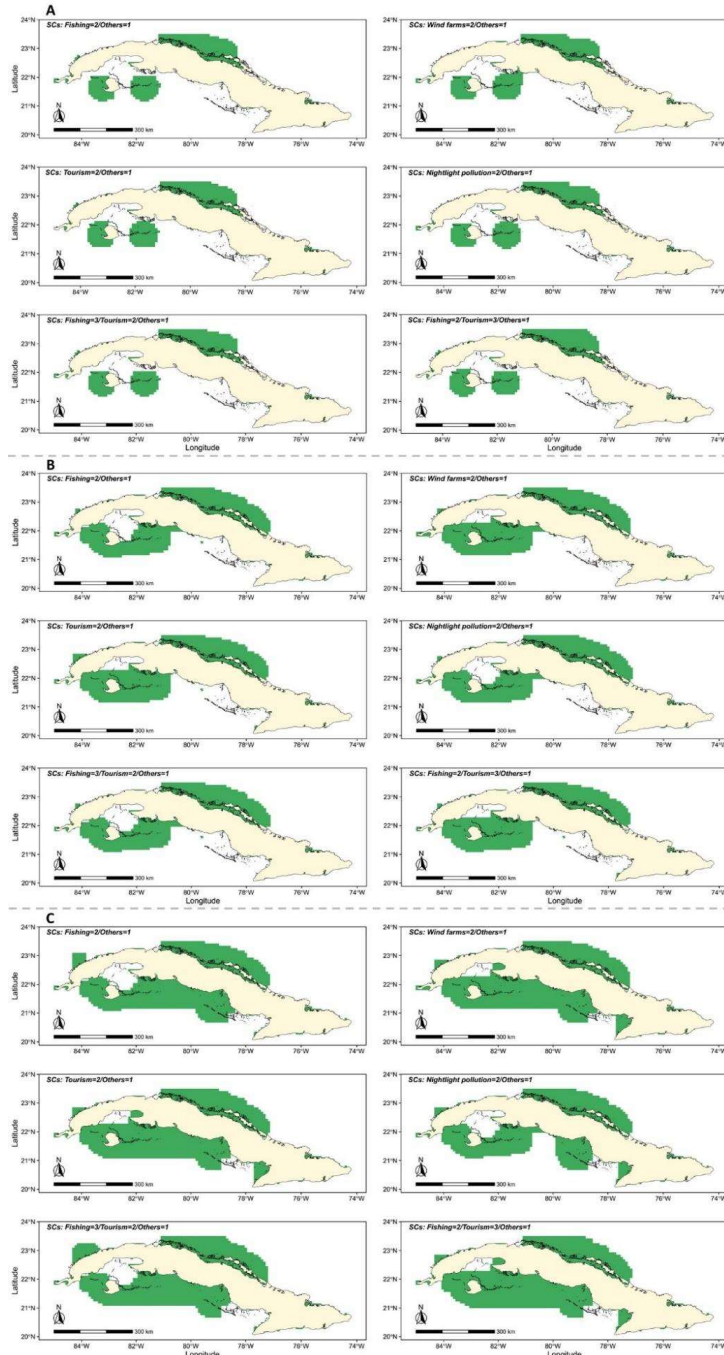
The reserve solutions using conservation targets of 50/50/90/50 % are highly similar (Table 7.2, Fig. 7.2A). In these scenarios, three large areas (belonging to the Sabana-Camagüey and Canarreos archipelagos) and some small patches (mainly in the western and northeastern regions) were identified as priority areas for conservation (Figs. 7.1 & 7.2A). The modeled areas ranged from 44 550 to 46 008 km<sup>2</sup> when nightlight pollution and coastal tourism, followed by fishing were the most important socioeconomic costs (Table 7.2).

The reserve solutions using the 75/75/90/75% target were also consistent in general (Table 7.2, Fig. 7.2B). The scenarios agreed on protecting almost the entire Sabana-Camagüey archipelago and small patches on the northeastern coast, the western extreme and within Los Colorados archipelago (Figs. 7.1 & 7.2B). The other conservation area covered a large part of the Canarreos archipelago and two coastal parts of southwestern Cuba (Figs. 7.1 & 7.2B). The modeled areas ranged from 76 302 to 82 134 km<sup>2</sup> when fishing and wind farms were the most important socioeconomic costs, respectively (Table 7.2).

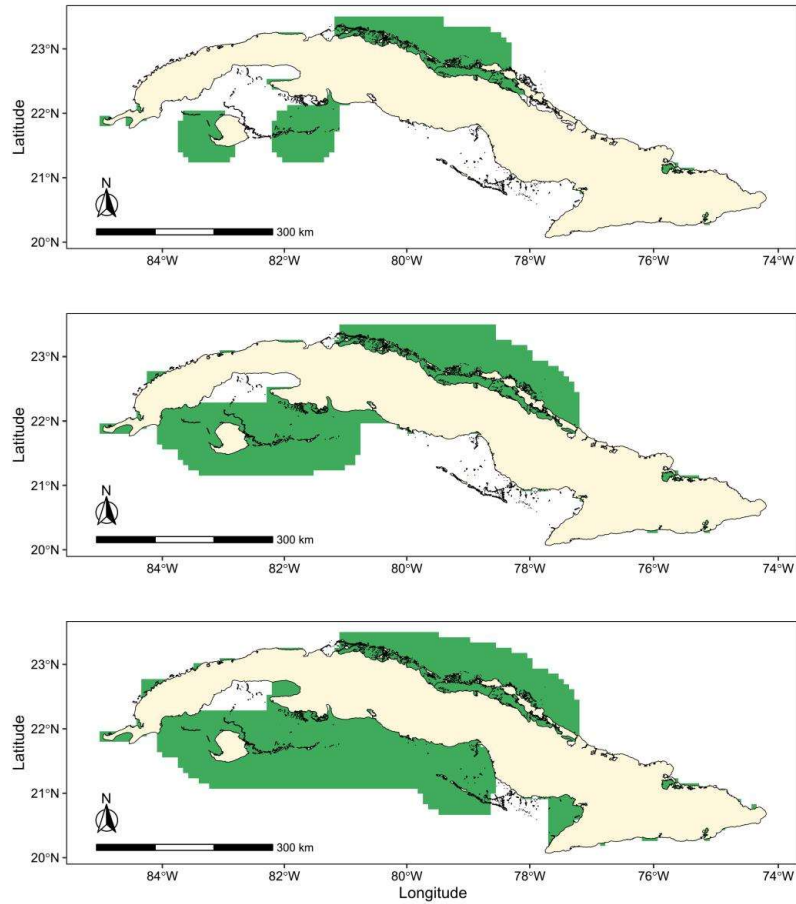
Despite their general consistency, the scenarios involving 90/90/90/90% targets, exhibited significantly different reserve solutions (Table 7.2, Fig. 7.2C). The entire Sabana-Camagüey archipelago and small patches on the northeastern coast and the western extreme were identified as priorities. However, in the two scenarios that prioritized fishing, protection coverage increased in Los Colorados archipelago but decreased in the Gulf of Guacanayabo (southeastern Cuba) (Figs. 7.1 & 7.2C). The largest conservation area extended from southwest to south-central Cuba, including almost the entire Canarreos archipelago and south-central coasts, until the western half of Jardines de la Reina archipelago (Figs. 7.1 & 7.2C). The spatial coverage of this area was reduced only when nightlight pollution was prioritized (Fig. 7.2C). The computed areas ranged from 99 225 to 119 799 km<sup>2</sup> when nightlight pollution, coastal tourism and fishing (in that order) were the most important socioeconomic costs (Table 7.2). In general, the largest target and cost values were achieved when nightlight pollution had the heaviest weights while the opposite occurred in the scenario with wind farms with the largest weight, regardless of the values of conservation targets (Table 7.2, Fig. 7.2).

Taking into account the future Cuban development plan of wind farms, the spatial patterns of priority conservation areas were highly similar to the current wind farm conditions scenarios previously computed (Table 7.2, Figs. 7.2 & 7.3). The predicted future areas covered 45 441, 83 349 and 117 207 km<sup>2</sup> for conservation targets of 50/50/90/50%, 75/75/90/75% and 90/90/90/90%, respectively. These values increased the area to be protected by 0.18, 1.48 and 1.97% in relation to the corresponding current scenarios. But implying a decrease of the objective (and consequent cost reduction) by 2.63, 3.14 and 3.41% for the aforementioned target scenarios.

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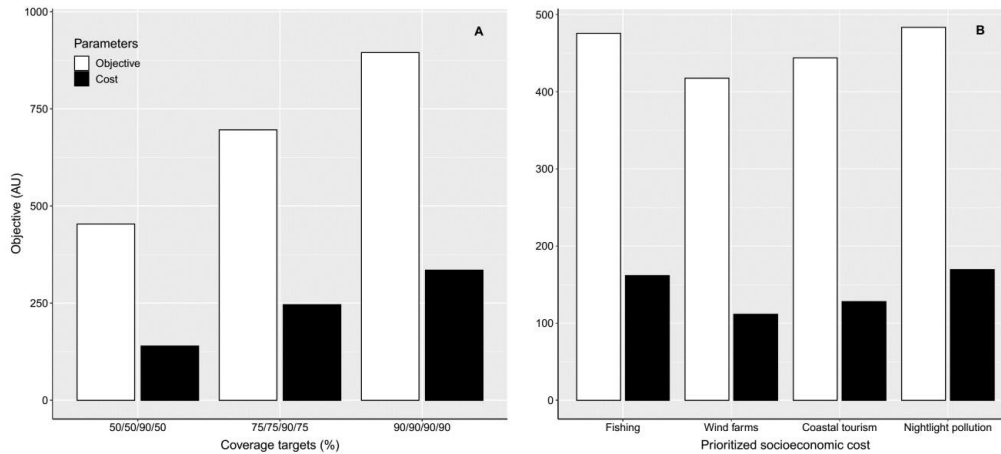
**Figure 7.2.** The reserve solutions modeled for the conservation of Laridae breeding habitats in Cuba considering different weights of four socioeconomic costs (SCs). Scenarios A, B and C respectively using 50/50/90/50%, 75/75/90/75% and 90/90/90/90% for the conservation targets.



**Figure 7.3.** Future conservation areas for the conservation of Laridae breeding habitats in Cuba considering four socioeconomic costs (prioritizing wind farms) in scenarios with conservation features targets = 50/50/90/50 % (top), 75/75/90/75 % (middle) and 90/90/90/90 % (bottom).

### 7.3.2 Sensitivity analysis

When we consider increasing conservation targets, we observe that both the objective value and cost of the reserve selection are notably increasing (Fig. 7.4A). This result was expected because the reserve solution is expanding to meet the increasing conservation targets. On the other hand, minor differences were observed among the prioritized socioeconomic costs based on both the objective and cost of reserve selection (Fig. 7.4B). The protection of Laridae in scenarios where fishing and nightlight pollution are prioritized has largest cost than that under scenarios with tourism and wind farms prioritized.



**Figure 7.4.** Sensitivity analysis to assess the influence of the coverage target (A) and socioeconomic cost (B) parameters on the objective function and cost value of the optimal reserve solution for breeding Laridae in Cuba. AU = arbitrary unit.

### 7.3.3 Overlap of the priority conservation areas identified from the model with current Cuban MPAs

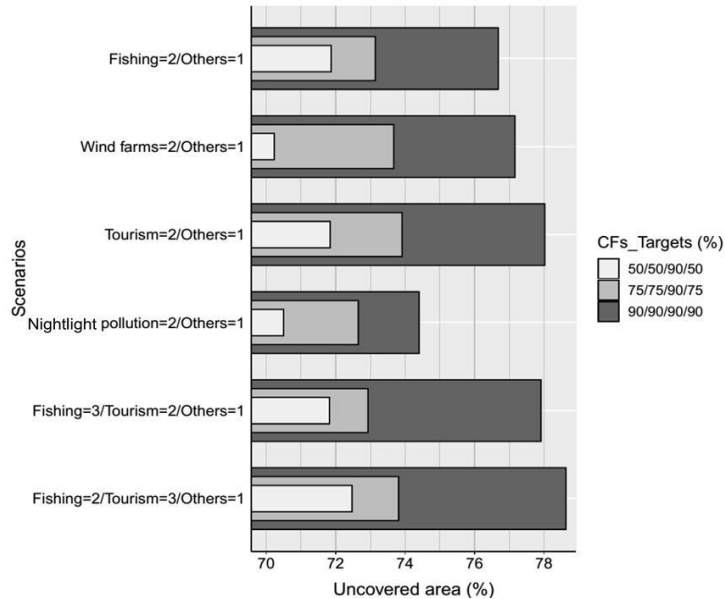
In all considered scenarios, more than 70% of the modelled priority conservation areas for Laridae was not covered by the current Cuban MPAs (Fig. 7.5). As expected, the discrepancy between current MPAs and modelled priority conservation areas was largest and smallest under the conservation targets 50/50/90/50% and 90/90/90/90% respectively (Fig. 7.5). As far as cost is concerned, the largest discrepancies were observed when tourism and fishing had the larger weights, with the 50/50/90/50% and 90/90/90/90% conservation targets and when tourism had the larger weight with the 75/75/90/75% conservation target (Fig. 7.5).

## 7.4 Discussion

### 7.4.1 Conservation areas for the protection of breeding Laridae from current and future human disturbance

Areas of importance for breeding Laridae, proposed considering the lowest conservation targets (50/50/90/50%), were highly similar among socioeconomic scenarios. Given the minimum coverage requirements to be protected, the overall pattern of conservation areas appeared to be highly influenced by the spatial distribution of threatened breeding species and the number of breeding species (Annex 11). The remaining small patches were identified primarily from habitat suitability estimated under the 2021 conditions (Annex 11). Despite the larger differences among scenarios with 75/75/90/75% target, the general pattern of coverage to be protected included the characteristics of those proposed with the 50/50/90/50% targets but adding a spatial connectivity between the two more important archipelagos for breeding Laridae (Sabana-Camagüey and Canarreos). The largest variations occurred in the coverage of the Canarreos archipelago, but always preserving the connectivity of the proposed reserve. The

greatest contrasts in coverage were obtained with the 90/90/90/90/90% target, especially in the scenario that prioritized nightlight pollution (the lowest coverage). Nevertheless, a convergent spatial pattern was identified, characterized by the extension of the previous coverages until covering a large part of the Jardines de la Reina and Los Colorados archipelagos. In this context, the conservation area solution was highly connected.



**Figure 7.5.** Proportion of the priority conservation areas identified from the model, uncovered by the current Cuban MPAs. Area discrepancies were computed for scenarios with different targets for conservation features (CFs) and different weighting of the human activities.

Regardless of conservation features targets, proposed protected areas had greater cost when more weight was given to nightlight pollution and fishing. This is probably because these sources of disturbance occupied a larger spatial extent than the others (Annex 11), what increases the cost penalty during optimisation. However, they also constituted the solutions that achieved the greatest objective. Finally, the integration of all the produced conservation areas (combining socioeconomic scenarios and conservation targets) allows the identification of common regions that can be considered key for the conservation of breeding Laridae in Cuba. At first place was most of the Sabana-Camagüey archipelago, the largest in the country (470 km) that includes a large number of highly heterogeneous and remote cays, islets and sandbanks. It was followed by the western (including part of the Isla de la Juventud) and eastern sectors of the Canarreos archipelago (148 km of length), where remote small cays predominate with little landscape heterogeneity. The rest were minor areas associated with the western end of the country (Guanahacabibes peninsula) which has sandy coastal areas, marshes and cliffs; some mangrove cays with sandy shores in the central part of the Los Colorados archipelago; and several bays in the east of the country (from Nicaro to Sagua de Tánamo in the north, and

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Guantánamo in the south). Other important minor sites were located in some coastal areas at the south of the main island.

The feasibility of the computed conservation areas should not be compared among scenarios as this depends on the socioeconomic priorities established by the governance institutions. In this work, we considered socioeconomic costs from important activities for the country in question, but which have also been recognized as stressors for seabirds. Historically, one of the greatest conservation problems for colonial breeding seabirds is human disturbance (Anderson and Keith, 1980). Despite that seabirds can develop tolerance to some degree of disturbance (Nisbet, 2000; Yorio *et al.*, 2001), this habituation is species-specific and requires proper planning of anthropogenic activities (Schwemmer *et al.*, 2011). Our results constitute a tool to assist stakeholders and decision-makers in the development and refinement of sustainable marine spatial planning. But the final coverage and location of the protected areas will depend on the political priorities identified by them.

From a similar perspective, Harvey *et al.* (2021) focused on marine vertebrates (including only four non-Laridae seabird species) to identify potential Key Biodiversity Areas (KBAs) in the Greater Caribbean region. To this end, they used point data, distribution maps, threat statuses, population estimates, political and marine ecoregional boundaries, habitat distribution, and measures of cumulative human impacts. By overlaying map layers, they were able to detect gaps in the effectiveness of coverage in existing MPAs. Here, no potential new KBAs were found outside the boundaries of Cuba's MPAs.

Our framework also contributes to future planning based on forecasts of socioeconomic activities. This was demonstrated using the planned design of wind development in Cuba, where the simulated results facilitate the prediction of impacts on the conservation of breeding Laridae. These conservation areas considering the planned wind farms to be built were slightly smaller than those currently identified. This was due to the contribution of the socioeconomic cost in question (wind farms were the least contributing factor in the optimisation model), characterized by a limited spatial representativeness.

We emphasize the potential of this decision support tool for conservation based on its flexibility and capability to integrate current and future ecological and socioeconomic interests, that in fact, has been applied to design several scenarios in both marine and terrestrial systems (Brunel *et al.*, 2022; Proudfoot *et al.*, 2020). In this sense, the effectiveness of the solutions will depend on the information available for optimisation modelling. The more accurate the data on conservation features and socioeconomic costs, the more accurate the model reserve solutions will be. In this study we used basic information, but finer results can be produced if other variables are considered. For example, the inclusion of fishing fleet size, catch rates and used fishing gear, effective number of tourists practicing nautical activities, berthing points and boat trajectories, and spatial planning of coastal tourism development would contribute substantially to the quality of the estimations. The integration capability of this approach constitutes an indirect form of cumulative human impact assessment, which helps to decision makers and planners to target and prioritize management actions (Loiseau *et al.*, 2021). In addition, this

type of tool has an added value in the face of logistical and financial limitations frequent in developing countries, as it contributes substantially to the optimal use of economic resources.

#### **7.4.2 Sensitivity analysis**

The increase of the objective and cost of reserves with the increase of the conservation features targets was expected from the sensitivity analysis. But the proportions of these increases were contrasting. The fact that the objective would increase substantially with a small increase in cost could facilitate the approval of large conservation areas (because it implies low socioeconomic costs). Effective marine conservation planning requires the consideration of spatial scale, especially for highly mobile species such as seabirds (Opper *et al.*, 2018; Yorio, 2009), which can cross ecological and political boundaries (Lescroël *et al.*, 2016). In this sense, the larger the protected area, the greater could be the effectiveness of the conservation of breeding Laridae in Cuba.

On the other hand, the sensitivity analysis showed similar effects when prioritizing each socioeconomic cost (highlighting a large target/cost difference). The low-cost effect of wind farms to compute the reserve could derive from the lower spatial representativeness of this source of human disturbance. This facilitates the reduction of the cost to design MPAs when prioritizing that factor, but at the same time decreases the objective due to the synergistic influence of the other disturbance sources during the optimisation process. Few differences could be expected among the proposed MPAs considering different socioeconomic prioritization scenarios. However, the weights chosen can greatly influence the differences between scenarios.

#### **7.4.3 Coverage of the modeled conservation areas by Cuba's MPAs**

The current MPAs system offers remarkably insufficient coverage of conservation areas for the conservation of breeding Laridae in Cuba. This suggests that the establishment of MPAs has been focused primarily on other conservation objects (*e.g.* coral reefs, fish, mangroves, chelonians, seascapes) or from an incomplete perspective for the effective protection of breeding seabirds. Considering the degree of spatial overlap among MPAs and priority areas for Laridae, it is possible to detect that most of the unprotected portion corresponds to marine areas with potential foraging use. This may be due to an inadequate perception of the reproductive ecology of colonial seabirds, since these species require protection measures that cover from colony establishment to adult foraging areas (Opper *et al.*, 2018).

On the other hand, the largest protection gaps in the important areas for breeding Laridae resulted in the scenarios where marine-coastal tourism was prioritized. This denotes a high spatial coincidence among the infrastructure and activities associated to this socioeconomic factor and Cuba's MPAs. Normally, within protected areas, frequent monitoring should be carried out to update measures to reduce human impacts (Lieske *et al.*, 2019). In this sense, an in-depth analysis of the effects of marine-coastal tourism on biodiversity in MPAs seems advisable. This would also constitute a way to assess the MPAs' effectiveness, beyond the misleading conservation approach based on spatial coverage (see Meehan *et al.*, 2020). There

is an improvement in the methods used for marine conservation planning, which have evolved from a static conservation approach to the protection of important ecological processes (Proudfoot *et al.*, 2020).

The permissibility of tourism activities in seabird breeding areas (protected or not) should be treated with extreme caution. The increase of this type of scenarios worldwide has caused behavioral impacts on animals and other important disturbances on natural conservation values (Marcella *et al.*, 2017; Velando and Munilla, 2011; Yorio *et al.*, 2001). Within MPAs, ecotourism in particular can bring economic benefits at the cost of low impact on populations of species occupying high trophic positions (Marcella *et al.*, 2017). This could be the case of many seabirds such as breeding Laridae, but generally the effectiveness of MPAs is insufficient in highly mobile bird species (Yorio, 2009).

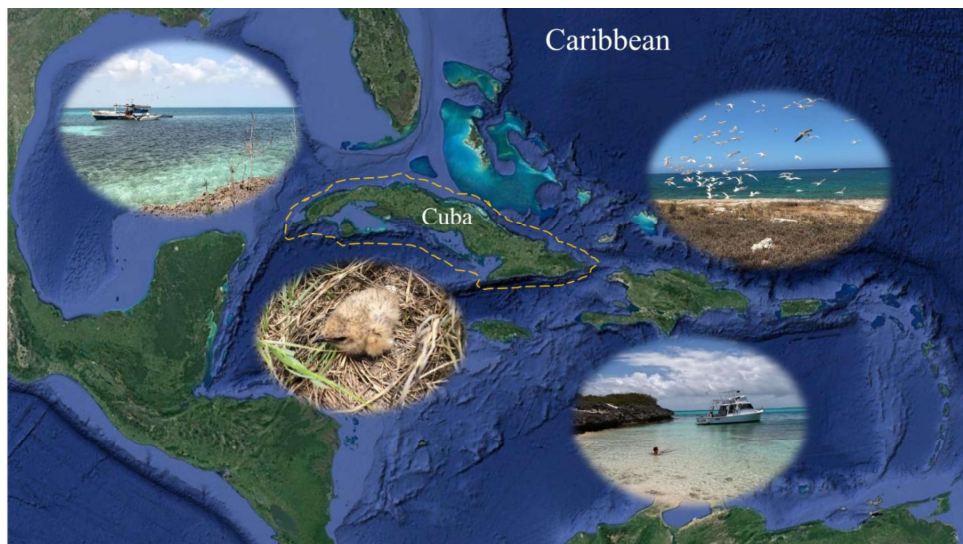
The importance of MPAs for the management and conservation of marine biodiversity has been widely recognized (Devillers *et al.*, 2020, 2015; Proudfoot *et al.*, 2020; Schultz *et al.*, 2022), as well as their contribution to climate change mitigation and adaptation (Jacquemont *et al.*, 2022). However, their effectiveness depends on management objectives, appropriateness of zoning and levels of compliance (Devillers *et al.*, 2015). One of the major criticisms of MPAs is the extent of human activities allowed within them, legally supported by flexible or weak management categories (Driedger *et al.*, 2023; Lescroël *et al.*, 2016).

Only 23 MPAs (out of a total of 65) in Cuba have one of the three most restrictive management categories (Natural Reserve, National Park and Ecological Reserve) representing 32.33% of the total coverage of the MPAs system. In addition, 43.48% of these areas with the highest level of protection are nested within other more flexible and larger areas (Annex 12). This suggests the need to evaluate the level of effective conservation -apparently insufficient- in such MPAs system. The superiority in effectiveness of fully or highly protected MPAs over less restrictive areas has been clearly demonstrated (Driedger *et al.*, 2023; Jacquemont *et al.*, 2022; Schultz *et al.*, 2022). The percentage of protection coverage in the priority areas for breeding Laridae in Cuba was obtained from the non-nested MPAs (which have a low levels of protection mostly), since they constituted the maximum limits of general protection. Thus, it is possible to detect the main gaps in the conservation of Laridae breeders, taking into account the low protection coverage in their priority areas and the fact that the current protection depends highly from low-restrictive MPAs.

Often lack of political will or limited resources obstruct the establishment of restrictive MPAs (Schultz *et al.*, 2022). Also, the number and spatial extent of protected areas in general may appear to be indicators of successful conservation for governments, NGOs and the public, with severe impacts on marine biodiversity going unnoticed (Devillers *et al.*, 2015). Therefore, we emphasize the importance of systematically assessing the link among marine biota, human disturbance and MPAs through detailed and updated information for the achievement of effective conservation. This takes an added value when dealing with highly dynamic biological groups and indicators of environmental change such as breeding seabirds.



**Chapter 8:**  
**General Discussion**



This work brings new information and results that contribute to scientific knowledge from two main viewpoints. On the one hand, it fills important information gaps about the breeding ecology of tropical larids in general, and in the Caribbean in particular. On the other hand, the methodological approaches applied to the study of several aspects of the reproduction and conservation of larids in Cuba, expose and/or confirm their efficacy beyond their traditional uses. The research carried out during this PhD combines traditional, modern and state-of-the-art approaches to deal with ecological processes that typify the reproduction of seabirds in general. Finally, the obtained results represent essential cornerstones for the course of new studies that delve deeper into the interesting world of seabirds in the tropics, and why not, in the rest of the world as well.

### **8.1 Reproduction and conservation of tropical larids: from Cuba to the Caribbean and beyond**

The Cuban archipelago is an area of high importance for the reproduction of seabirds, especially larids, which represent more than 60% of the local breeding seabird species (Jiménez *et al.*, 2009). However, little was known beyond inventories of species and breeding sites, counts (not always regular) of the number of eggs and chicks in colonies and punctual characterizations of the habitat at nesting sites. The main objective of this research was thus to fill several knowledge gaps about the breeding ecology of the best represented group of seabirds in Cuba, by using a mix of traditional and cutting edge methodologies, existing fragmentary information and acquiring new data. Taking into account the lack of ecological information on larids in Cuba, this thesis makes substantial contributions to the understanding of several key aspects of the ecology of these animals. At the same time, it opens the road for new studies to answer other research questions. Habitat selection (widely recognized as crucial), trophic interactions based on segregation mechanisms and phenological dynamic during reproduction are essential topics to understand the ecology of seabirds. On the other hand, planned conservation based on human-environment interaction is a clear way to protect biological resources, such as seabirds.

Habitat plays an essential role in the ecology of any species and becomes particularly important during reproduction. In animals such as seabirds, which are highly mobile and dependent on contrasting landscapes for breeding, the selection of suitable habitats is crucial for breeding success. The ability of seabirds to use various spatial scales during breeding habitat selection and foraging contributes to their aforementioned evolutionary success as well as to their management and conservation (Eveillard-Buchoux *et al.*, 2019; McGowan *et al.*, 2013). In this sense, Chapters 2 and 3 were focused on the breeding macro- and microhabitat, respectively, of larids in Cuba. The suitability and selection of the breeding macrohabitat were approached considering three important aspects to adjust the study as close as possible to reality: the definition of breeding macrohabitat or breeding site, interspecific sympatry during reproduction and the multiscale approach associated with foraging at sea.

Since seabirds breed on land and forage at sea, variables from both marine and terrestrial ecosystems were considered to define breeding sites for larids in Cuba. The simultaneous integration of sea and land components has been poorly represented in studies of habitat selection in seabirds (Burger & Shisler, 1978). This lack of a holistic approach probably limits

our ecological understanding of habitat selection in seabirds. With respect to sympatric breeding, the breeding sites were studied as a whole (regardless of breeding species composition) since macrohabitat breeding requirements often match among several species, resulting in the formation of multi-species colonies. This co-nesting results in the joint exploitation of the surrounding marine resources but tends to avoid competition from the different interspecific foraging radii. For this reason, three spatial scales (radii of 10, 50 and 100 km) around the colonies were considered in this study as part of the definition of breeding macrohabitat.

To our knowledge, these land and sea features have not been considered simultaneously in existing habitat selection studies in seabirds. Our results suggested that SST and Chl *a* at 100 km foraging radius were preponderant variables in the multispecies selection of breeding macrohabitat for the larids in Cuba. Something similar could occur in other parts of the Caribbean or other tropical regions with similar characteristics to Cuba, as warm waters tend to have little thermic and oceanographic variability (Jaquemet *et al.*, 2008).

The evaluation of breeding microhabitat or nesting site selection also included several larid species. However, it was analyzed separately since, at the local scale, species segregate to select their nesting site (Fasola & Canova, 1992) following specific patterns. Thus, the multispecific approach used facilitated the understanding of the basis for successful co-nesting among larid species. In essence, the larids in Cuba chose breeding microhabitats following different patterns according to the ecological niche breadth of the species and the habitats available at the breeding sites. Terns were more specialized with respect to gulls, but the results highlighted the generally determinant role of some variables in nesting site selection. Dominant plant species, minimum distance to the cay edge, vegetation cover and substratum at nesting sites were among the most important explanatory variables in this regard. The obtained patterns could contribute to the planning and carrying out of censuses or sampling in breeding colonies of these species in tropical areas. Thus, it would be easier to design the sampling scheme (sampling method, schedules, number of people required) knowing the cay area with the colony and the characteristics of the possible nesting sites of the species of interest. This could also help to optimize human, material and financial resources needed for a systematic monitoring of colonies, especially in countries with high logistical and economic limitations.

The analysis of stable isotopes of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  from blood, down and feathers of adults and chicks provided important elements to understand some aspects of the trophic ecology of larids in Cuba (Chapters 4 and 5), possibly reflecting more general pattern of the Caribbean. The simple quantification of isotope ratios constitutes an important contribution to the former nonexistent record of data on Cuban seabirds, as well as to the quite limited data set available on Caribbean and tropical seabirds in general. The need to increase knowledge on the trophic (and isotopic) ecology of tropical seabirds has been highlighted, as most studies have been biased toward temperate and polar species (Weimerskirch, 2007). However, this study went further by applying the relatively recent concept of the isotopic niche (Newsome *et al.*, 2007) as an integrative and representative measure of the trophic niche. The isotopic niche has been quantified in several seabird species, including some that breed in the Caribbean (Sebastiano *et al.*, 2016, 2017).

In Chapter 4, an extensive scheme was followed to evaluate the spatial and temporal variability of the isotopic niche in breeding communities of larids in Cuba. This allowed us to study the plasticity and trophic overlap of species during reproduction, in order to understand the basis for successful co-nesting in tropical marine ecosystems that are not very productive. In this sense, we detected trends towards little interspecific overlap between isotopic niches, as well as groups of species with contrasting niche widths (broad vs. narrow). Temporally, some species showed reductions in their niches from the pre-laying to the chick-feeding phase. Overall, the set of characteristics and patterns of isotopic variability detected suggests the existence of interspecific trophic segregation mechanisms (by types of prey consumed and foraging localities) that support joint nesting in the study areas.

Also using stable isotopes (Chapter 5), we assessed for the first time the trophic plasticity in the annual cycle of Bridled Tern (*Onychoprion anaethetus*), a highly abundant pantropical tern whose ecology has been very little studied (Bretagnolle & Benoit, 1997; Tayefeh *et al.*, 2017). This species has many breeding colonies in areas such as the Caribbean, which implies a high consumption of marine prey. This could be exploited to assess the possibility of using this species as a bioindicator of the state of the regional marine ecosystem. Bridled Tern showed important variations of its isotopic niche, especially between the nonbreeding and breeding phases. Within the reproductive period it was also possible to identify trophic changes between phases.

The description of the breeding phenology of several larid species constituted a significant contribution to the basic knowledge on the reproduction of these birds in Cuba and the Caribbean (Chapter 6). The dates and duration of each phenological phase could be similar in the Caribbean region considering its climatic stability and similarity in general. However, this should be assessed in other areas outside Cuba given the dependence of seabirds on the availability of prey for breeding. As we know, the sea is a highly dynamic and unpredictable ecosystem (Jaquemet *et al.*, 2008; Pinaud *et al.*, 2005).

From the description of the breeding phenology it was possible to precisely identify the timing of early and late laying. This laying asynchrony can impact several factors, such as oological morphology, which influence breeding success in colonies (Cram *et al.*, 2019; Zhang *et al.*, 2015). However, in general, the comparison of morphometric variables between early and late eggs of larids in Cuba did not reflect significant differences. Only the shape of the eggs of two species showed differences between the earlier and the later laying. There were also cases that evidenced the need to increase the sample sizes to obtain accurate results. Thus, a general recommendation could be to extend the experiment both spatially and temporally to refine the potential of tropical larid eggs to reflect the effects of laying asynchrony.

Last but not least, in Chapter 7, we worked on the question of the conservation of breeding sites (certain and probable) of larids in Cuba. This was done by simultaneously considering conservation features and socioeconomic costs derived from prioritized activities at the country level. The approach used stands out because it is based on the premise of "conservation and sustainable development", which increases the conservation interest of policies, leaders, decision-makers and other stakeholders. It is important to highlight the concatenation between

the results of this and Chapter 2 because the modeled breeding habitat suitability was used as one of the conservation features. The evaluation of important areas for the conservation of breeding habitats for the larids included a representativeness analysis for the current MPAs system in Cuba. Most striking was the low spatial coverage of the current MPAs network with respect to the areas identified as important for breeding larids, as well as the presumed spatial overlap between MPAs and activities associated with marine-coastal tourism. Conservation of natural resources has become an important element for management and sustainable development in small island countries (such as Cuba), highly impacted by the effects of climate change and anthropization. This work was able to propose a first prioritization of areas of interest for the conservation of larids.

## **8.2 Use of classic, modern and state-of-the-art methods: unity is strength**

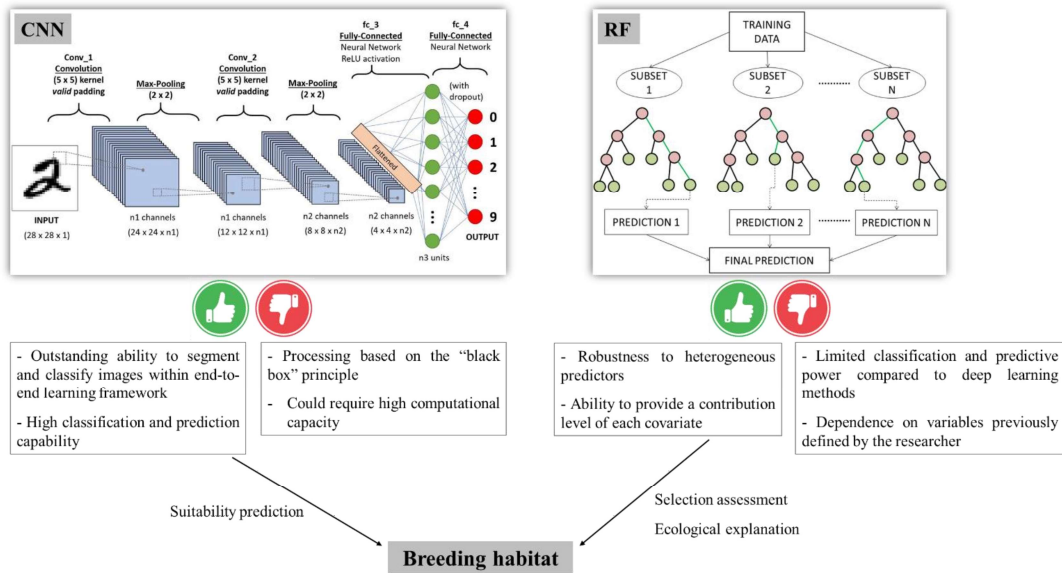
### **8.2.1 Habitat modelling**

Regardless of their strengths and potential, no data analysis or modeling method is perfect. There are usually assumptions and limitations that must be considered during the application of each method. Therefore, in this study several methods were combined to obtain the results under a complementarity approach. Classical, modern and state-of-the-art methods were used to answer several ecological questions that contribute to fill important information gaps at the regional level. Furthermore, some of the novel methodological frameworks implemented here could be extended to other biological groups and regions of the world. Also, this complementarity between methods can lead to the generation of valuable scientific information while minimizing the costs associated with field work at sea, thanks to recent technological and computing advances.

In chapters 2 and 3, data were collected on the breeding habitat of larids by processing Landsat satellite images (macro- and microhabitat) and directly in the field (microhabitat). Undoubtedly, the use of satellite images offers the possibility of working on large spatial scales at no other cost than that associated with internet access. This considerably empowers the work and expands the scope of ecological research. Then, random forest models (RF) were implemented to evaluate the strength of selection (use vs. availability) and the relative importance of environmental covariates in breeding habitat selection.

Considering the well-known advantages for predictive modelling of deep learning methods over machine learning methods (Kattenborn *et al.*, 2021; Mahdianpari *et al.*, 2018, Fig. 8.1), a convolutional neural network model (CNN) was developed to predict the suitability of breeding habitats across Cuba. CNN used only a few bands of satellite images to be trained, classify and predict suitable areas for breeding larids; and they showed high predictive performance despite the limited sample size. The "black box" functioning of CNN (as far as the explanation is concerned) was balanced by the estimation of the contribution of the covariates by the random forest models (guaranteeing the spatial and temporal coincidence of the sites used in both model types). Thus, we demonstrated that the complementary use of the CNN and RF offers the possibility of addressing the issue of breeding habitat from an integrative perspective, addressing both explanatory and predictive challenges. Through CNN we predicted suitability

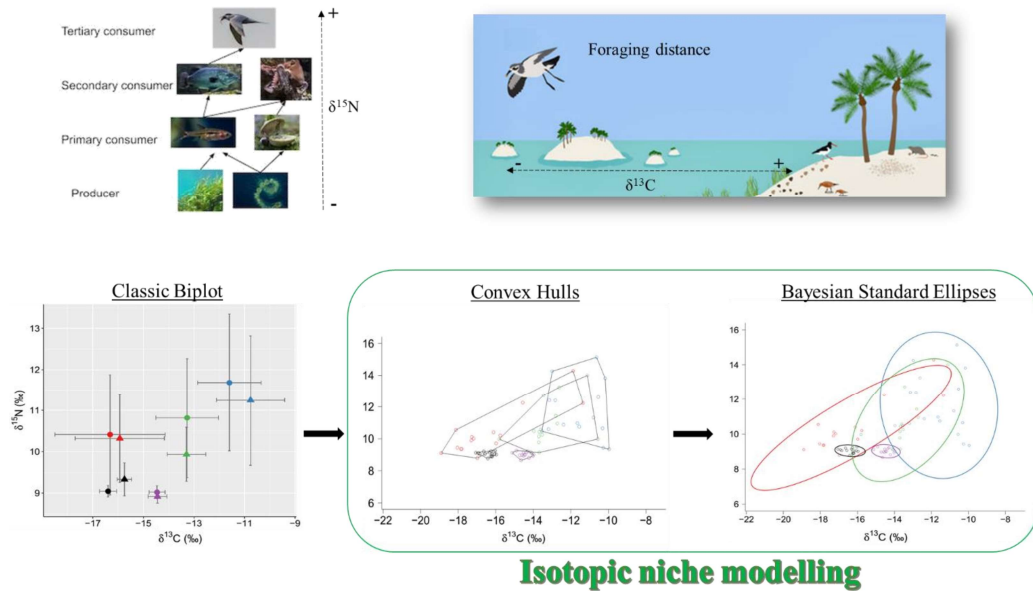
and with RF we explained the ecological basis of breeding macrohabitat selection by larids (Fig. 8.1).



**Figure 8.1.** Complementarity approach between Convolutional Neural Networks (CNN) and Random Forest (RF) models to study seabird breeding habitat.

### 8.2.2 Trophic niche modelling

On another aspect of this work, the evolution from the simple quantification of stable isotope ratios to the computation of the isotopic niche represents an important impetus for biochemistry applied to trophic ecology (Fig. 8.2). Isotopic signatures allow the calculation of trends, variability and ranges in the linear dimension, thus leading to fragmented analysis of isotopes as representatives of species' trophic traits. However, a more holistic vision is obtained by the isotopic niche, which projects the n-dimensions of the trophic niche on a reduced number of axes and can be interpreted as a proxy for the latter (Grecian *et al.*, 2015; Newsome *et al.*, 2007; Fig. 8.2). The isotopic niche includes measures of spatial breadth and shape, two properties impossible to obtain from separate isotopic ratios. The integrative nature of the isotopic niche allows a more complete assessment of the trophic niche, as well as the degree of overlap between these niches. In this regard, the use of the isotopic niche as a proxy for the trophic niche has gradually increased in ecological research (*e.g.* Bratton *et al.*, 2022; Kiszka *et al.*, 2015; Marinao *et al.*, 2019; Newsome *et al.*, 2012; Schwartz-Narbonne *et al.*, 2019).



**Figure 8.2.** Meaning of the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  variability along marine food webs and the open ocean-coastal gradient, respectively (up), and evolution of isotopic data processing methods as proxies of the trophic niche (bottom).

In this study, the isotopic niches of several species of breeding larids in Cuba were calculated as an exploratory tool of the trophic ecology of these birds, especially because there are no isotopic baselines or precise data on their diets and foraging. Thus, by means of a methodological design that included spatial and temporal analyses at the intra- and interspecific level, it was possible to infer some trophic characteristics of the species. Patterns with different levels of variability and isotopic overlap were identified that seem to explain the characteristics of the trophic interactions between co-breeding species. All this provided valuable information taking into account the existing gaps in knowledge and set the basis for future research on the trophic ecology of larids in Cuba. Also, as an added value, the theoretical and practical training given to the participants in the sampling and storage of bird tissues for the quantification of stable isotopes (Fig. 8.3) should be highlighted. These transfers of knowledge and skills for working with isotopes can broaden the spectrum of marine ecology studies in Cuba.

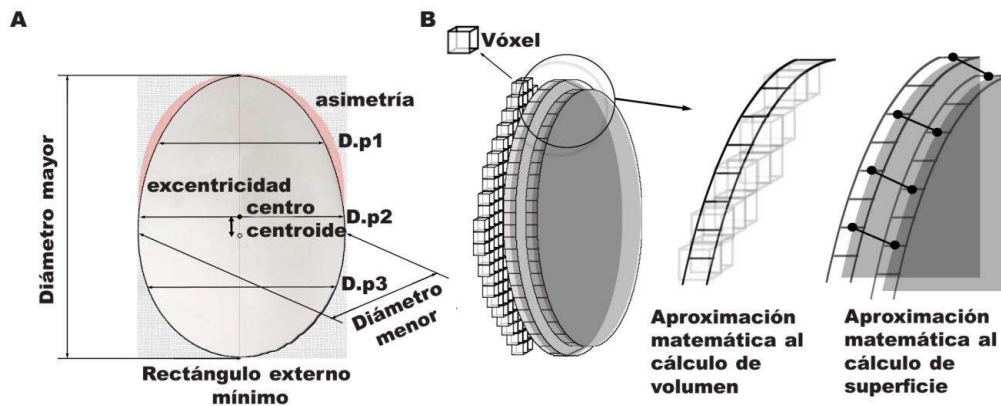


**Figure 8.3.** Cuban researchers learning how to take tissue samples (blood, down and feathers) from seabirds for stable isotope analysis, and banding and weighing the individuals.

### 8.2.3 Egg morphometry description

Morphometric analysis of larid eggs from semi-automated processing of digital photographs offered several advantages. First, it reduced the handling of the eggs and thus the risk of accidents or damage to the developing embryo. It is known that direct measurements in the field with manual instruments tend to introduce manipulation and observer errors (Ramírez–Arrieta *et al.*, 2021). Digital processing also allows the measurement of a greater number of morphometric variables than can be recorded in the field, leading to more comprehensive analyses of the object of study. Another advantage is that it facilitates the research work, since field work is limited to taking standardized photographs for subsequent computer processing.

Several digital photo processing methods have been developed for the morphometric description of avian eggs (*e.g.* Bridge *et al.*, 2007; Chowdhury *et al.*, 2020; Nedomová & Buchar, 2014), producing positive and promising results in this field. This study employed the standardized protocol of Ramírez–Arrieta *et al.* (2021) to quantify six morphometric variables of eggs of four larid species (see Fig. 8.4 for the general procedure). These variables were then compared between two groups according to egg-laying date to evaluate possible differences due to asynchrony. If measurements had been made in the field, very few oological variables would have been recorded directly (*e.g.* length and width), and others would have to be estimated by models or coefficients with recognized shortcomings (Ramírez–Arrieta *et al.*, 2021). This study showed an example of the application of digital photo processing to study the effects of egg-laying asynchrony on larid eggs. At the same time, it also highlights the potential of this method for the study of other biological structures and phenomena.



**Figure 8.4.** Representation of egg measurements extracted from calibrated digital pictures (A) and numerical approximation when using estimates from voxels or mathematical equations (B). D.p1, D.p2, D.p3: transversal diameter at each quartile of longitudinal axis. Taken from Ramírez-Arrieta *et al.* (2021).

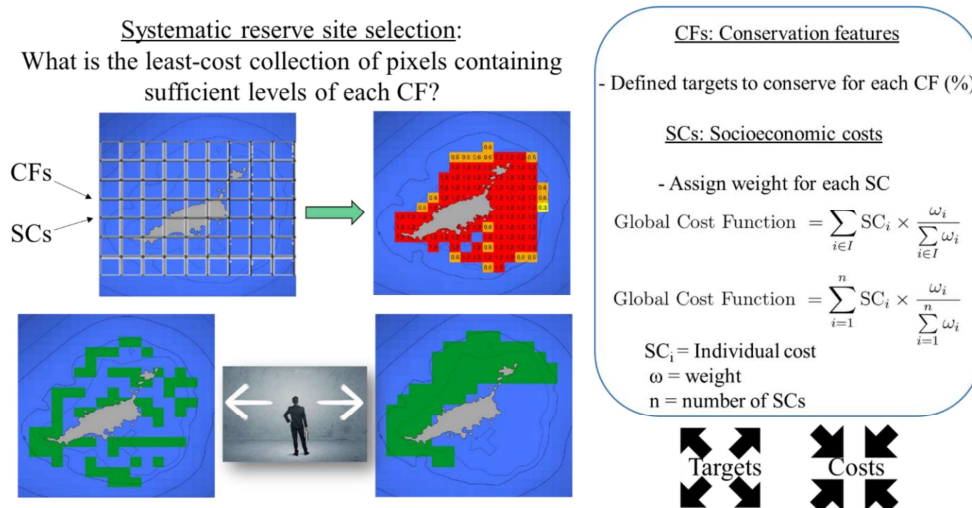
### 8.2.4 Conservation priorities modelling

From the conservation point of view, decision support models are a highly valuable tool. These methods transcend the classical view of strict conservation in an increasingly industrialized,



dollarized and natural resource exploitative world. The optimization principle that governs the systematic reserve selection model implemented in this work represents a balance between conservation and socioeconomic interests, something that could be more attractive to decision-makers and stakeholders (Fig. 8.5).

The prioritized conservation scenarios in this thesis can contribute to the spatial management of socioeconomic activities, a key aspect of marine spatial planning. As an added value, the model used here stands out for its flexibility and integration of diverse interests, both in current and future scenarios (Brunel *et al.*, 2022; Proudfoot *et al.*, 2020). Moreover, it gives the possibility of being implemented in diverse contexts. The spatial overlay approach of conservation features and socioeconomic costs with which this tool works generates proposals for conservation areas that minimize costs and maximize natural values (Fig. 8.5). This could be crucial to solve or avoid some of the reported insufficiencies in MPAs design, such as low levels of activity restriction (Driedger *et al.*, 2023) and residual MPAs (Devillers *et al.*, 2015).



**Figure 8.5.** The optimization principle that governs the systematic reserve selection model implemented in this work. Maps were taken from Brunel & Lanco Bertrand (2023).

### 8.3 Ecology of the larids in Cuba and the Caribbean: challenges and perspectives

The general inventory by Bradley & Norton (2009) is among the few compilations of seabird breeding data in the Caribbean, where larids are highly represented. From this compilation, some conservation and research priorities were identified as well as the need to create standardized protocols for collecting seabird field data. These authors recommended deepening the regional inventory of breeding sites and colonies, given the great potential of the region for seabird reproduction. There is also a risk of underestimation of the information recorded due to logistical limitations and insufficient political and governmental interest in several Caribbean territories. Other identified knowledge gaps correspond to the breeding dynamics at colonies

and at-sea activity (Bradley & Norton, 2009). The need for accurate assessments of emerging pressures such as those associated with climate change and some anthropogenic activities is also highlighted. Particularly for Cuba's seabirds, insufficient protection coverage has been detected at some important colonies (Jiménez *et al.*, 2009). Among the research needs are greater efforts to carry out inventories and continuous monitoring, the evaluation of population trends and breeding success, and the standardization of monitoring methods (Jiménez *et al.*, 2009). Another important aspect is the search for funding mechanisms to train, care for and preserve human resources and MPAs, in order to keep alive the infrastructure linked to the conservation (Jiménez *et al.*, 2009).

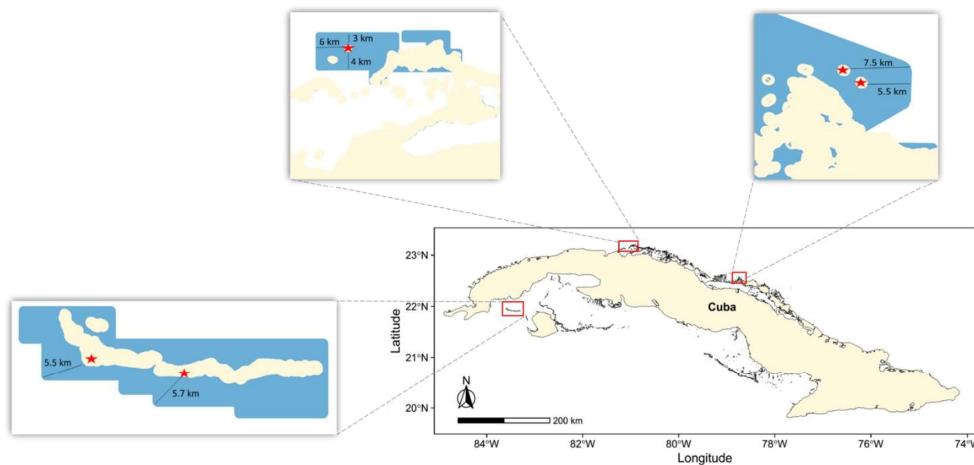
New challenges may also arise from this thesis. The analysis of interannual dynamics of habitat characteristics for laying and of oceanographic conditions (representative of prey availability) seems to be essential to evaluate selection patterns and trends. This becomes even more important in a region such as the Caribbean, which is frequently impacted by intense hurricanes that cause remarkable transformations in marine and terrestrial ecosystems (Fig. 8.6). It also remains to evaluate the potential of egg morphology and growth of chicks as indicators of laying asynchrony. Another imminent task for Cuba is the need to develop the perspective of the close link between larids (and seabirds in general) and the sea. Although the food dependence of these animals on marine resources is well known, current approaches to research, management and conservation of seabirds are not in line with this. It is therefore recommended that the trophic niche of seabirds in Cuba be evaluated in depth using various research methods (sample collection, stable isotope analysis, GPS and GLS tracking, satellite image processing) to obtain information at the lowest possible cost. In addition, it is necessary to study some currently ignored aspects such as contaminants at sea, especially mercury, which in high concentrations can severely affect marine ecosystems and human health.



**Figure 8.6.** Impacts of Hurricane Irma (September 2017) on the flora, fauna and coasts of the northern cays of Cuba.

Uncertainty persists about the effective conservation of seabirds in Cuba. A better quantification and spatio-temporal representation of the socioeconomic activities that constitute

disturbances or threats to seabirds and their habitats is needed. This has been identified as an essential requirement for developing effective conservation strategies for the sustainable use of environmental resources (Anderson & Keith, 1980; Lieske *et al.*, 2019). In relation to Cuba's MPAs, it seems advisable to conduct several studies aimed to assess their effectiveness based on the spatial coverage and restriction levels of their categories. The spatial coverage of the current MPAs is insufficient for the protection of breeding larids, mainly because the foraging areas around the breeding colonies are poorly covered by MPAs (Fig. 8.7). And the larids, like all the other seabirds, usually travel long distances while foraging at sea.



**Figure 8.7.** Examples of the low spatial coverage of the foraging areas around breeding colonies of larids (red stars) by the current Marine Protected Areas (blue) of Cuba. Notice the short distances from cays with colonies to the protection boundaries.

The development of tourism and recreational activities in some areas with more flexible categories may cause negative effects (often unnoticed by humans) on the colonies of larids and other seabird species. It may be worth considering the introduction of novel approaches to the design and establish more effective MPAs. For example, moving from a static to a dynamic vision to MPA establishment could benefit the conservation of important ecological processes in addition to natural values *per se* (Proudfoot *et al.*, 2020).

Finally, a call is made to encourage the development of new approaches to marine ecology research in Cuba and the Caribbean. First, the perspective of the functional interrelationship between strictly marine biota, climatic and oceanographic conditions/phenomena, and biota dependent on marine resources (*e.g.* crocodiles, seabirds) should be encouraged. This will allow answering broader research questions within tropical marine ecology. Second, the numerical and predictive approaches to research must be strengthened to better understand the functioning of the highly dynamic marine ecosystem. Moving beyond local scale work to quantify resources, phenomena and processes on larger spatial scales. This will yield significant volumes of data to assess and predict scenarios, situations and anomalies in the marine environment. Consequently, more effective biodiversity management and conservation actions could be implemented.

## References

- Acosta M, Mugica L, Rodríguez A, Jiménez A (2011) A general overview of waterbird communities in Cuba. *Journal of Caribbean Ornithology* 24:10-19
- Acosta M, Mugica L, Rodríguez-Ochoa A, González A, Aguilar S, Aguilar K (2022) Caracterización de la colonia reproductiva de aves marinas en Cayo Hijo de los Ballenatos, Archipiélago de los Canarreos, Cuba. *Revista Cubana de Ciencias Biológicas* 10(1):1-8
- Afán I, Navarro J, Grémillet D, Coll M, Forero MG (2019) Maiden voyage into death: are fisheries affecting seabird juvenile survival during the first days at sea? *Royal Society Open Science* 6:181151. <https://doi.org/10.1098/rsos.181151>
- Anderson CM, Iverson SA, Black A, Mallory ML, Hedd A, Merkel F, Provencher JF (2018) Modelling demographic impacts of a growing Arctic fishery on a seabird population in Canada and Greenland. *Marine Environmental Research* 142:80-90. <https://doi.org/10.1016/j.marenvres.2018.09.021>
- Anderson DW, Keith JO (1980) The human influence on seabird nesting success: Conservation implications. *Biological Conservation* 18:65-80. [https://doi.org/10.1016/0006-3207\(80\)90067-1](https://doi.org/10.1016/0006-3207(80)90067-1)
- Angulo-Valdes J, Pina-Amargos F, Figueredo-Martin T, Fujita R, Haukebo S, Miller V, Boné-Morón E, Whittle D (2022) Managing marine recreational fisheries in Cuba for sustainability and economic development with emphasis on the tourism sector. *Marine Policy* 145:105254. <https://doi.org/10.1016/j.marpol.2022.105254>
- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473
- Ausems ANMA, Skrzypek G, Wojczulanis-Jakubas K, Jakubas D (2020) Sharing menus and kids' specials: Inter- and intraspecific differences in stable isotope niches between sympatrically breeding storm-petrels. *Science of The Total Environment* 728:138768
- Aygen D, Emslie SD (2006) Royal Tern (*Sterna maxima*) chick diet at Fisherman Island National Wildlife Refuge, Virginia. *Waterbirds* 29:395–400
- Baird PH (1990) Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. *Ornis Scandinavica* 21:224-235. <https://doi.org/10.2307/3676782>
- Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H (2012) Effects of climate change and fisheries bycatch on Southern Ocean seabirds: A review. *Marine Ecology Progress Series* 454:285-307. <https://doi.org/10.3354/meps09616>
- Barbraud C, Weimerskirch H (2001). Emperor penguins and climate change. *Nature* 411(6834):183–186. <https://doi.org/10.1038/35075554>

## References

- Barrett RT, Camphuysen K, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Hüppop O, Leopold MF, Montevecchi WA, Veit RR (2007) Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Science* 64:1675–1691
- Beale CM, Monaghan P (2004) Human disturbance: people as predation-free predators? *Journal of Applied Ecology* 41:335–343
- Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* 75(5):451–458. <https://doi.org/10.1086/342800>
- Becker PH, Goutner V, Ryan PG, González-Solís J (2016) Feather mercury concentrations in Southern Ocean seabirds: Variation by species, site and time. *Environmental Pollution* 216:253–263. <https://doi.org/10.1016/j.envpol.2016.05.061>
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)* 57:289–300
- Beyer HL, Dujardin Y, Watts ME, Possingham HP (2016) Solving conservation planning problems with integer linear programming. *Ecological Modelling* 328:14–22. <https://doi.org/10.1016/j.ecolmodel.2016.02.005>
- Bezanson J, Edelman A, Karpinski S, Shah VB (2015) Julia: A Fresh Approach to Numerical Computing. *ArXiv14111607cs ArXiv* 14111607
- Bezanson J, Karpinski S, Shah VB, Edelman A (2012) Julia: A Fast Dynamic Language for Technical Computing
- Birt V, Birt T, Goulet D, Cairns D, Montevecchi W (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* 40:205–208. <https://doi.org/10.3354/meps040205>
- Black C, Collen B, Lunn D, Filby D, Winnard S, Hart T (2018) Time-lapse cameras reveal latitude and season influence breeding phenology durations in penguins. *Ecology and Evolution* 8(16):8286–8296. <https://doi.org/10.1002/ece3.4160>
- Blanco P (2012) *Sterna dougallii*. In: González H, Rodríguez L, Rodríguez A, Mancina CA, Ramos I (eds) *Libro Rojo de Los Vertebrados de Cuba*. Editorial Academia, La Habana, pp. 227–229
- Blanco PR, Peris JA, Sánchez BO (2001) Las aves limícolas (Charadriiformes) nidificantes de Cuba: Su distribución y reproducción. *Centro Iberoamericano de la Biodiversidad*. 62 pp.
- Block WM, Brennan LA (1993) The habitat concept in ornithology: Theory and applications. In: Power DM (ed) *Current Ornithology*, Vol. 11, pp. 35–91. Plenum Press, New York, USA.
- Boersma PD, Rebstock GA (2010) Calculating egg volume when shape differs: When are equations appropriate?: Calculating Egg Volume. *Journal of Field Ornithology* 81(4):442–448. <https://doi.org/10.1111/j.1557-9263.2010.00300.x>

## References

- Bolton M, Conolly G, Carroll M, Wakefield ED, Caldow R (2019) A review of the occurrence of inter-colony segregation of seabird foraging areas and the implications for marine environmental impact assessment. *Ibis* 161:241–259
- Bost CA, Maho YL (1993) Seabirds as bio-indicators of changing marine ecosystems: new perspectives. *Acta Oecologica* 14:463–470
- Bradley P, Norton R (2009) An inventory of breeding seabirds of the Caribbean. University Press of Florida, Florida, USA.
- Brandl HB, Griffith SC, Schuett W (2019) Wild zebra finches choose neighbours for synchronized breeding. *Animal Behaviour* 151:21-28. <https://doi.org/10.1016/j.anbehav.2019.03.002>
- Bratton RM, Legett HD, Shannon P, Yakola KC, Gerson AR, Staudinger MD (2022) Pre-breeding foraging ecology of three tern species nesting in the Gulf of Maine. *Avian Conservation and Ecology* 17:19. <https://doi.org/10.5751/ACE-02112-170119>
- Breiman L, Cutler A, Liaw A, Wiener M (2018) randomForest: Breiman and Cutler’s Random Forests for Classification and Regression. R package version 4.6-14, <https://CRAN.R-project.org/package=randomForest>
- Bretagnolle V, Benoit MP (1997) Distribution, status and notes on the breeding biology of the Bridled Tern *Sterna anaethetus* in New Caledonia. *Emu* 97(4):310-315. <https://doi.org/10.1071/MU97045>
- Bridge ES, Voelker G, Thompson CW, Jones AW, Baker AJ (2007) Effects of Size and Migratory Behavior on the Evolution of Wing Molt in terns (Sternae): A Phylogenetic-Comparative Study. *The Auk* 124(3):841-856
- Brooke M de I, Bonnaud E, Dilley BJ, Flint EN, Holmes ND, Jones HP, Provost P, Rocamora G, Ryan PG, Surman C, Buxton RT (2018) Seabird population changes following mammal eradications on islands. *Animal Conservation* 21:3-12. <https://doi.org/10.1111/acv.12344>
- Brown RGB (1980) Seabirds as marine animals. In: Burger J, Olla BL, Winn HE (eds) Behavior of marine animals. Current Perspectives in Research. Plenum Press, New York-London
- Brunel A, Lanco Bertrand S (2023) Strengths and weaknesses of decision support tools: A didactic example on the archipelago of Fernando de Noronha. In: Bonnin M, Lanco Bertrand S (eds.) *Marine Spatial Planning in the Tropical Atlantic, from a Tower of Babel to the Organization of a Collective Intelligence*. p. 52. IRD Edition, France.
- Brunel A, Omer J, Lanco Bertrand S (2022) Producing a Diverse Set of Near-Optimal Reserve Solutions with Exact Optimisation. *Environmental Modeling & Assessment*:1-16. <https://doi.org/10.1007/s10666-022-09862-1>
- Buckley FG, Buckley PA (1980) Habitat selection and marine birds. In: Burger J, Olla BL, Winn HE (eds) *Behavior of Marine Animals*. Boston, MA: Springer, [https://doi.org/10.1007/978-1-4684-2988-6\\_3](https://doi.org/10.1007/978-1-4684-2988-6_3)

## References

- Bugoni L, Vooren CM (2004) Feeding ecology of the Common Tern *Sterna hirundo* in a wintering area in southern Brazil. *Ibis* 146:438-453
- Bukacinska M, Bukacinsky D (1993) The effect of habitat structure and density of nests on territory size and territorial behaviour in the Black-headed Gull (*Larus ridibundus* L.). *Ethology* 94:306-316
- Burger J (1977) Role of visibility in nesting behavior of *Larus* Gulls. *Journal of Comparative and Physiological Psychology* 91(6):1347-1358
- Burger J (1988) Foraging behavior in gulls: differences in method, prey, and habitat. *Colonial Waterbirds* 11(1):9-23
- Burger J, Gochfeld M (1981) Nest site selection by Kelp Gulls in Southern Africa. *The Condor* 83:243-251
- Burger J, Gochfeld M (1986) Nest Site Selection in Sooty Terns (*Sterna fuscata*) in Puerto Rico and Hawaii. *Colonial Waterbirds* 9(1):31. <https://doi.org/10.2307/1521141>
- Burger J, Gochfeld M (1991) Lead, mercury, and cadmium in feathers of tropical terns in Puerto Rico and Australia. *Archives of Environmental Contamination and Toxicology* 21(2):311-315. <https://doi.org/10.1007/BF01055351>
- Burger J, Shisler J (1978) Nest site selection and competitive interactions of Herring and Laughing Gulls in New Jersey. *The Auk* 95:252-266
- Carey MJ (2009) The effects of investigator disturbance on procellariiform seabirds: A review. *New Zealand Journal of Zoology* 36:367-377. <https://doi.org/10.1080/03014220909510161>
- Carr P, Votier S, Koldewey H, Godley B, Wood H, Nicoll MAC (2020) Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. *Bird Conservation International* 31:14-34. <https://doi.org/10.1017/S0959270920000295>
- Carroll M, Butler A, Owen E, Ewing S, Cole T, Green J, Soanes L, Arnould J, Newton S, Baer J, Daunt F, Wanless S, Newell M, Robertson G, Mavor R, Bolton M (2015) Effects of sea temperature and stratification changes on seabird breeding success. *Climate Research* 66(1):75-89. <https://doi.org/10.3354/cr01332>
- Catry T, Ramos JA, Le Corre M, Kojadinovic J, Bustamante P (2008) The role of stable isotopes and mercury concentrations to describe seabird foraging ecology in tropical environments. *Marine Biology* 155(6):637-647. <https://doi.org/10.1007/s00227-008-1060-6>
- Centro Nacional de Áreas Protegidas (2013) Plan del Sistema Nacional de Áreas Protegidas 2014-2020. Ministerio de Ciencia, Tecnología y Medio Ambiente. La Habana, Cuba
- Champagnon J, Lebreton JD, Drummond H, Anderson DJ (2018) Pacific Decadal and El Niño oscillations shape survival of a seabird. *Ecology* 99(5):1063-1072

## References

- Chatfield-Taylor W (2017) Caribbean Audubon's Shearwaters *Puffinus lherminieri* choose nesting locations that improve male and female pre-laying exodus foraging strategies. *Marine Ornithology* 45:103-106
- Cherel Y, Corre M, Jaquemet S, Ménard F, Richard P, Weimerskirch H (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. *Marine Ecology Progress Series* 366:281-291
- Cherel Y, Hobson K (2007) Geographical variation in carbon stable isotope signatures of marine predators: A tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series* 329:281-287. <https://doi.org/10.3354/meps329281>
- Cherel Y, Hobson KA, Weimerskirch H (2000) Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia* 122(2):155-162. <https://doi.org/10.1007/PL00008843>
- Chilson C, Avery K, McGovern A, Bridge E, Sheldon D, Kelly J (2019) Automated detection of bird roosts using NEXRAD radar data and Convolutional Neural Networks. *Remote Sensing in Ecology and Conservation* 5(1):20-32. <https://doi.org/10.1002/rse2.92>
- Chowdhury WS, Lu G, Hossain MM (2020) Three-dimensional reconstruction and measurement of avian eggs through digital imaging. 2020 IEEE International Instrumentation and Measurement Technology Conference (I2MTC):1-5. <https://doi.org/10.1109/I2MTC43012.2020.9129156>
- Clark TJ, Matthiopoulos J, Bonnet-Lebrun A-S, Campioni L, Catry P, Marengo I, Poncet S, Wakefield E (2019) Integrating habitat and partial survey data to estimate the regional population of a globally declining seabird species, the Sooty Shearwater. *Global Ecology and Conservation* 17:e00554. <https://doi.org/10.1016/j.gecco.2019.e00554>
- Claudet J, Loiseau C, Sostres M, Zupan M (2020) Underprotected Marine Protected Areas in a Global Biodiversity Hotspot. *One Earth*, 2(4):380–384. <https://doi.org/10.1016/j.oneear.2020.03.008>
- Clay TA, Oppel S, Lavers JL, Phillips RA, Brooke M de L (2019) Divergent foraging strategies during incubation of an unusually wide-ranging seabird, the Murphy's petrel. *Marine Biology* 166:1-14
- Cocks KD, Baird IA (1989) Using mathematical programming to address the multiple reserve selection problem: An example from the Eyre Peninsula, South Australia. *Biological Conservation* 49:113-130. [https://doi.org/10.1016/0006-3207\(89\)90083-9](https://doi.org/10.1016/0006-3207(89)90083-9)
- Córdoba-Córdoba S, Ouyang JQ, Hauck SJ (2010) Nesting preferences and population estimates of a new Black Noddy *Anous minutus* breeding colony on one tree island, great barrier reef, Australia. *Marine Ornithology* 38:79-84
- Coulson JC (2002) Colonial breeding in seabirds. In: Schreiber EA, Burger J (eds) *Biology of Marine Birds*. Boca Raton, FL: CRC Press. <https://doi.org/10.1201/9781420036305>



## References

- Cram DL, Jungwirth A, Spence-Jones H, Clutton-Brock T (2019) Reproductive conflict resolution in cooperative breeders. *Behavioral Ecology* 30(6):1743-1750. <https://doi.org/10.1093/beheco/arz143>
- Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International* 22:1-34. <https://doi.org/10.1017/S0959270912000020>
- Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology* 79(7):2415-2428. [https://doi.org/10.1890/0012-9658\(1998\)079\[2415:CRSABH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2415:CRSABH]2.0.CO;2)
- Danchin E, Wagner RH (1997) The evolution of coloniality: The emergence of new perspectives. *Trends in Ecology & Evolution* 12(9):342-347. [https://doi.org/10.1016/S0169-5347\(97\)01124-5](https://doi.org/10.1016/S0169-5347(97)01124-5)
- Deneu B, Servajean M, Bonnet P, Botella C, Munoz F, Joly A (2021) Convolutional neural networks improve species distribution modelling by capturing the spatial structure of the environment. *PLOS Computational Biology* 17(4):e1008856. <https://doi.org/10.1371/journal.pcbi.1008856>
- Denis D (2014) Aplicación de las funciones elípticas de Fourier para la descripción de la forma de los huevos de las aves. *Revista de Biología Tropical* 62(4):1469-1480. <https://doi.org/10.15517/rbt.v62i4.12992>
- Denis D, Olavarrieta U (2011) ¿Existe isomorfia en los huevos de las especies de la familia Ardeidae (Aves, Ciconiiformes)? *Animal Biodiversity and Conservation* 34(1):35-45
- Devillers R, Pressey RL, Grech A, Kittinger JN, Edgar GJ, Ward T, Watson R (2015) Reinventing residual reserves in the sea: are we favouring ease of establishment over need for protection? *Aquatic Conservation: Marine and Freshwater Ecosystems* 25:480-504. <https://doi.org/10.1002/aqc.2445>
- Devillers R, Pressey RL, Ward TJ, Grech A, Kittinger JN, Edgar GJ, Watson RA (2020) Residual marine protected areas five years on: Are we still favouring ease of establishment over need for protection? *Aquatic Conservation: Marine and Freshwater Ecosystems* 30:1758-1764. <https://doi.org/10.1002/aqc.3374>
- Devney CA, Congdon BC (2009) Testing the efficacy of a boundary fence at an important tropical seabird breeding colony and key tourist destination. *Wildlife Research* 36:353-360. <https://doi.org/10.1071/WR08143>
- Diamond AW (1976) Subannual breeding and moult cycles in the Bridled Tern *Sterna anaethetus* in the Seychelles. *Ibis* 118(3):414-419. <https://doi.org/10.1111/j.1474-919X.1976.tb02029.x>
- Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Garcia Borboroglu P, Croxall JP (2019) Threats to seabirds: A global assessment. *Biological Conservation* 237:525-537. <https://doi.org/10.1016/j.biocon.2019.06.033>

## References

- Dobson FS, Becker PH, Arnaud CM, Bouwhuis S, Charmantier A (2017) Plasticity results in delayed breeding in a long-distant migrant seabird. *Ecology and Evolution* 7(9):3100-3109. <https://doi.org/10.1002/ece3.2777>
- Doligez B, Danchin E, Clobert J (2002) Public information and breeding habitat selection in a wild bird population. *Science* 297(5584):1168-1170. <https://doi.org/10.1126/science.1072838>
- Dosch JJ (2003) Movement patterns of adult Laughing Gulls *Larus atricilla* during the nesting season. *Acta Ornithologica* 38:15–25
- Driedger A, Sletten J, Colegrove C, Vincent T, Zetterlind V, Claudet J, Horta e Costa B (2023) Guidance on marine protected area protection level assignments when faced with unknown regulatory information. *Marine Policy* 148:105441. <https://doi.org/10.1016/j.marpol.2022.105441>
- Dunlop JN (2011) Comparative foraging ecology in the dark tern guild breeding off southwestern Australia - insights from stable isotope analysis. *Marine Ornithology* 39:201–206
- Dunlop JN, Surman CA (2012) The role of foraging ecology in the contrasting responses of two dark terns to a changing ocean climate. *Marine Ornithology* 40:105–110
- Dunn PO, Møller AP (2014) Changes in breeding phenology and population size of birds. *Journal of Animal Ecology* 83(3):729-739. <https://doi.org/10.1111/1365-2656.12162>
- Dunning I, Huchette J, Lubin M (2017) JuMP: A Modeling Language for Mathematical Optimization. *SIAM Review* 59:295-320. <https://doi.org/10.1137/15M1020575>
- Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* 95:6-13. <https://doi.org/10.1016/j.fishres.2008.09.024>
- Elvidge CD, Zhizhin M, Ghosh T, Hsu FC, Taneja J (2021) Annual time series of global VIIRS nighttime lights derived from monthly averages:2012 to 2019. *Remote Sensing* 13(5):922. <https://doi.org/doi:10.3390/rs13050922>
- Englert Duursma D, Gallagher RV, Griffith SC (2018) Effects of El Niño Southern Oscillation on avian breeding phenology. *Diversity and Distributions* 24(8):1061-1071. <https://doi.org/10.1111/ddi.12750>
- Eveillard-Buchoux M, Beninger PG, Chadenas C, Sellier D (2019) Small-scale natural landscape features and seabird nesting sites: The importance of geodiversity for conservation. *Landscape Ecology* 34:2295-2306. <https://doi.org/10.1007/s10980-019-00879-8>
- Fasola M, Canova L (1992) Nest habitat selection by eight syntopic species of mediterranean gulls and terns. *Colonial Waterbirds* 15(2):169-291. <https://doi.org/10.2307/1521450>
- Faul F, Erdfelder E, Lang A-G, Buchner A (2007) G\*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods* 39:175-191

## References

- Fernández GJ, Reboreda JC (2008) Between and within clutch variation of egg size in Greater Rheas. *The Wilson Journal of Ornithology* 120(4):674-682. <https://doi.org/10.1676/07-176.1>
- Fincham JI, Wilson C, Barry J, Bolam S, French G (2020) Developing the use of convolutional neural networking in benthic habitat classification and species distribution modelling. *ICES Journal of Marine Science* 77(7–8):3074-3082. <https://doi.org/10.1093/icesjms/fsaa208>
- Forbes LS, Kaiser GW (1994) Habitat choice in breeding seabirds: when to cross the information barrier. *Oikos* 70:377-384. <https://doi.org/10.2307/3545775>
- Forero MG, Hobson KA (2003) Using stable isotopes of nitrogen and carbon to study seabird ecology: applications in the Mediterranean seabird community. *Scientia Marina* 67:23-32. <https://doi.org/10.3989/scimar.2003.67s223>
- Forrest J, Ralphs T, Vigerske S, Hafer L, Kristjansson B, Fasano JP, Straver E, Lubin M, Gambini Santos H, Lougee R, Saltzman M (2018) Coin-Or/Cbc: Version 2.9.9.
- Furness RW, Monaghan P (1987) *Seabird Ecology*. Springer New York, NY. 166 pp.
- Gaglio D (2017) Investigating the foraging ecology and energy requirements of a seabird population increasing in an intensely exploited marine environment. PhD thesis, University of Cape Town, South Africa
- Gaglio D, Cook TR, McInnes A, Sherley RB, Ryan PG (2018) Foraging plasticity in seabirds: A non-invasive study of the diet of greater crested terns breeding in the Benguela region. *PLOS ONE* 13(1):e0190444. <https://doi.org/10.1371/journal.pone.0190444>
- Gaiotto JV, Nunes GT, Bugoni L (2022) Dissipation of seabird-derived nutrients in a terrestrial insular trophic web. *Austral Ecology* 47:1037–1048. <https://doi.org/10.1111/aec.13196>
- Gao B (1996) NDWI-a normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment* 58:257-266
- Garavanta CAM, Wooller RD (2000) Courtship behaviour and breeding biology of Bridled Terns *Sterna anaethetus* on Penguin Island, Western Australia. *Emu* 100(3):169-174. <https://doi.org/10.1071/MU9859>
- García Borboroglu P, Yorio P (2007) Breeding habitat requirements and selection by Olrog's Gull (*Larus atlanticus*), a threatened species. *The Auk* 124:1201-1212
- Garcia-Quintas A, Denis D, Barbraud C, Lanco Bertrand S (2023) Breeding microhabitat patterns among sympatric tropical larids. *Marine Ornithology* 51:97-107
- García-Quintas A, González L, González A (2020) Novedades sobre la reproducción de dos especies de aves marinas poco comunes en Cuba. *Journal of Caribbean Ornithology* 33:54-57
- Garrido OH, Kirkconnell A (2011) *Aves de Cuba*. Cornell University, New York, USA
- Gatto A, Yorio P, Doldan MS, Gomila LV (2019) Spatial and temporal foraging movement patterns in Royal Terns (*Thalasseus maximus*) and Cayenne Terns (*Thalasseus sandvicensis eurygnathus*) in Northern Patagonia, Argentina. *Waterbirds* 42:217-224

## References

- Genovart M, Sanz-Aguilar A, Fernández-Chacón A, Igual JM, Pradel R, Forero MG, Oro D (2013) Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. *Journal of Animal Ecology* 82(1):121–130. <https://doi.org/10.1111/j.1365-2656.2012.02015.x>
- Ghanbari H, Mahdianpari M, Homayouni S, Mohammadimanesh F (2021) A meta-analysis of Convolutional Neural Networks for remote sensing applications. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* 14:3602-3613. <https://doi.org/10.1109/JSTARS.2021.3065569>
- Gilmour ME, Hudson SAT, Lamborg C, Fleishman AB, Young HS, Shaffer SA (2019) Tropical seabirds sample broadscale patterns of marine contaminants. *Science of The Total Environment* 691:631-643. <https://doi.org/10.1016/j.scitotenv.2019.07.147>
- Giménez E, Ramos I, Valle S (2016) Análisis de la productividad pesquera de la plataforma suroriental de Cuba. *Revista Cubana de Investigaciones Pesqueras* 33:43-52
- Gineste B, Souquet M, Couzi F-X, Giloux Y, Philippe J-S, Hoarau C, Tourmetz J, Potin G, Le Corre M (2017) Tropical Shearwater population stability at Reunion Island, despite light pollution. *Journal of Ornithology* 158:385-394. <https://doi.org/10.1007/s10336-016-1396-5>
- González H, Rodríguez L, Rodríguez A, Mancina CA, Ramos I (2012) Libro Rojo de los Vertebrados de Cuba. Editorial Academia, La Habana.
- González-Leiva L, González-Pérez D (2021) Flora y vegetación en tres cayuelos del archipiélago de Sabana-Camagüey, Cuba. *Acta Botánica Cubana* 220. <http://revistasgeotech.com/index.php/abc/article/view/372>
- González-Medina E, Castillo-Guerrero JA, Masero JA, Fernández G (2020) Too salty for you? Changes of diet in the Laughing Gull nestlings during the growing period. *Journal of Avian Biology* 51(8):jav.02432. <https://doi.org/10.1111/jav.02432>
- González-Sansón G, Aguilar C, Hernández I, Cabrera Y, Curry RA (2009) The influence of habitat and fishing on reef fish assemblages in Cuba. *Gulf and Caribbean Research* 21:13-21. <https://doi.org/10.18785/gcr.2101.02>
- Good TP (2002) Breeding success in the Western Gull x Glaucous-Winged Gull complex: the influence of habitat and nest-site characteristics. *The Condor* 104:353-365
- Gorke M, Brandl R (1986) How to live in colonies: spatial foraging strategies of the Black-headed Gull. *Oecologia* 70:288–290
- Graham BS, Koch PL, Newsome SD, McMahon KW, Auriolos D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) *Isoscapes: Understanding movement, pattern, and process on earth through isotope mapping*. Springer Science & Business Media, Netherlands, pp. 299–318

## References

- Grecian WJ, McGill RAR, Phillips RA, Ryan PG, Furness RW (2015) Quantifying variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes within and between feathers and individuals: Is one sample enough? *Marine Biology* 162(4):733-741. <https://doi.org/10.1007/s00227-015-2618-8>
- Greer RD, Cordes CL, Anderson SH (1988) Habitat relationships of island nesting seabirds along coastal Louisiana. *Colonial Waterbirds* 11(2):181-188. <https://doi.org/10.2307/1520999>
- Gronstol GB (1997) Correlates of egg-size variation in polygynously breeding Northern Lapwings. *The Auk* 114(3):507-512. <https://doi.org/10.2307/4089255>
- Hamer KC, Schreiber EA, Burger J (2002) Breeding biology, life histories, and life history-environment interactions in seabirds. In: Schreiber EA, Burger J (eds) *Biology of marine birds*. CRC Press
- Hanson JO, Schuster R, Morrell N, Strimas-Mackey M, Edwards BPM, Watts ME, Arcese P, Bennett J, Possingham HP (2022) prioritizr: Systematic Conservation Prioritization in R
- Hanson JO, Schuster R, Strimas-Mackey M, Bennett JR (2019) Optimality in prioritizing conservation projects. *Methods in Ecology and Evolution* 10:1655-1663. <https://doi.org/10.1111/2041-210X.13264>
- Harrison P, Perrow M, Larsson H (2021) *Seabirds: the new identification guide*.
- Harvey MS, Ralph GM, Polidoro BA, Maxwell SM, Carpenter KE (2021) Identifying key biodiversity areas as marine conservation priorities in the greater Caribbean. *Biodiversity and Conservation* 30:4039-4059. <https://doi.org/10.1007/s10531-021-02291-8>
- Hazen EL, Abrahms B, Brodie S, Carroll G, Jacox MG, Savoca MS, Scales KL, Sydeman WJ, Bograd SJ (2019) Marine top predators as climate and ecosystem sentinels. *Frontiers in Ecology and the Environment* 17(10):565-574. <https://doi.org/10.1002/fee.2125>
- Hindell MA, Bradshaw CJA, Brook BW, Fordham DA, Kerry K, Hull C, McMahon CR (2012) Long-term breeding phenology shift in royal penguins: Phenology in Antarctic Seabirds. *Ecology and Evolution* 2(7):1563-1571. <https://doi.org/10.1002/ece3.281>
- Hobson KA (1990) Stable Isotope Analysis of Marbled Murrelets: Evidence for freshwater feeding and determination of trophic level. *The Condor* 92:897-903
- Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes II: Factors influencing diet-tissue fractionation. *The Condor* 94(1):189-197. <https://doi.org/10.2307/1368808>
- Hockey P, Wilson W (2003) Reproductive traits of marine terns (Sternidae): Evidence for food limitation in the tropics? *Ostrich* 74(1-2):110-116. <https://doi.org/10.2989/00306520309485376>
- Hong P, Wiley DN, Powers KD, Michener RH, Kaufman L, Hatch KA (2019) Stable isotope analyses of multiple tissues of Great Shearwaters (*Ardenna gravis*) reveals long-term dietary stability, short-term changes in diet, and can be used as a tool to monitor food webs. *Diversity* 11(9):163. <https://doi.org/doi:10.3390/d11090163>

## References

- Hu G, Feeley KJ, Wu J, Xu G, Yu M (2011) Determinants of plant species richness and patterns of nestedness in fragmented landscapes: Evidence from land-bridge islands. *Landscape Ecology* 26(10):1405-1417. <https://doi.org/10.1007/s10980-011-9662-7>
- Hulsman K, Langham NPE (1985) Breeding biology of the Bridled Tern *Sterna anaethetus*. *Emu* 85(4):240-249. <https://doi.org/10.1071/MU9850240>
- Hunt GL, Hunt MW (1973) Habitat partitioning by foraging gulls in Maine and Northwestern Europe. *The Auk* 90:827-839. <https://doi.org/10.2307/4084363>
- Inger R, Bearhop S (2008) Applications of stable isotope analyses to avian ecology: Avian stable isotope analysis. *Ibis* 150:447-461
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R: Bayesian isotopic niche metrics. *Journal of Animal Ecology* 80(3):595-602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Jacquemont J, Blasiak R, Le Cam C, Le Gouellec M, Claudet J (2022) Ocean conservation boosts climate change mitigation and adaptation. *One Earth* 5:1126-1138. <https://doi.org/10.1016/j.oneear.2022.09.002>
- Jaeger A, Feare CJ, Summers RW, Lebarbenchon C, Larose CS, Le Corre M (2017) Geolocation reveals year-round at-sea distribution and activity of a superabundant tropical seabird, the Sooty Tern *Onychoprion fuscatus*. *Frontiers in Marine Science* 4:394. <https://doi.org/10.3389/fmars.2017.00394>
- Jaquemet S, Potier M, Cherel Y, Kojadinovic J, Bustamante P, Richard P, Catry T, Ramos JA, Le Corre M (2008) Comparative foraging ecology and ecological niche of a superabundant tropical seabird: The Sooty Tern *Sterna fuscata* in the southwest Indian Ocean. *Marine Biology* 155(5):505-520. <https://doi.org/10.1007/s00227-008-1049-1>
- Jiménez A, Rodríguez P, Blanco P (2009) Cuba. In: Bradley P, Norton R (eds) *An inventory of breeding seabirds of the Caribbean*. University Press of Florida, USA, pp. 47-57
- Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR (2008) Severity of the effects of invasive rats on seabirds: A global review. *Conservation Biology* 22:16-26. <https://doi.org/10.1111/j.1523-1739.2007.00859.x>
- Kalinowski T, Falbel D, Allaire JJ, Chollet F, Tang Y, Van Der Bijl W, Studer M, Keydana S (2021) keras: R Interface to 'Keras'. R package version 2.6.1, <https://cran.r-project.org/web/packages=keras>
- Kattenborn T, Leitloff J, Schiefer F, Hinz S (2021) Review on Convolutional Neural Networks (CNN) in vegetation remote sensing. *ISPRS Journal of Photogrammetry and Remote Sensing* 173:24-49. <https://doi.org/10.1016/j.isprsjprs.2020.12.010>
- Kiszka JJ, Aubail A, Hussey NE, Heithaus MR, Caurant F, Bustamante P (2015) Plasticity of trophic interactions among sharks from the oceanic south-western Indian Ocean revealed by

## References

- stable isotope and mercury analyses. *Deep Sea Research Part I: Oceanographic Research Papers* 96:49-58. <https://doi.org/10.1016/j.dsr.2014.11.006>
- Kohno H, Kishimoto H (1991) Prey of the Bridled Tern *Sterna anaethetus* on Nakanokamishima Island, South Ryukyus, Japan. *Japanese Journal of Ornithology* 40:15–25
- Kokko H, Harris MP, Wanless S (2004) Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the Common Guillemot *Uria aalge*. *Journal of Animal Ecology* 73:367-376
- Komar O, Rodriguez W (1996) A major Bridled Tern (*Sterna anaethetus*) colony in the Gulf of Fonseca, Nicaragua. *Colonial Waterbirds* 19(2):264. <https://doi.org/10.2307/1521868>
- Krishna ST, Kalluri HK (2019) Deep learning and transfer learning approaches for image classification. *International Journal of Recent Technology and Engineering (IJRTE)*:7(5S4)
- Kristan III WB (2006) Sources and expectations for hierarchical structure in bird-habitat associations. *The Condor* 108:5-12
- Kussul N, Lavreniuk M, Skakun S, Shelestov A (2017) Deep learning classification of land cover and crop types using remote sensing data. *IEEE Geoscience and Remote Sensing Letters* 14(5):778-782. <https://doi.org/10.1109/LGRS.2017.2681128>
- Labbé AMT (2017) Effects of age on reproduction and chick rearing in Bridled Terns (*Onychoprion anaethetus*) at Penguin Island, Western Australia. PhD thesis, Murdoch University, Western Australia
- Labbé AMT, Dunlop JN, Loneragan NR (2013) Central place foraging and feather regrowth rate in Bridled Terns (*Onychoprion anaethetus*): An insight from stable isotopes. *Marine and Freshwater Research* 64(12):1184-1191. <https://doi.org/10.1071/MF12334>
- Lamb JS, Satgé YG, Jodice PGR (2017) Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. *Ecology and Evolution* 7:6469-6481
- Langham NP (1983) Growth strategies in marine terns. *Studies in Avian Biology* 8:73-83
- Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48
- Lescroël A, Mathevet R, Péron C, Authier M, Provost P, Takahashi A, Grémillet D (2016) Seeing the ocean through the eyes of seabirds: A new path for marine conservation? *Marine Policy* 68:212-220. <https://doi.org/10.1016/j.marpol.2016.02.015>
- Liechty JS, Fontenot QC, Pierce AR (2016) Diet Composition of Royal Tern (*Thalasseus maximus*) and Sandwich Tern (*Thalasseus sandvicensis*) at Isles Dernieres Barrier Island Refuge, Louisiana, USA. *Waterbirds* 39:58–68

## References

- Lieske DJ, Tranquilla LM, Ronconi R, Abbott S (2019) Synthesizing expert opinion to assess the at-sea risks to seabirds in the western North Atlantic. *Biological Conservation* 233:41-50. <https://doi.org/10.1016/j.biocon.2019.02.026>
- Lieske DJ, Tranquilla LM, Ronconi RA, Abbott S (2020) “Seas of risk”: Assessing the threats to colonial-nesting seabirds in Eastern Canada. *Marine Policy* 115:103863. <https://doi.org/10.1016/j.marpol.2020.103863>
- Lindén A (2018) Adaptive and nonadaptive changes in phenological synchrony. *Proceedings of the National Academy of Sciences* 115(20):5057-5059. <https://doi.org/10.1073/pnas.1805698115>
- Linhares BDA, Bugoni L (2022) Seabirds subsidize terrestrial food webs and coral reefs in a tropical rat-invaded archipelago. *Ecological Applications* 33:<https://doi.org/10.1002/eap.2733>
- Lisnizer N, Yorio P (2019) Trophic niche expansion during the non-breeding season in Kelp Gulls of known breeding colony. *Marine Biology* 166:12. <https://doi.org/10.1007/s00227-018-3460-6>
- Loiseau C, Thiault L, Devillers R, Claudet J (2021) Cumulative impact assessments highlight the benefits of integrating land-based management with marine spatial planning. *Science of The Total Environment* 787:147339. <https://doi.org/10.1016/j.scitotenv.2021.147339>
- Lorentsen S, Mattisson J, Christensen-Dalsgaard S (2019) Reproductive success in the European Shag is linked to annual variation in diet and foraging trip metrics. *Marine Ecology Progress Series* 619:137–147
- Lorrain A, Houlbrèque F, Benzoni F, Barjon L, Tremblay-Boyer L, Menkes C, Gillikin DP, Payri C, Jourdan H, Boussarie G, Verheyden A, Vidal E (2017) Seabirds supply nitrogen to reef-building corals on remote Pacific islets. *Scientific Reports* 7:3721. <https://doi.org/10.1038/s41598-017-03781-y>
- Lougee-Heimer R (2003) The Common Optimization INterface for Operations Research: Promoting open-source software in the operations research community. *IBM Journal of Research and Development* 47:57-66. <https://doi.org/10.1147/rd.471.0057>
- Ma L, Liu Y, Zhang X, Ye Y, Yin G, Johnson BA (2019) Deep learning in remote sensing applications: A meta-analysis and review. *ISPRS Journal of Photogrammetry and Remote Sensing* 152:166-177. <https://doi.org/10.1016/j.isprsjprs.2019.04.015>
- Madden H, Eggermont E (2020) First evidence of plastic ingestion by Red-billed Tropicbirds *Phaethon aethereus* from St. Eustatius, Caribbean Netherlands. *Marine Ornithology* 48:157–160
- Mahdianpari M, Salehi B, Rezaee M, Mohammadimanesh F, Zhang Y (2018) Very deep convolutional neural networks for complex land cover mapping using multispectral remote sensing imagery. *Remote Sensing* 10(7):1119. <https://doi.org/10.3390/rs10071119>



## References

- Marcella TK, Gende SM, Roby DD, Allignol A (2017) Disturbance of a rare seabird by ship-based tourism in a marine protected area. *PLOS ONE* 12:e0176176. <https://doi.org/10.1371/journal.pone.0176176>
- Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature* 405:243-253
- Marinao C, Suárez N, Gatto A, Yorio P (2019) Forage fish to growing chicks: shared food resources between two closely related tern species. *Marine Biology* 166:121. <https://doi.org/10.1007/s00227-019-3570-9>
- Massaro M, Davis LS (2004) The influence of laying date and maternal age on eggshell thickness and pore density in Yellow-Eyed Penguins. *The Condor* 106:496-505
- McGinnis TW, Emslie SD (2001) The foraging ecology of Royal and Sandwich Terns in North Carolina, USA. *Waterbirds* 24:361-370
- McGowan J, Hines E, Elliott M, Howar J, Dransfield A, Nur N, Jahncke J (2013) Using seabird habitat modeling to inform marine spatial planning in central California's national marine sanctuaries. *PLOS ONE* 8(8):e71406. <https://doi.org/10.1371/journal.pone.0071406>
- Meehan MC, Ban NC, Devillers R, Singh GG, Claudet J (2020) How far have we come? A review of MPA network performance indicators in reaching qualitative elements of Aichi Target 11. *Conservation Letters* 13:e12746. <https://doi.org/10.1111/conl.12746>
- Meier RE, Votier SC, Wynn RB, Guilford T, Grivé MM, Rodríguez A, Newton J, Maurice L, Chouvelon T, Dessier A, Trueman CN (2017) Tracking, feather moult and stable isotopes reveal foraging behaviour of a critically endangered seabird during the non-breeding season. *Diversity and Distribution* 23:130–145
- Mejías MA, Wingate DB, Hetzel E, Nisbet ICT (2020) Nesting of Roseate Terns (*Sterna dougallii*) in Bermuda after extirpation for nearly 150 years. *Waterbirds* 43:101. <https://doi.org/10.1675/063.043.0111>
- Menéndez L, Capote RP, Vilamajó D, Ricardo N, Guzmán JM, Rodríguez L (2014) Vegetación: Formaciones vegetales presentes en el archipiélago de Sabana-Camagüey. In: Rodríguez D, Arias A, Ruiz E (eds) *Fauna Terrestre del Archipiélago de Sabana-Camagüey, Cuba*. Editorial Academia, La Habana, Cuba
- Mínguez E, Oro D, De Juana E, Martínez-Abraín A (2003) Mediterranean seabird conservation: what can we do? *Scientia Marina* 67:3-6. <https://doi.org/10.3989/scimar.2003.67s23>
- Mitchell I, Daunt F, Frederiksen M, Wade K (2020) Impacts of climate change on seabirds, relevant to the coastal and marine environment around the UK. *MCCIP Science Review* 2020:382–399. <https://doi.org/10.14465/2020.ARC17.SBI>
- Moiron M, Araya-Ajoy YG, Teplitsky C, Bouwhuis S, Charmantier A (2020) Understanding the social dynamics of breeding phenology: Indirect genetic effects and assortative mating in a long-distance migrant. *The American Naturalist* 196(5):566-576. <https://doi.org/10.1086/711045>

## References

- Monticelli D, Ramos JA, Tavares PC, Bataille B, Lepoint G, Devillers P (2008) Diet and foraging ecology of Roseate Terns and Lesser Noddies breeding sympatrically on Aride Island, Seychelles. *Waterbirds* 31:231-240
- Moser ML, Lee DS (2012) Foraging over *Sargassum* by Western North Atlantic seabirds. *The Wilson Journal of Ornithology* 124(1):66-72. <https://doi.org/10.1676/11-067.1>
- Mugica L, Acosta M, Denis D (2006) Conservando las aves acuáticas. In: Mugica L, Denis D, Acosta M, Jiménez A, Rodríguez A (eds) *Aves acuáticas en los humedales de Cuba*, pp. 136-159. Ed. Científico-Técnica, La Habana, Cuba
- Mugica L, Acosta M, Jiménez A, Rodríguez A (2012) Current knowledge and conservation of cuban waterbirds and their habitats. *Journal of Caribbean Ornithology* 25:64-76
- Muzaffar SB, Gubiani R, Benjamin S (2015) Nest location influences hatching success in the Socotra Cormorant (*Phalacrocorax nigrogularis*) on Siniya Island, United Arab Emirates. *Wildlife Research* 42:13-18. <https://doi.org/10.1071/WR14225>
- Navarro N (2021) Annotated Checklist of the Birds of Cuba. Ediciones Nuevos Mundos, USA
- Nedomová Š, Buchar J (2014) Goose eggshell geometry. *Research in Agricultural Engineering* 60(3):100-106. <https://doi.org/10.17221/80/2012-RAE>
- Neumann JL, Larose CS, Brodin G, Feare CJ (2018) Foraging ranges of incubating Sooty Terns *Onychoprion fuscatus* on Bird island, Seychelles, during a transition from food plenty to scarcity, as revealed by gps loggers. *Marine Ornithology* 46:11-18
- Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5(8):429-436. <https://doi.org/10.1890/060150.1>
- Nisbet ICT (2000) Disturbance, habituation, and management of waterbird colonies. *Waterbirds* 23:312-332
- Nisbet ICT (2020) Distinguishing between Roseate and Common Terns at breeding colonies in the West Indies. *Journal of Caribbean Ornithology* 33:117-118
- Norton R (2009) Local, regional, and global threats. In: Bradley P, Norton R (eds) *An inventory of breeding seabirds of the Caribbean*. University Press of Florida, Florida, USA.
- Nunes GT, Bertrand S, Bugoni L (2018) Seabirds fighting for land: Phenotypic consequences of breeding area constraints at a small remote archipelago. *Scientific Reports* 8(1):665. <https://doi.org/10.1038/s41598-017-18808-7>
- Olier I, Orhobor OI, Dash T, Davis AM, Soldatova LN, Vanschoren J, King RD (2021) Transformational machine learning: Learning how to learn from many related scientific problems. *Proceedings of the National Academy of Sciences* 118(49):e2108013118. <https://doi.org/10.1073/pnas.2108013118>
- Oppel S, Beard A, Fox D, Mackley E, Leat E, Henry L, Clingham E, Fowler N, Sim J, Sommerfeld J, Weber N, Weber S, Bolton M (2015) Foraging distribution of a tropical seabird

## References

- supports Ashmole's hypothesis of population regulation. *Behavioral Ecology and Sociobiology* 69(6):915-926. <https://doi.org/10.1007/s00265-015-1903-3>
- Oppel S, Bolton M, Carneiro APB, Dias MP, Green JA, Masello JF, Phillips RA, Owen E, Quillfeldt P, Beard A, Bertrand S, Blackburn J, Boersma PD, Borges A, Broderick AC, Catry P, Cleasby I, Clingham E, Creuwels J, *et al.* (2018) Spatial scales of marine conservation management for breeding seabirds. *Marine Policy* 98:37-46. <https://doi.org/10.1016/j.marpol.2018.08.024>
- Orians GH, Wittenberger JF (1991) Spatial and temporal scales in habitat selection. *The American Naturalist* 137:29-49
- Oro D (2014) Seabirds and climate: Knowledge, pitfalls, and opportunities. *Frontiers in Ecology and Evolution* 2(79). <https://doi.org/10.3389/fevo.2014.00079>
- PAN-Tiburones (2015) Plan de Acción Nacional de Conservación y Manejo de Condrictios de la República de Cuba. Ministerio de la Industria Alimentaria, La Habana, Cuba
- Paredes R, Harding A, Irons D, Roby D, Suryan R, Orben R, Renner H, Young R, Kitaysky A (2012) Proximity to multiple foraging habitats enhances seabirds' resilience to local food shortages. *Marine Ecology Progress Series* 471:253-269. <https://doi.org/10.3354/meps10034>
- Paredes R, Orben R, Roby D, Irons D, Young R, Renner H, Tremblay Y, Will A, Harding A, Kitaysky A (2015) Foraging ecology during nesting influences body size in a pursuit-diving seabird. *Marine Ecology Progress Series* 533:261-276
- Parsons J (1976) Factors determining the number and size of eggs laid by the Herring Gull. *The Condor* 78(4):481-492. <https://doi.org/10.2307/1367097>
- Passuni G, Barbraud C, Chaigneau A, Demarcq H, Ledesma J, Bertrand A, Castillo R, Perea A, Mori J, Viblanc VA, Torres-Maita J, Bertrand S (2016) Seasonality in marine ecosystems: Peruvian seabirds, anchovy, and oceanographic conditions. *Ecology* 97(1):182-193. <https://doi.org/10.1890/14-1134.1>
- Perera S, Hernández A, González J, Moreno O, Cobián D, Ferro H, Milián E, Caballero H, Alcolado PM, Pina F, Hernández Z, Espinosa L, Rodríguez LF (2017) Marine protected areas in Cuba. *Bulletin of Marine Science* 94(2):423-442. <https://doi.org/10.5343/bms.2016.1129>
- Perrow MR, Harwood AJP, Skeate ER, Praca E, Eglington SM (2015) Use of multiple data sources and analytical approaches to derive a marine protected area for a breeding seabird. *Biological Conservation* 191:729-738. <https://doi.org/10.1016/j.biocon.2015.08.031>
- Perrow MR, Skeate ER, Gilroy JJ (2011) Visual tracking from a rigid-hulled inflatable boat to determine foraging movements of breeding terns: Visual tracking of terns. *Journal of Field Ornithology* 82:68-79
- Phillips RA, McGill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Marine Biology* 158:2199-2208

## References

- Piatt JF, Sydeman WJ, Wiese F (2007) Seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series* 352:199-204. <https://doi.org/10.3354/meps07070>
- Pinaud D, Cherel Y, Weimerskirch H (2005) Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Marine Ecology Progress Series* 298:295-304. <https://doi.org/10.3354/meps298295>
- Piper WH (2011) Making habitat selection more “familiar”: A review. *Behavioral Ecology and Sociobiology* 65(7):1329-1351. <https://doi.org/10.1007/s00265-011-1195-1>
- Planos E, Rivero R, Guevara V (2013) Impacto del cambio climático y medidas de adaptación en Cuba. Instituto de Meteorología, CITMA, La Habana, 430 pp.
- Polito MJ, Hinke JT, Hart T, Santos M, Houghton LA, Thorrold SR (2017) Stable isotope analyses of feather amino acids identify penguin migration strategies at ocean basin scales. *Biology Letters* 13:20170241. <https://doi.org/10.1098/rsbl.2017.0241>
- Ponchon A, Grémillet D, Doligez B, Chambert T, Tveraa T, González-Solís J, Boulinier T (2013) Tracking prospecting movements involved in breeding habitat selection: Insights, pitfalls and perspectives. *Methods in Ecology and Evolution* 4(2):143-150. <https://doi.org/10.1111/j.2041-210x.2012.00259.x>
- Pressey RL (1994) Ad hoc reservations: Forward or backward steps in developing representative reserve systems? *Conservation Biology* 8:662-668. <https://doi.org/10.1046/j.1523-1739.1994.08030662.x>
- Pressey RL, Tully SL (1994) The cost of ad hoc reservation: A case study in western New South Wales. *Australian Journal of Ecology* 19:375-384. <https://doi.org/10.1111/j.1442-9993.1994.tb00503.x>
- Proudfoot B, Devillers R, Brown CJ (2020) Integrating fine-scale seafloor mapping and spatial pattern metrics into marine conservation prioritization. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30:1613-1625. <https://doi.org/10.1002/aqc.3360>
- QGIS Development Team (2020) QGIS 3.10.2.
- Quillfeldt P, McGill RAR, Furness RW (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson’s Storm-petrel. *Marine Ecology Progress Series* 295:295–304
- Quintero I, González-Caro S, Zalamea P-C, Cadena CD (2014) Asynchrony of seasons: Genetic differentiation associated with geographic variation in climatic seasonality and reproductive phenology. *The American Naturalist* 184(3):352-363. <https://doi.org/10.1086/677261>
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rader JA, Newsome SD, Sabat P, Chesser RT, Dillon ME, Martínez del Rio C (2017) Isotopic niches support the resource breadth hypothesis. *Journal of Animal Ecology* 86(2):405-413. <https://doi.org/10.1111/1365-2656.12629>

## References

- Ramírez-Arrieta VM, Denis D, Ferrer-Sánchez Y (2021) Evaluación de un protocolo automatizado para la obtención de medidas morfométricas de huevos de aves a partir de fotografías digitales. *Animal Biodiversity and Conservation* 44(1):31-43. <https://doi.org/10.32800/abc.2021.44.0031>
- Ramos JA, Monticelli D (2012) The influence of early age at breeding on reproductive parameters of tropical Roseate Terns. *Ostrich* 83(1):7-12. <https://doi.org/10.2989/00306525.2012.677518>
- Ramos R, Reyes-González JM, Morera-Pujol V, Zajková Z, Militão T, González-Solís J (2020) Disentangling environmental from individual factors in isotopic ecology: A 17-year longitudinal study in a long-lived seabird exploiting the Canary Current. *Ecological Indicators* 111:105963. <https://doi.org/10.1016/j.ecolind.2019.105963>
- Raynor EJ, Pierce AR, Leumas CM, Rohwer FC (2012) Breeding habitat requirements and colony formation by Royal Terns (*Thalasseus maximus*) and Sandwich Terns (*T. sandvicensis*) on barrier islands in the Gulf of Mexico. *The Auk* 129(4):763-772. <https://doi.org/10.1525/auk.2012.11181>
- Reed TE, Warzybok P, Wilson AJ, Bradley RW, Wanless S, Sydeman WJ (2009) Timing is everything: Flexible phenology and shifting selection in a colonial seabird. *Journal of Animal Ecology* 78(2):376-387. <https://doi.org/10.1111/j.1365-2656.2008.01503.x>
- Reed WL, Turner AM, Sotherland PR (1999) Consequences of egg-size variation in the Red-Winged Blackbird. *The Auk* 116(2):549-552. <https://doi.org/10.2307/4089390>
- Ricklefs RE, Hahn DC, Montevecchi WA (1978) The Relationship between egg size and chick size in the Laughing Gull and Japanese Quail. *The Auk* 95(1):135-144. <https://doi.org/10.2307/4085504>
- Robert A, Paiva VH, Bolton M, Jiguet F, Bried J (2014) Nest fidelity is driven by multi-scale information in a long-lived seabird. *Proceedings of the Royal Society B: Biological Sciences* 281(1793):20141692. <https://doi.org/10.1098/rspb.2014.1692>
- Robertson GJ, Fifield D, Massaro M, Chardine JW (2001) Changes in nesting-habitat use of large gulls breeding in Witless Bay, Newfoundland. *Canadian Journal of Zoology* 79:2159-2167. doi: 10.1139/cjz-79-12-2159
- Robertson GS, Bolton M, Grecian WJ, Wilson LJ, Davies W, Monaghan P (2014) Resource partitioning in three congeneric sympatrically breeding seabirds: Foraging areas and prey utilization. *The Auk* 131:434-446
- Rodríguez P, Rodríguez D, Pérez E, Blanco P, Parada A, Ruiz E, Barrio O, Llanes A (2003) Distribución y composición de las colonias de nidificación de aves acuáticas en el Archipiélago de Sabana-Camagüey. CD-ROM Memorias VII Simposio de Botánica, La Habana, Cuba. ISBN: 959-270-029-X

## *References*

- Rolland C, Danchin E, de Fraipont M (1998) The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: A comparative analysis. *The American Naturalist* 151(6):514-529. <https://doi.org/10.1086/286137>
- Roman J (2018) The ecology and conservation of Cuba's coastal and marine ecosystems. *Bulletin of Marine Science* 94(2):149-169. <https://doi.org/10.5343/bms.2017.1164>
- Roura-Pérez P, Sistachs-Vega V, Vega R, Alpizar-Tirzo M (2018) Caracterización estadística climatológica de huracanes en Cuba durante el período 1791-2016. *Revista Cubana de Meteorología* 24(3):304-312
- Rouse JW Jr, Haas RH, Schell JA, Deering DW (1973) Monitoring vegetation systems in the Great Plains with ERTS. In *Third Earth Resources Technology Satellite-1 Symposium.: Vol. Technical presentations, Section A, Vol. I.* (pp. 309–317)
- Rstudio Team (2021) RStudio: Integrated Development for R. RStudio Inc. (1.4.1717). Boston, MA: PBC, URL <http://www.rstudio.com/>.
- Ruiz E, Primelles J, Rodríguez P, Barrio O, Rodríguez D, Hernández E (2014) Aves: Comunidades de aves acuáticas. In: Rodríguez D, Arias A, Ruiz E (eds) *Fauna Terrestre del Archipiélago de Sabana-Camagüey, Cuba*. Editorial Academia, La Habana, Cuba
- Salas R, Müller W, Vercrujssse H, Lens L, Stienen E (2020) Forced nest site relocations negatively affect reproductive investment in a colonial seabird species. *Biological Conservation* 246:108550. <https://doi.org/10.1016/j.biocon.2020.108550>
- Schreiber EA, Burger J (2002) *Biology of Marine Birds*. CRC Press
- Schultz M, Brun V, Wingate M, Cury P, Gaill F, Sicre M-A, Claudet J (2022) A framework to identify barriers and levers to increase the levels of protection of marine protected areas. *One Earth* 5:987-999. <https://doi.org/10.1016/j.oneear.2022.08.007>
- Schuster R, Hanson JO, Strimas-Mackey M, Bennett JR (2020) Exact integer linear programming solvers outperform simulated annealing for solving conservation planning problems. *PeerJ* 8:e9258. <https://doi.org/10.7717/peerj.9258>
- Schwartz-Narbonne R, Longstaffe FJ, Kardynal KJ, Druckenmiller P, Hobson KA, Jass CN, Metcalfe JZ, Zazula G (2019) Reframing the mammoth steppe: Insights from analysis of isotopic niches. *Quaternary Science Reviews* 215:1–21
- Schwemmer P, Adler S, Guse N, Markones N, Garthe S (2009) Influence of water flow velocity, water depth and colony distance on distribution and foraging patterns of terns in the Wadden Sea. *Fisheries Oceanography* 18:161-172. <https://doi.org/10.1111/j.1365-2419.2009.00504.x>
- Schwemmer P, Mendel B, Sonntag N, Dierschke V, Garthe S (2011) Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. *Ecological Applications* 21:1851-1860. <https://doi.org/10.1890/10-0615.1>
- Sebastiano M, Bustamante P, Costantini D, Eulaers I, Malarvannan G, Mendez-Fernandez P, Churlaud C, Blévin P, Hauselmann A, Dell’Omo G, Covaci A, Eens M, Chastel O (2016)

## References

- High levels of mercury and low levels of persistent organic pollutants in a tropical seabird in French Guiana, the Magnificent Frigatebird, *Fregata magnificens*. *Environmental Pollution* 214:384-393. <https://doi.org/10.1016/j.envpol.2016.03.070>
- Sebastiano M, Bustamante P, Eulaers I, Malarvannan G, Mendez-Fernandez P, Churlaud C, Blévin P, Hauselmann A, Covaci A, Eens M, Costantini D, Chastel O (2017) Trophic ecology drives contaminant concentrations within a tropical seabird community. *Environmental Pollution* 227:183-193
- Shealer DA (1996) Foraging habitat use and profitability in Tropical Roseate Terns and Sandwich Terns. *The Auk* 113:209-217
- Shipley ON, Matich P (2020) Studying animal niches using bulk stable isotope ratios: An updated synthesis. *Oecologia* 193(1):27-51. <https://doi.org/10.1007/s00442-020-04654-4>
- Soanes LM, Bright JA, Bolton M, Millett J, Mukhida F, Green JA (2015) Foraging behaviour of Brown Boobies *Sula leucogaster* in Anguilla, Lesser Antilles: Preliminary identification of at-sea distribution using a time-in-area approach. *Bird Conservation International* 25:87-96
- Soanes LM, Bright JA, Carter D, Dias MP, Fleming T, Gumbs K, Hughes G, Mukhida F, Green JA (2016) Important foraging areas of seabirds from Anguilla, Caribbean: Implications for marine spatial planning. *Marine Policy* 70:85-92
- Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: Stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology* 78(2):460-467. <https://doi.org/10.1111/j.1365-2656.2008.01492.x>
- Su J-H, Piao Y-C, Luo Z, Yan B-P (2018) Modeling habitat suitability of migratory birds from remote sensing images using convolutional neural networks. *Animals* 8(5):66. <https://doi.org/10.3390/ani8050066>
- Surman C, Nicholson L, Santora J (2012) Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. *Marine Ecology Progress Series* 454:147-157. <https://doi.org/10.3354/meps09729>
- Surman CA, Wooller RD (2003) Comparative foraging ecology of five sympatric terns at a sub-tropical island in the eastern Indian Ocean. *Journal of Zoology (London)* 259:219-230
- Sydeman WJ, Emslie SD (1992) Effects of parental age on hatching asynchrony, egg size and third-chick disadvantage in Western Gulls. *The Auk* 109(2):242-248. <https://doi.org/10.2307/4088192>
- Tayefeh FH, Zakaria M, Amini H, Mohammadnejad J, Darvishi K, Karami S (2014) Dietary segregation between breeding tern species on the Persian Gulf Islands, Iran. *Waterbirds* 37(3):307-318. <https://doi.org/10.1675/063.037.0309>
- Tayefeh FH, Zakaria M, Ghayoumi R, Amini H (2017) Breeding biology of the Bridled Tern *Sterna anaethetus* on Nakhilu Island, Persian Gulf, Iran. *Podoces* 12(1):1-12

## References

- Thaxter CB, Lascelles B, Sugar K, Cook ASCP, Roos S, Bolton M, Langston RHW, Burton NHK (2012) Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation* 156:53-61. <https://doi.org/10.1016/j.biocon.2011.12.009>
- Thompson D, Torres L, Taylor G, Rayner M, Sagar P, Shaffer S, Phillips R, Bury S (2015) Stable isotope values delineate the non-breeding distributions of Sooty Shearwaters *Puffinus griseus* in the North Pacific Ocean. *Marine Ecology Progress Series* 521:277-282
- Tree AJ, Connan M, Whittington PA (2019) Roseate Terns *Sterna dougallii* on the southeast coast of South Africa: Information on moult and migratory status. *Ostrich* 90(4):303-313. <https://doi.org/10.2989/00306525.2019.1642253>
- Tremblay Y, Bertrand S, Henry R, Kappes M, Costa D, Shaffer S (2009) Analytical approaches to investigating seabird–environment interactions: a review. *Marine Ecology Progress Series* 391:153-163. <https://doi.org/10.3354/meps08146>
- Trevaill AM, Green JA, Bolton M, Daunt F, Harris SM, Miller PI, Newton S, Owen E, Polton JA, Robertson G, Sharples J, Patrick SC (2021) Environmental heterogeneity promotes individual specialisation in habitat selection in a widely distributed seabird. *Journal of Animal Ecology* 90(12):2875-2887. <https://doi.org/10.1111/1365-2656.13588>
- Troisi G, Barton S, Bexton S (2016) Impacts of oil spills on seabirds: Unsustainable impacts of non-renewable energy. *International Journal of Hydrogen Energy* 41:16549-16555. <https://doi.org/10.1016/j.ijhydene.2016.04.011>
- Valdés V (1984) Datos de nidificación sobre las aves que crían en Cuba. *Poeyana* 282:1-10
- Velando A, Munilla I (2011) Disturbance to a foraging seabird by sea-based tourism: Implications for reserve management in marine protected areas. *Biological Conservation* 144:1167-1174. <https://doi.org/10.1016/j.biocon.2011.01.004>
- Vilchis L, Ballance L, Fiedler P (2006) Pelagic habitat of seabirds in the eastern tropical Pacific: Effects of foraging ecology on habitat selection. *Marine Ecology Progress Series* 315:279-292. <https://doi.org/10.3354/meps315279>
- Villard P, Bretagnolle V (2010) Breeding biology of the Bridled Tern (*Sterna anaethetus*) in New Caledonia. *Waterbirds* 33(2):246-250. <https://doi.org/10.1675/063.033.0214>
- Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21:1-16
- Wakefield ED, Bodey TW, Bearhop S, Blackburn J, Colhoun K, Davies R, Dwyer RG, Green JA, Grémillet D, Jackson AL, Jessopp MJ, Kane A, Langston RHW, Lescroël A, Murray S, Le Nuz M, Patrick SC, Péron C, Soanes LM, Wanless S, Votier SC, Hamer KC (2013) Space partitioning without territoriality in Gannets. *Science* 341(6141):68–70. <https://doi.org/10.1126/science.1236077>



## *References*

- Wakefield ED, Phillips RA, Trathan PN, Arata J, Gales R, Huin N, Robertson G, Waugh SM, Weimerskirch H, Matthiopoulos J (2011) Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs* 81(1):141-167. <https://doi.org/10.1890/09-0763.1>
- Wallace GE, González H, McNicholl MK, Rodríguez D, Oviedo R, Llanes A, Sánchez B, Wallace EAH (1996) Winter surveys of forest-dwelling Neotropical migrant and resident birds in three regions of Cuba. *The Condor* 98(4):745-768.
- Wang Z, Wang J, Lin C, Han Y, Wang Z, Ji L (2021) Identifying habitat elements from bird images using deep convolutional neural networks. *Animals* 11(5):1263. <https://doi.org/10.3390/ani11051263>
- Washburn BE, Bernhardt GE, Kutschbach-Brohl L, Chipman RB, Francoeur LC (2013) Foraging ecology of four gull species at a coastal–urban interface. *The Condor* 115:67-76
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography* 54:211-223
- Weimerskirch H, Bertrand S, Silva J, Marques JC, Goya E (2010) Use of social information in seabirds: Compass rafts indicate the heading of food patches. *PLoS ONE* 5:e9928. <https://doi.org/10.1371/journal.pone.0009928>
- Wiley AE, Rossman S, Ostrom PH, France CAM, Penniman J, Bailey C, Duvall F, Zipkin EF, James HF (2019) From ecologically equivalent individuals to contrasting colonies: quantifying isotopic niche and individual foraging specialization in an endangered oceanic seabird. *Marine Biology* 166:39. <https://doi.org/10.1007/s00227-019-3483-7>
- Williams TD (1994) Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* 69(1):35-59. <https://doi.org/10.1111/j.1469-185X.1994.tb01485.x>
- Winkler DW, Billerman SM, Lovette IJ (2020) Gulls, Terns, and Skimmers (Laridae), version 1.0. In: Billerman SM, Keeney BK, Rodewal PG, Schulenberg TS (eds) *Birds of the World*. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.larida1.01>
- Yorio P (2009) Marine protected areas, spatial scales, and governance: implications for the conservation of breeding seabirds. *Conservation Letters* 2:171-178. <https://doi.org/10.1111/j.1755-263X.2009.00062.x>
- Yorio P, Frere E, Gandini P, Schiavini A (2001) Tourism and recreation at seabird breeding sites in Patagonia, Argentina: current concerns and future prospects. *Bird Conservation International* 11:231-245. <https://doi.org/10.1017/S0959270901000314>
- Zarn AM, Valle CA, Brasso R, Fetzner WD, Emslie SD (2020) Stable isotope and mercury analyses of the Galapagos Islands seabird community. *Marine Ornithology* 48:71-80

*References*

- Zavalaga CB, Halls J, Dell'Omo G (2010) Marine habitat use of Peruvian boobies: A geographic and oceanographic comparison between inshore and offshore islands. *ICES Journal of Marine Science* 67(5):940-951
- Zhang H, Vedder O, Becker PH, Bouwhuis S (2015) Age-dependent trait variation: The relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. *Journal of Animal Ecology* 84(3):797-807. <https://doi.org/10.1111/1365-2656.12321>

## Annexes

**Annex 1** List of the breeding and available sites of Laridae registered in Cuba. LAGU = Laughing Gull *Leucophaeus atricilla*, BRNO = Brown Noddy *Anous stolidus*, SOTE = Sooty Tern *Onychoprion fuscatus*, BRTE = Bridled Tern *Onychoprion anaethetus*, LETE = Least Tern *Sternula antillarum*, GBTE = Gull-Billed Tern *Gelochelidon nilotica*, ROST = Roseate Tern *Sterna dougallii*, ROYT = Royal Tern *Thalasseus maximus*, SATE = Sandwich Tern *Thalasseus sandvicensis*.

Site	Longitude	Latitude	Date of last register	Nesting species	Source
Rincón del Guanal point	-82.83345	21.45010	1980	LETE	2, 7
Borracho cay	-79.15140	22.65071	1989	LAGU, BRNO, SOTE	7
Caimán de Sotavento cay	-78.96420	22.69748	1989	LAGU, BRNO, BRTE, ROYT	7
Monos de Jutías cay	-79.85020	22.96936	1989	SOTE, BRTE, LETE	7
Dios cays	-81.17457	21.63407	1991	BRNO, SOTE, BRTE	7
La Vela cay	-79.75536	22.94368	1998	BRNO, BRTE, LETE, ROST, ROYT	7
Grande cay	-79.21170	20.99063	1998	LETE	12
Tortuga cay	-79.37771	21.28699	1998	LAGU, ROYT, SATE	12
Dune of Bergantines	-78.83738	20.93286	1998	LAGU	7
Hicacos point	-81.14283	23.20414	2000	LETE, ROST	7
Máximo river mouth	-77.46020	21.70534	2001	LAGU	7
Cinco Leguas cay	-80.84182	23.12689	2002	LAGU, ROYT	3
Galindo cay	-80.87131	23.25341	2002	LAGU, LETE, ROYT	3
Palma cay	-79.10301	22.38926	2002	ROYT	7
Jaula cay	-78.51431	22.56962	2002	LAGU, BRNO, SOTE, BRTE, ROYT	9
Cruz cay	-77.77895	22.19509	2002	LETE	3
Fogón cay	-77.73093	22.08174	2002	LAGU	9
South of Guajaba cay	-77.50694	21.80528	2002	LAGU, LETE	9
East of Sifonte cay	-77.41333	21.72945	2002	GBTE	3
Lengua de Pájaro, Sabinal cay	-77.38889	21.71979	2002	LAGU, LETE	1
Nuevitas bay	-77.26694	21.49167	2002	LETE	3
Tío Pepe cay	-79.15389	22.62917	2003	LETE	3
Juan García cay	-83.62580	21.97959	2003	LETE	7
Leonero lagoon	-77.04925	20.64129	2003	LAGU, LETE, ROYT	7
Mono Grande cay	-81.08951	23.26596	2004	BRNO, SOTE, BRTE, ROST	3
Jato inlet	-77.34083	21.64556	2004	GBTE	1, 7
Sijú cay	-83.51313	21.94642	2004	LETE	7
Las Salinas	-81.27723	22.11073	2004	LAGU, LETE	3
Dune Palo Quemado, Fragoso cay	-79.61961	22.80563	2005	LETE, ROYT	7
Fragoso cay	-79.47301	22.71754	2005	LETE, ROYT	7
Marcos cays	-79.65007	22.80607	2005	BRTE, SATE	7
Pajonal cays	-79.68842	22.85227	2006	ROST, SATE	7

Francés point	-83.19415	21.63073	2006	LETE, ROST	8
Español de Afuera cay	-79.13443	22.65377	2007	LAGU, SOTE, BRTE, ROYT, SATE	10
Mono cay	-79.68358	22.84578	2007	BRTE, ROST, SATE	7
Caimán de los Cayuelos cays	-78.90530	22.69279	2007	LAGU, BRNO	10
Caimán de Barlovento cay	-78.87128	22.68394	2007	LAGU, BRTE	10
Caimán cay at Northwest of Caimán de Bella	-78.84632	22.67453	2007	BRTE	10
Caimán de Bella cay	-78.84143	22.66959	2007	LETE	10
Dutton or Pajonal Anegado cay	-79.67746	22.89152	2008	BRTE, ROST, SATE	7
Yuraguanal cay	-77.77126	22.11570	2013	ROYT	4
Verde cay	-77.64759	22.11741	2013	LAGU, LETE	3, 4
Los Ballenatos cay	-81.63857	21.57841	2013	LAGU, BRTE, LETE, ROST, ROYT, SATE	3, 7
Loma del Puerto beach, Coco cay	-78.42420	22.55401	2014	LETE	5
Pescador cay	-83.74932	22.80580	2017	LETE	11
Inés de Soto cay	-83.77728	22.81612	2019	LETE	11
Felipe de Sotavento cay	-78.64486	22.62660	2021	LAGU, BRNO, SOTE, BRTE	5, 9
Felipe de Barlovento cay	-78.62352	22.61220	2021	LAGU, BRNO, SOTE, BRTE, ROST, ROYT, SATE	6, 9
Paredón de Lado cay	-78.21316	22.47886	2021	LAGU, BRNO, SOTE, BRTE, ROYT	5, 9
Available 1	-81.14300	23.20400	2020	-	Fieldwork
Available 2	-79.18600	22.59600	2020	-	Fieldwork
Available 3	-78.75800	22.38400	2020	-	Fieldwork
Available 4	-78.68900	22.62700	2020	-	Fieldwork
Available 5	-78.62500	22.61400	2020	-	Fieldwork
Available 6	-78.33100	22.52500	2020	-	Fieldwork
Available 7	-78.35700	22.52300	2020	-	Fieldwork
Available 8	-78.17000	22.48200	2020	-	Fieldwork
Available 9	-78.14800	22.48300	2020	-	Fieldwork
Available 10	-78.14600	22.44000	2020	-	Fieldwork
Available 11	-78.08900	22.42600	2020	-	Fieldwork
Available 12	-77.87100	22.21100	2020	-	Fieldwork
Available 13	-77.74400	22.12900	2020	-	Fieldwork
Available 14	-77.32700	21.73100	2020	-	Fieldwork
Available 15	-77.14000	21.661	2020	-	Fieldwork
Available 16	-76.31000	21.25100	2020	-	Fieldwork
Available 17	-77.02600	20.54400	2020	-	Fieldwork
Available 18	-75.86300	20.00000	2020	-	Fieldwork
Available 19	-78.43000	20.63600	2020	-	Fieldwork
Available 20	-78.55400	20.69400	2020	-	Fieldwork
Available 21	-78.71800	20.66600	2020	-	Fieldwork
Available 22	-78.75100	20.67800	2020	-	Fieldwork
Available 23	-78.94500	20.80700	2020	-	Fieldwork

Available 24	-78.88400	20.80400	2020	-	Fieldwork
Available 25	-78.75900	20.78800	2020	-	Fieldwork
Available 26	-78.96500	20.87000	2020	-	Fieldwork
Available 27	-78.93200	20.97900	2020	-	Fieldwork
Available 28	-78.95400	21.07500	2020	-	Fieldwork
Available 29	-78.80400	21.39400	2020	-	Fieldwork
Available 30	-78.73700	21.53700	2020	-	Fieldwork
Available 31	-78.88700	21.53400	2020	-	Fieldwork
Available 32	-78.66700	22.22600	2020	-	Fieldwork
Available 33	-78.32600	22.24400	2020	-	Fieldwork
Available 34	-79.35200	21.08100	2020	-	Fieldwork
Available 35	-79.45700	21.12800	2020	-	Fieldwork
Available 36	-79.19000	21.01400	2020	-	Fieldwork
Available 37	-79.97400	21.72800	2020	-	Fieldwork
Available 38	-80.42100	22.07700	2020	-	Fieldwork
Available 39	-79.14800	22.40000	2020	-	Fieldwork
Available 40	-77.28300	20.69400	2020	-	Fieldwork
Available 41	-78.58300	22.51800	2020	-	Fieldwork
Available 42	-77.91900	22.31300	2020	-	Fieldwork
Available 43	-77.84400	22.16100	2020	-	Fieldwork
Available 44	-77.21600	21.52100	2020	-	Fieldwork
Available 45	-78.96700	22.66500	2020	-	Fieldwork
Available 46	-78.54000	22.29400	2020	-	Fieldwork
Available 47	-77.90500	22.25400	2020	-	Fieldwork
Available 48	-77.43600	20.61500	2020	-	Fieldwork
Available 49	-79.04200	21.20100	2020	-	Fieldwork
Available 50	-79.19900	21.17900	2020	-	Fieldwork
Available 51	-83.65500	22.83600	2020	-	Fieldwork
Available 52	-83.70500	22.80700	2020	-	Fieldwork

<sup>1</sup>Barrio, O., Soriano, R. & Paneca, G. (2001). Colonias de nidificación de aves acuáticas en Cayo Sabinal. *Informe Proyecto Sabana-Camagüey CUB/98/G32*. Centro de Investigaciones de Medio Ambiente de Camagüey, 6 pp.

<sup>2</sup>Berovides, V., & Smith, R. (1983). Aspectos ecológicos de la nidificación de *Sterna hirundo* y *Sterna albifrons*. *Ciencias Biológicas*, 9, 128-131.

<sup>3</sup>Blanco, P. (2006). Distribución y áreas de importancia para las aves del orden Charadriiformes en Cuba. *Tesis de Doctorado*. Universidad de La Habana, Cuba. Pp: 87.

<sup>4</sup>Figueredo-Martín, T., Hernández-Fernández, L., García-Quintas, A. & Marichal, E. (2013). Solicitud de Licencia Ambiental a Sweet Spa: "Actividad de Pesca Recreativa en Cayo Cruz". *Informe de servicio científico-técnico*. Centro de Investigaciones de Ecosistemas Costeros, Cuba.

<sup>5</sup>García-Quintas, A. (pers.com.). Ornithologist, Centro de Investigaciones de Ecosistemas Costeros, Cuba.

<sup>6</sup>García-Quintas, A., González, L. & González, A. (2020). Novedades sobre la reproducción de dos especies de aves marinas poco comunes en Cuba. *Journal of Caribbean Ornithology*, 33, 54-57.

- <sup>7</sup> Jiménez, A., Rodríguez, P., & Blanco, P. (2009). Cuba. In P. Bradley & R. Norton (Eds.), *An inventory of breeding seabirds of the Caribbean* (pp. 47-57). University Press of Florida.
- <sup>8</sup> Rodríguez, A., Rodríguez, P. & Zayas, R. (2009). Nidificación de la Gaviotica (*Sternula antillarum*) y la Gaviota Común (*Sterna hirundo*) en el sur de la Isla de la Juventud, Cuba. *Journal of Caribbean Ornithology*, 22, 96-97.
- <sup>9</sup> Rodríguez, P., Rodríguez, D., Pérez, E., Llanes, A., Blanco, P., Barrio, O., Parada, A., Ruiz, E., Socarrás, E., Hernández, A., & Cejas, F. (2003). Distribución y composición de las colonias de nidificación de aves acuáticas en el Archipiélago de Sabana-Camagüey. *CD-ROM Memorias del VII Simposio de Botánica*. ISBN: 959-270-029-X3.
- <sup>10</sup> Ruiz, E., Arias, A., Más, L., Romero, M., García, J. M. & Arias, R. (2010). Breve caracterización de las colonias reproductivas de aves acuáticas (Charadriiformes) presentes en los cayos del noreste de Villa Clara, Cuba. *ECOVIDA*, 2(2), 57-68.
- <sup>11</sup> Ruiz, I. (pers.com.). Conservation specialist of the Los Colorados protected area, National Company for the Flora and Fauna Conservation, Cuba.
- <sup>12</sup> Socarrás, E., Parada, A., López, M., Gómez, R. & Aguilar, A. (2006). Biota terrestre del ecosistema Jardines de la Reina. In *Ecosistemas costeros: biodiversidad y gestión de recursos naturales*. Compilación por el XV Aniversario del CIEC. Sección II. Ecosistema Jardines de la Reina. CIEC. Editorial CUJAE. ISBN: 959-261-254-4.

**Annex 2** List of satellite images used to characterize the breeding habitat and predict its suitability for Laridae of Cuba. A = derived images since Landsat 5 -7 and Sentinel-2 satellites, B = derived images since MODIS-Aqua satellite that cover a general scene of Cuba.

A)

Satellite	Scene	Date acquired (yy-mm-dd)
Landsat 5	14/44	1989-09-19
Landsat 5	15/45	1991-04-09
Landsat 5	15/45	1991-09-16
Landsat 5	13/46	1998-05-16
Landsat 5	13/46	1998-06-01
Landsat 5	13/46	1998-07-19
Landsat 5	13/46	1998-08-20
Landsat 5	14/44	1998-05-07
Landsat 5	14/44	1998-06-08
Landsat 5	14/44	1998-07-10
Landsat 5	14/44	1998-08-27
Landsat 5	14/45	1998-05-07
Landsat 5	14/45	1998-06-08
Landsat 5	14/45	1998-07-10
Landsat 5	14/45	1998-08-11
Landsat 5	14/45	2000-05-03
Landsat 5	14/45	2000-06-20
Landsat 7	15/44	2000-07-30
Landsat 7	15/44	2000-08-15
Landsat 7	12/45	2001-05-25
Landsat 7	12/45	2001-06-10
Landsat 7	12/45	2001-07-12
Landsat 7	12/45	2001-08-29
Landsat 7	12/45	2002-04-26
Landsat 7	12/45	2002-06-29
Landsat 7	12/45	2002-07-15
Landsat 7	13/44	2002-04-17
Landsat 7	13/44	2002-07-22
Landsat 7	13/44	2002-08-23
Landsat 7	13/45	2002-04-17
Landsat 7	13/45	2002-06-04
Landsat 7	13/45	2002-08-23
Landsat 7	14/44	2002-05-10
Landsat 7	14/44	2002-06-27

Landsat 7	14/44	2002-07-29
Landsat 7	14/44	2002-08-30
Landsat 7	15/44	2002-05-17
Landsat 7	15/44	2002-07-04
Landsat 7	15/44	2002-08-05
Landsat 7	12/46	2003-05-15
Landsat 7	12/46	2003-08-03
Landsat 7	14/44	2003-05-13
Landsat 5	14/44	2003-07-08
Landsat 7	14/44	2003-08-17
Landsat 7	16/45	2003-04-25
Landsat 7	16/45	2003-08-15
Landsat 7	12/45	2004-05-17
Landsat 7	12/45	2004-06-18
Landsat 7	12/45	2004-07-20
Landsat 7	12/45	2004-08-21
Landsat 5	15/44	2004-05-30
Landsat 7	15/44	2004-06-07
Landsat 7	15/44	2004-08-10
Landsat 7	15/45	2004-05-22
Landsat 7	15/45	2004-06-07
Landsat 7	15/45	2004-08-10
Landsat 7	16/45	2004-05-13
Landsat 7	16/45	2004-08-17
Landsat 7	14/44	2005-05-02
Landsat 5	14/44	2005-08-14
Landsat 7	14/44	2006-05-05
Landsat 7	14/44	2006-06-22
Landsat 7	14/44	2006-07-08
Landsat 7	14/44	2006-08-25
Landsat 7	16/45	2006-05-19
Landsat 7	16/45	2006-06-04
Landsat 7	16/45	2006-07-22
Landsat 7	16/45	2006-08-23
Landsat 7	13/44	2007-05-01
Landsat 7	13/44	2007-06-18
Landsat 7	13/44	2007-09-06
Landsat 7	14/44	2007-05-08
Landsat 7	14/44	2007-06-09
Landsat 7	14/44	2007-09-13

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Landsat 7	14/44	2008-05-26
Landsat 7	14/44	2008-08-14
Landsat 7	13/45	2013-05-01
Landsat 7	13/45	2013-07-20
Landsat 7	13/45	2013-09-06
Landsat 7	15/45	2013-05-15
Landsat 7	15/45	2013-08-03
Landsat 7	13/44	2014-05-20
Landsat 7	13/44	2014-06-21
Landsat 7	13/44	2014-07-23
Landsat 7	13/44	2014-08-08
Landsat 7	10-46	2015-05-18
Landsat 7	10-46	2015-08-22
Landsat 7	11/46	2020-05-06
Landsat 7	11/46	2020-06-23
Landsat 7	11/46	2020-07-09
Landsat 7	11/46	2020-08-10
Landsat 7	12/45	2020-05-29
Landsat 7	12/45	2020-06-30
Landsat 7	12/45	2020-07-16
Landsat 7	12/45	2020-08-17
Landsat 7	12/46	2020-05-13
Landsat 7	12/46	2020-06-30
Landsat 7	12/46	2020-07-16
Landsat 7	12/46	2020-08-17
Landsat 7	13/44	2020-05-04
Landsat 7	13/44	2020-06-05
Landsat 7	13/44	2020-07-07
Landsat 7	13/44	2020-08-08
Landsat 7	13/45	2020-05-04
Landsat 7	13/45	2020-06-05
Landsat 7	13/45	2020-07-07
Landsat 7	13/45	2020-08-08
Landsat 7	13/46	2020-05-04
Landsat 7	13/46	2020-06-05
Landsat 7	13/46	2020-07-23
Landsat 7	13/46	2020-08-08
Landsat 7	14/44	2020-05-27
Landsat 7	14/44	2020-06-28
Landsat 7	14/44	2020-07-14

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Landsat 7	14/44	2020-08-31
Landsat 7	14/45	2020-05-27
Landsat 7	14/45	2020-06-28
Landsat 7	14/45	2020-07-14
Landsat 7	14/45	2020-08-31
Landsat 7	15/44	2020-05-02
Landsat 7	15/44	2020-08-22
Landsat 7	17/44	2020-05-16
Landsat 7	17/44	2020-06-01
Landsat 7	17/44	2020-07-03
Landsat 7	11-45	2021-07-12
Landsat 7	11-45	2021-08-29
Landsat 7	11-46	2021-06-04
Landsat 7	11-46	2021-07-06
Landsat 7	11-46	2021-08-29
Landsat 7	12-45	2021-05-16
Landsat 7	12-45	2021-07-03
Landsat 7	12-46	2021-07-03
Landsat 7	13-44	2021-05-07
Landsat 7	13-44	2021-06-08
Landsat 7	13-44	2021-07-26
Landsat 7	13-45	2021-05-07
Landsat 7	13-45	2021-06-24
Landsat 7	13-46	2021-05-23
Landsat 7	13-46	2021-06-24
Landsat 7	13-46	2021-07-10
Landsat 7	14-44	2021-05-30
Landsat 7	14-44	2021-07-17
Landsat 7	14-45	2021-05-14
Landsat 7	14-45	2021-07-17
Landsat 7	15-44	2021-07-08
Landsat 7	15-44	2021-08-25
Landsat 7	15-45	2021-07-24
Landsat 7	15-45	2021-08-25
Landsat 7	16-44	2021-07-31
Landsat 7	16-44	2021-09-01
Landsat 7	16-45	2021-05-28
Landsat 7	16-45	2021-09-01
Landsat 7	17-44	2021-08-07
Landsat 7	17-45	2021-08-23

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Sentinel-2 # 17QQF 2021-05-27  
Sentinel-2 # 17QQE 2021-06-01

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B)

Starting date (mm-dd)	Ending date (mm-dd)	Year
07-04	07-29	2002
08-07	08-31	2002
05-01	08-31	2003
05-01	08-31	2004
05-01	08-31	2005
05-01	08-31	2006
05-01	08-31	2007
05-01	08-31	2008
05-01	08-31	2009
05-01	08-31	2010
05-01	08-31	2011
05-01	08-31	2012
05-01	08-31	2013
05-01	08-31	2014
05-01	08-31	2015
05-01	08-31	2016
05-01	08-31	2017
05-01	08-31	2018
05-01	08-31	2019
05-01	08-31	2020
05-01	08-31	2021

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**Annex 3** Characteristics of two variants of a dataset (since six channels of Landsat images) and best architectures (dense layers, processing units and epochs) of convolutional neural networks models used to classify breeding localities of Laridae in Cuba. Performance indicators (accuracy and F1-score) are expressed in %. Channels used were red, green, blue, near infrared, shortwave infrared 1 and shortwave infrared 2.

Datasets	Images by habitat classes (breeding vs available)	Training sample size (70% of data)	Validation sample size (30% of data)	Dense layers	Units	Epochs	Validation accuracy (by image)	Validation F1-score (by image)	Validation accuracy (by locality)	Validation F1-score (by locality)
Images with any cloud cover	149 vs 208	254	103	5	156	25	75.7	76.2	86.7	85.7
Images with cloud cover < 30%	132 vs 176	216	92	5	512	25	72.8	73.7	86.7	84.6

**Annex 4** Overview of the most frequently used performance indicators (derived since confusion matrix) for classification purposes. TP = true positives, TN = true negatives, FP = false positives, FN = false negatives. Indicators values vary between 0 to 1 and can be expressed in %.

Indicators	Formula	Description
Overall Accuracy	$TP + TN / (TP + TN + FP + FN)$	Ratio of true predictions (positive and negative) and the total number of observations.
Precision	$TP / (TP + FP)$	Ratio of true presences classified correctly and the number of all positive predictions. Assesses how many of the predicted presences are actually true.
Recall	$TP / (TP + FN)$	Ratio of true presences classified correctly and the total number of instances belonging to the classes (true positive and false negative). Assess how many of the actual presences were classified as true.
F1-score	$2 \times (\text{precision} \times \text{recall}) / (\text{precision} + \text{recall})$	Harmonic mean of recall and precision. Constitute a balanced accuracy metric that is sensitive to both under- and overestimation.

**Annex 5** Maximum foraging ranges of nine Laridae species during the breeding season at different world localities and its estimated values for the Cuban archipelago.

Species	Foraging habitat <sup>a</sup>	Mean maximum foraging range (km)	Estimated maximum foraging range in Cuba (km)	Arguments for the estimations
Laughing gull <i>Leucophaeus atricilla</i>	Nearshore	45.0 <sup>14</sup> 30.0 <sup>16</sup> >40.0 <sup>20</sup>	45.0	This species has large reproductive colonies (up to 250 pairs) in Cuba despite the fact that the collected information corresponds to foraging in open oceans.
Brown noddy ( <i>Anous stolidus</i> )	Between Nearshore and Offshore	24.0 and 80.5 <sup>4</sup> ≈180.0 <sup>15</sup> 54.9 <sup>21</sup> 269.0 <sup>24</sup>	55.0	Selected value that correspond to the foraging localities at seas/gulfs (similar to the Cuban context); moreover two references belong to a geographic area near to Cuba (Caribbean Sea and the northeast of the Gulf of Mexico).
Sooty tern ( <i>Onychoprion fuscatus</i> )	Offshore	420.0-1130.0 and 50.0-130.0 <sup>4</sup> 450.0 <sup>8</sup> 480.0-600.0 <sup>15</sup> 895.0 <sup>23</sup> 128.0 <sup>24</sup>	100.0	Selected value that correspond to the foraging localities at seas/gulfs (similar to Cuban context); moreover two references belong to a geographic area near to Cuba (Caribbean Sea and the NE of the Gulf of Mexico).
Bridled tern ( <i>Onychoprion anaethetus</i> )	Nearshore and Offshore	28.0 <sup>5</sup> 2.5 <sup>6</sup> 30.0 <sup>9</sup> 80.0 <sup>18</sup>	30.0	Selected value that correspond to the foraging localities at seas/gulfs (similar to the Cuban context).
Least tern ( <i>Sternula antillarum</i> )	Nearshore	4.9 <sup>1</sup> <5.0 <sup>2</sup> 5.0 and 8.0 <sup>4</sup> 1.5 <sup>10</sup> 12.0 <sup>12</sup>	8.0	Selected value that correspond to the foraging localities at seas/gulfs (similar to the Cuban context); reference that shows the value = 12 km belongs to a scenery (salt flat in Oklahoma, USA) less frequent in Cuba.
Gull-billed tern ( <i>Gelochelidon nilotica</i> )	Nearshore	<5.0 <sup>2</sup> ≈45.0 <sup>3</sup> 45.0 <sup>4</sup>	45.0	Selected value that correspond to the foraging localities at seas/gulfs (similar to the Cuban context).
Roseate tern ( <i>Sterna dougallii</i> )	Nearshore	5.0 and 22.0 <sup>4</sup> 60.0 <sup>15</sup> 30.0 <sup>19</sup>	22.0	Selected value that correspond to the foraging localities at seas/gulfs (similar to the Cuban context).
Royal tern ( <i>Thalasseus maximus</i> )	Nearshore	65.0 <sup>4</sup> 50.0 <sup>11</sup> 55.0 <sup>13</sup> 30.0 <sup>16</sup>	55.0	Selected value because all compiled data correspond to the foraging localities in open oceans (tendency to major ranges); 158 km is an atypical value derived of 13

		158.0 <sup>24</sup> ≈42.0 <sup>25</sup>		sampled individuals in Senegal (median = 36); value=65 km was resulted of inaccurate methods; moreover, the colonies in Cuba are not large (<90 pairs).
Sandwich tern ( <i>Thalasseus sandvicensis</i> )	Nearshore	25.0 <sup>4</sup> 16.0 <sup>7</sup> 31.0 <sup>13</sup> 30.0 <sup>16</sup> 54.0 <sup>17</sup> 54.0 <sup>19</sup> 61.0 <sup>22</sup> ≈42.0 <sup>25</sup>	54.0	Selected value that correspond to the foraging localities at seas/gulfs (similar to the Cuban context); Thaxter <i>et al.</i> (2012) show summary values of world's compilations; 61 km is an exceptional value when the central tendency statistics are analyzed (in Fijn <i>et al.</i> , 2017).

<sup>1</sup>Tomkins, I. R. (1959). Life History Notes on the Least Tern. *The Wilson Bulletin*, 71(4), 313–322.

<sup>2</sup>Erwin, R. M. (1978). Coloniality in terns: The role of social feeding. *The Condor*, 80(2), 211. <https://doi.org/10.2307/1367920>

<sup>3</sup>Møller, A. P. (1982). Coloniality and colony structure in Gull-billed Terns *Gelochelidon nilotica*. *Journal für Ornithologie*, 123(1), 41-53.

<sup>4</sup>Clapp, R.B., D. Morgan-Jacobs, & Banks, R.C. (1983). Marine birds of the Southeastern United States. US Fish and Wildlife Service, FWS/OBS 83/30, Washington, DC.

<sup>5</sup>Hulsman, K. (1984). Survey of seabird colonies in the Capricornia Section of the Great Barrier Reef Marine Park 111. Population parameters and management strategies. *Research Report to Great Barrier Reef Marine Park Authority*.

<sup>6</sup>Hulsman, K., & Langham, N. P. E. (1985). Breeding biology of the Bridled Tern *Sterna anaethetus*. *Emu*, 85(4), 240-249.

<sup>7</sup>Fasola, M., & Bogliani, G. (1990). Foraging ranges of an assemblage of Mediterranean seabirds. *Colonial Waterbirds*, 13(1), 72–74.

<sup>8</sup>Flint, E. N. (1991). Time and energy limits to the foraging radius of Sooty Terns *Sterna fuscata*. *Ibis*, 133(1), 43–46. <https://doi.org/10.1111/j.1474-919X.1991.tb04808.x>

<sup>9</sup>Kohno, H., & Kishimoto, H. (1991). Prey of the Bridled Tern *Sterna anaethetus* on Nakanokamishima Island, South Ryukyus, Japan. *Japanese Journal of Ornithology*, 40(1), 15–25. <https://doi.org/10.3838/jjo.40.15>

<sup>10</sup>Wilson, E. C., Hubert, W. A., & Anderson, S. H. (1993). Nesting and foraging of Least Terns on Sand Pits in Central Nebraska. *The Southwestern Naturalist*, 38(1), 9. <https://doi.org/10.2307/3671637>

<sup>11</sup>Lee, D. S. (1995). Marine birds off the coast of North Carolina. *The Chat*, 59, 113-188.

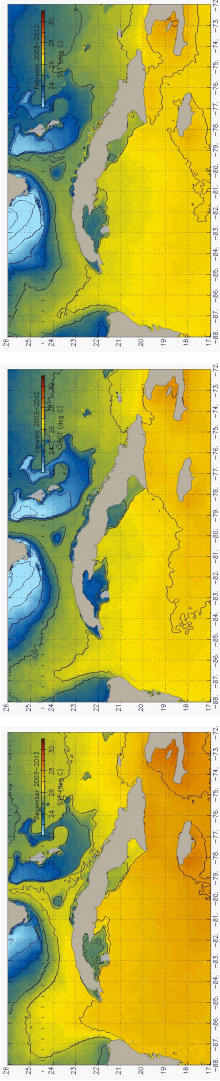
<sup>12</sup>Schweitzer, S. H., & Leslie, D. M. (1996). Foraging patterns of the Least Tern (*Sterna antillarum*) in North-Central Oklahoma. *The Southwestern Naturalist*, 41(3), 307–314.

- <sup>13</sup>McGinnis, T. W., & Emslie, S. D. (2001). The Foraging Ecology of Royal and Sandwich Terns in North Carolina, USA. *Waterbirds: The International Journal of Waterbird Biology*, 24(3), 361. <https://doi.org/10.2307/1522066>
- <sup>14</sup>Dosch, J. J. (2003). Movement Patterns of Adult Laughing Gulls *Larus atricilla* During the Nesting Season. *Acta Ornithologica*, 38(1), 15–25. <https://doi.org/10.3161/068.038.0106>
- <sup>15</sup>Surman, C. A., & Wooller, R. D. (2003). Comparative foraging ecology of five sympatric terns at a subtropical island in the eastern Indian Ocean. *J. Zool., Lond.*, 259, 219–230.
- <sup>16</sup>Wickliffe, L. C., & Jodice, P. G. R. (2010). *Seabird attendance at shrimp trawlers in nearshore waters of South Carolina*. 10.
- <sup>17</sup>Perrow, M. R., Skeate, E. R., & Gilroy, J. J. (2011). Visual tracking from a rigid-hulled inflatable boat to determine foraging movements of breeding terns: Visual Tracking of Terns. *Journal of Field Ornithology*, 82(1), 68–79. <https://doi.org/10.1111/j.1557-9263.2010.00309.x>
- <sup>18</sup>Dunlop, J. N., & Surman, C. A. (2012). The role of foraging ecology in the contrasting responses of two dark terns to a changing ocean climate. *Marine Ornithology*, 40, 105–110.
- <sup>19</sup>Thaxter, C. B., Lascelles, B., Sugar, K., Cook, A. S. C. P., Roos, S., Bolton, M., Langston, R. H. W., & Burton, N. H. K. (2012). Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation*, 156, 53–61. <https://doi.org/10.1016/j.biocon.2011.12.009>
- <sup>20</sup>Washburn, B. E., Bernhardt, G. E., Kutschbach-Brohl, L., Chipman, R. B., & Francoeur, L. C. (2013). Foraging ecology of four gull species at a coastal–urban interface. *The Condor*, 115(1), 67–76.
- <sup>21</sup>Maxwell, S. M., Connors, M. G., Sisson, N. B., & Dawson, T. M. (2016). Potential Benefits and Shortcomings of Marine Protected Areas for Small Seabirds Revealed Using Miniature Tags. *Frontiers in Marine Science*, 3. <https://doi.org/10.3389/fmars.2016.00264>
- <sup>22</sup>Fijn, R. C., de Jong, J., Courtens, W., Verstraete, H., Stienen, E. W. M., & Poot, M. J. M. (2017). GPS-tracking and colony observations reveal variation in offshore habitat use and foraging ecology of breeding Sandwich Terns. *Journal of Sea Research*, 127, 203–211. <https://doi.org/10.1016/j.seares.2016.11.005>
- <sup>23</sup>Neumann, J. L., Larose, C. S., Brodin, G., & Feare, C. J. (2018). Foraging ranges of incubating Sooty Terns *Onychoprion fuscatus* on Bird island, Seychelles, during a transition from food plenty to scarcity, as revealed by gps loggers. *Marine Ornithology*, 46, 11–18.
- <sup>24</sup>Oppel, S., Bolton, M., Carneiro, A. P. B., Dias, M. P., Green, J. A., Masello, J. F., Phillips, R. A., Owen, E., Quillfeldt, P., Beard, A., Bertrand, S., Blackburn, J., Boersma, P. D., Borges, A., Broderick, A. C., Catry, P., Cleasby, I., Clingham, E., Creuwels, J., ... Croxall, J. (2018). Spatial scales of marine conservation management for breeding seabirds. *Marine Policy*, 98, 37–46. <https://doi.org/10.1016/j.marpol.2018.08.024>
- <sup>25</sup>Gatto, A., Yorio, P., Doldan, M. S., & Gomila, L. V. (2019). Spatial and temporal foraging movement patterns in Royal Terns (*Thalasseus maximus*) and Cayenne Terns (*Thalasseus sandvicensis eurygnathus*) in Northern Patagonia, Argentina. *Waterbirds*, 42(2), 217. <https://doi.org/10.1675/063.042.0209>

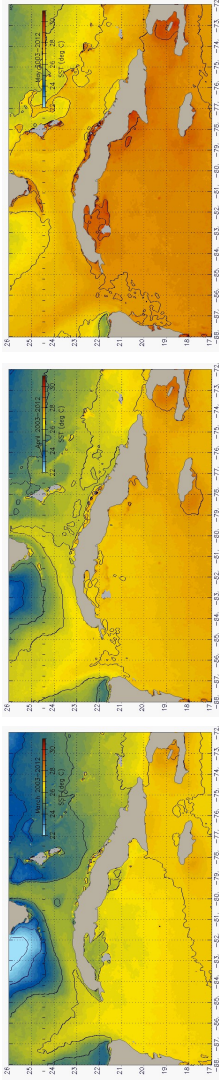


**Annex 6** Summaries of general interannually variability of Sea Surface Temperature (SST, first four pages) and Chlorophyll *a* (Chl *a*, last three pages) oceanographic variables in Cuba.

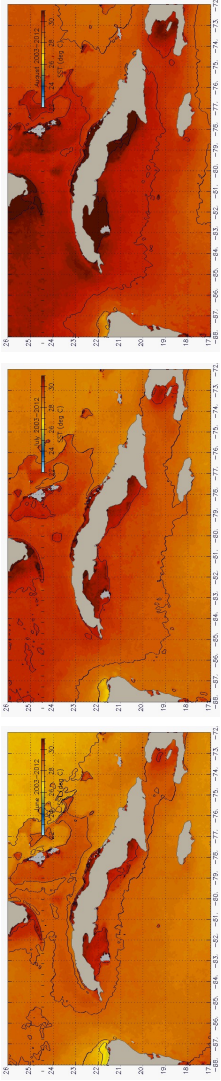
DJF



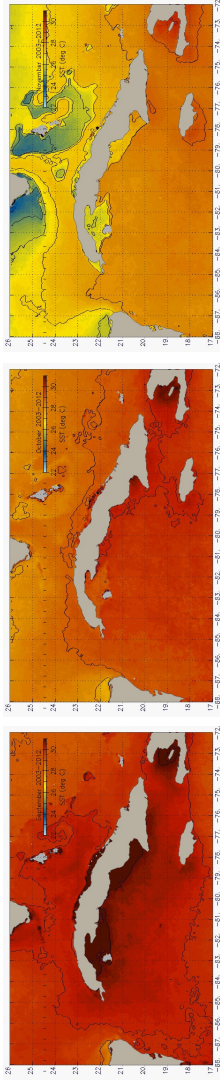
MAM



JJA

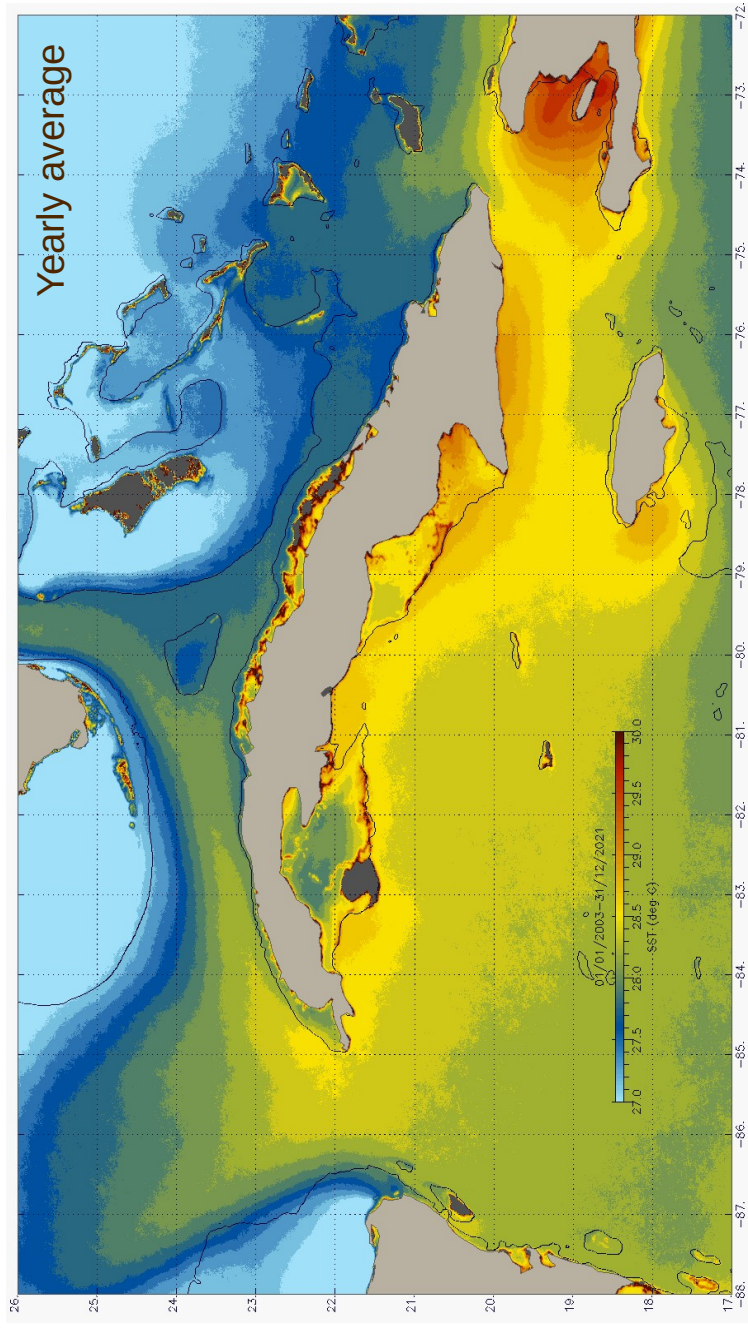


SON



## 1-km resolution data (area "cuba1")

Checking the variability (seasonal and interannual)  
cd /data/areas/cuba1/modis/R2019/sst2/1m\_ci/bil/  
avg\_l, cuba1\_modis\_sst2\_1km\_1m\_2003\* 2021\*-AQUA.R2019.0.qual1.avg.avg.gz', /std  
v, cuba1\_modis\_sst2\_1km\_19y\_20030101\_20211231.AQUA.R2019.0.qual1.avg.avg.gz', min=27, max=30, xcbo=0.15, ycbo=0.15, /fil, /mar, g\_s=1, bathy=200, /png  
v, cuba1\_modis\_sst2std\_1km\_19y\_20030101\_20211231.AQUA.R2019.0.qual1.avg.sst2.gz', min=0.5, max=3, xcbo=0.15, ycbo=0.15, /mar, g\_s=1, bathy=200, /fil, /png.gz', max=1



## 1-km resolution data (area "cuba1")

Checking the variability (seasonal and interannual)

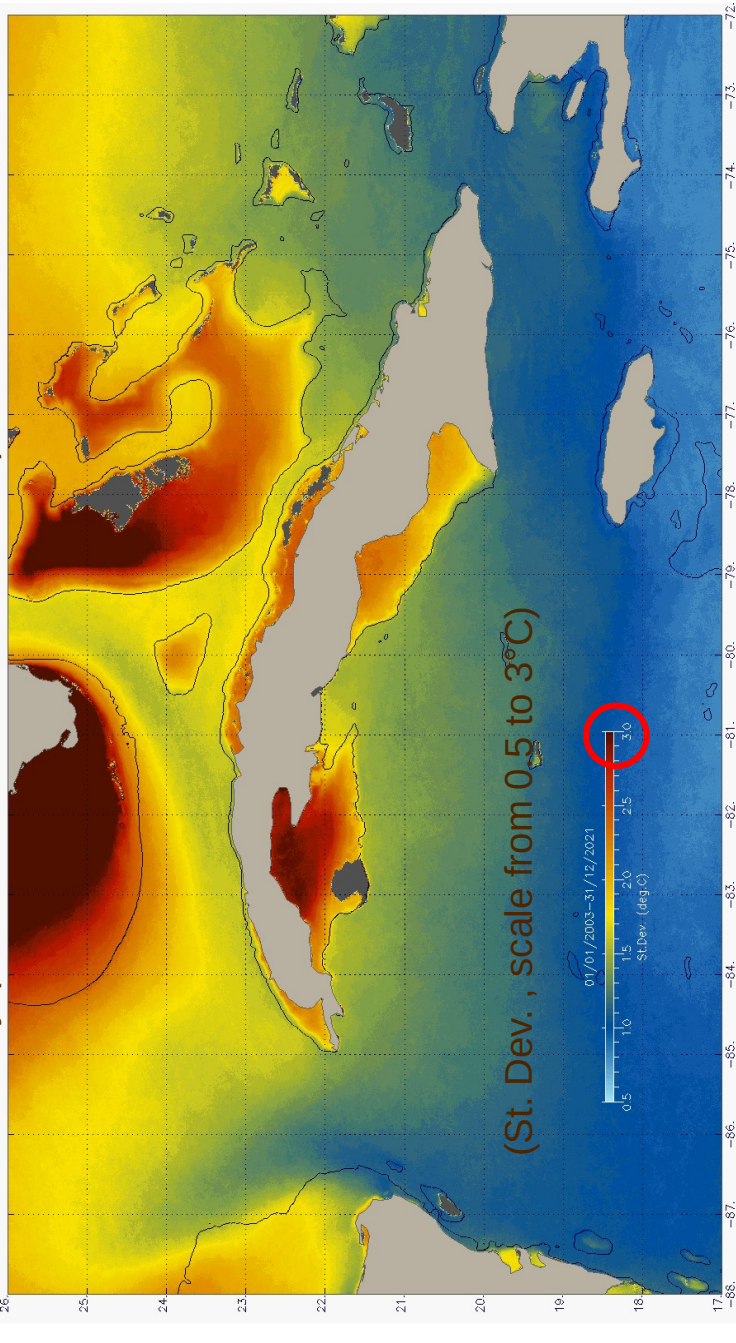
```
cd /data/areas/cuba1/modis/R2019/sst2/1m_c1/bil/
```

```
avg_l_cuba1_modis_sst2_1km_1m_2003* 2021*-AQUA.R2019.0.qual1.avg.gz', /std
```

```
v_cuba1_modis_sst2_1km_19y_20030101_20211231.AQUA.R2019.0.qual1.avg.gz', min=27, max=30, /fill, /mar, g_s=1, bathy=200, /png
```

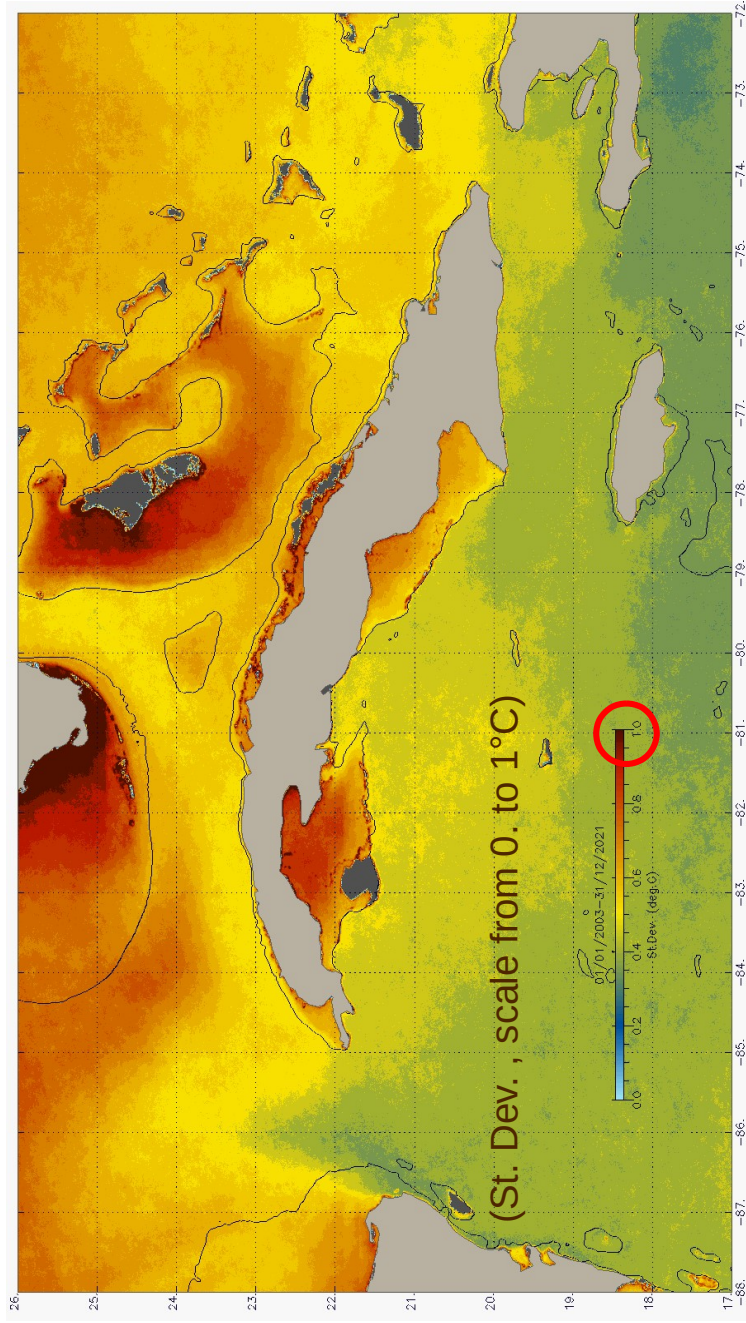
```
v_cuba1_modis_sst2std_1km_19y_20030101_20211231.AQUA.R2019.0.qual1.avg.sst2.gz', min=0.5, max=3, xcbo=0.15, ycbo=0.15, color=1, /mar, g_s=1, bathy=200, /fil, /png
```

## Seasonal variability (St. Dev. , scale from 0.5 to 3°C)

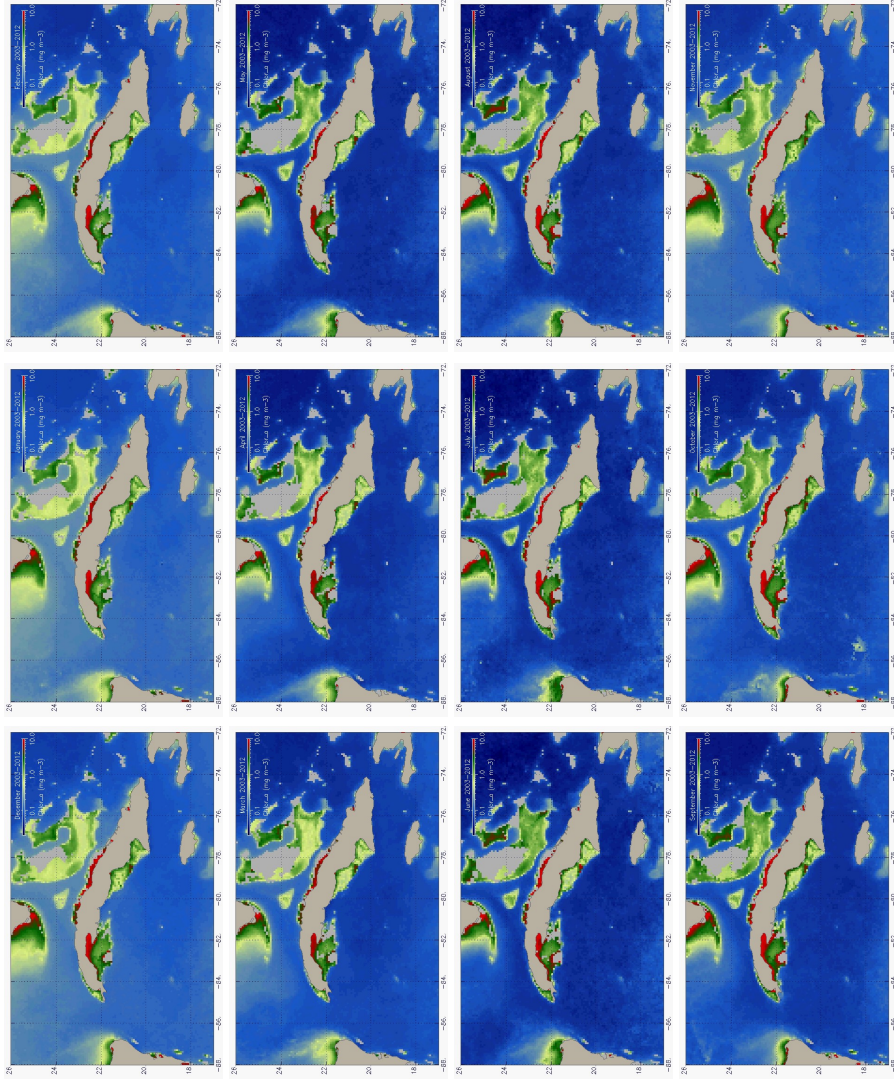


## Interannual variability (much lower (about 30%) than the seasonal var. )

(seasonally averaged) from 12 months of SSTstd  
/data/areas/cuba1/modis/R2019/sst2/1m/bil/  
avg\_cl\_month, cuba1\_modis\_sst2\_1km\_1m \* AQUA.R2019.0.qual1.avg.gz', /std, 2003, 2021  
avg\_l, cuba1\_modis\_sst2std\_1km\_1m\_2003\* 2021 \* AQUA.R2019.0.qual1.avg.sst2.gz'  
v, cuba1\_modis\_sst2std\_1km\_19y\_20030101\_20211231.AQUA.R2019.0.qual1.avg.sst2.avg.gz', min=0., max=1, xcbo=0.15, ycbo=0.15, color=0, /mar, g\_s=1, bathy=200, /fil, /png



DJF



MAM

JJA

SON

## 1-km resolution data (area "cuba1")

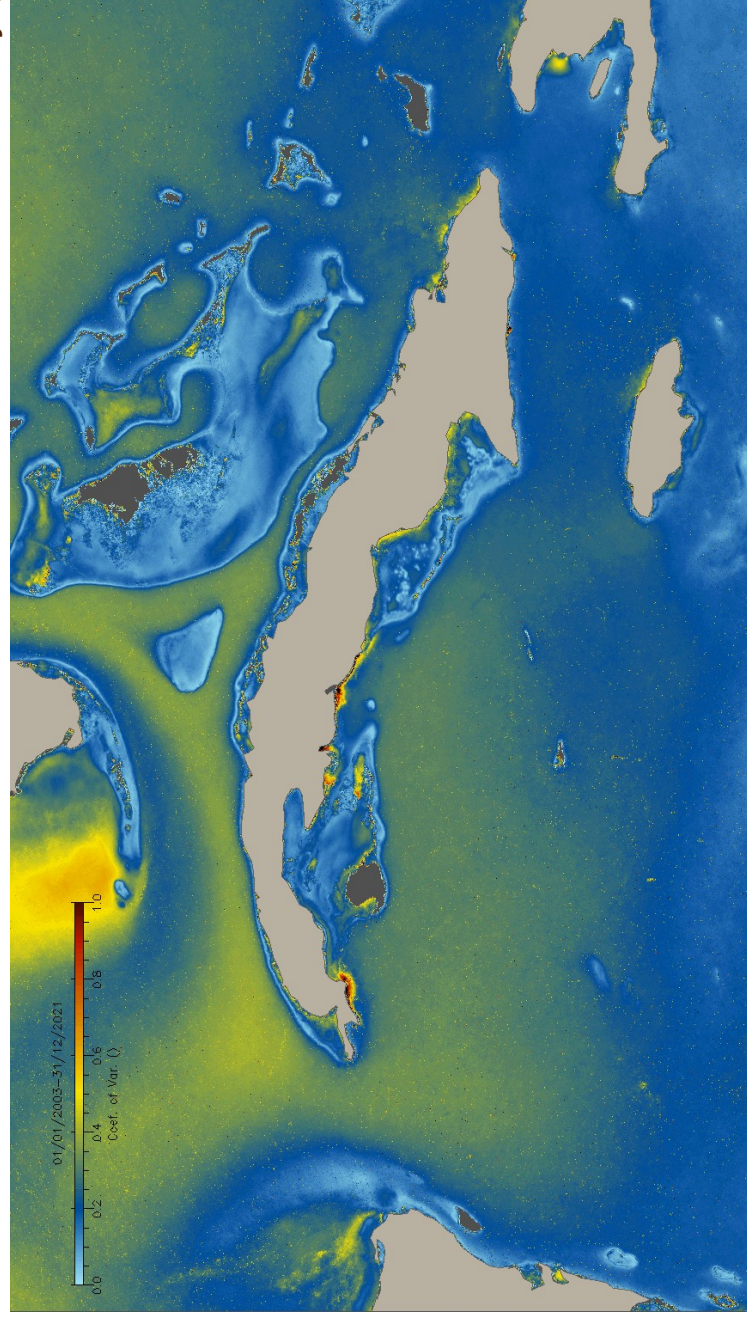
Checking the variability (seasonal and interannual)

```
v, 'cuba1_modis_cvar_1km_1m_2003*_2021*.AQUA.R2018.0.avg.chla.gz', /w, max=1, /pix, /png
```

```
avg_l, 'cuba1_modis_chla_1km_1m_20030101_20210131.AQUA.R2018.0.avg.avg.gz', /cv
```

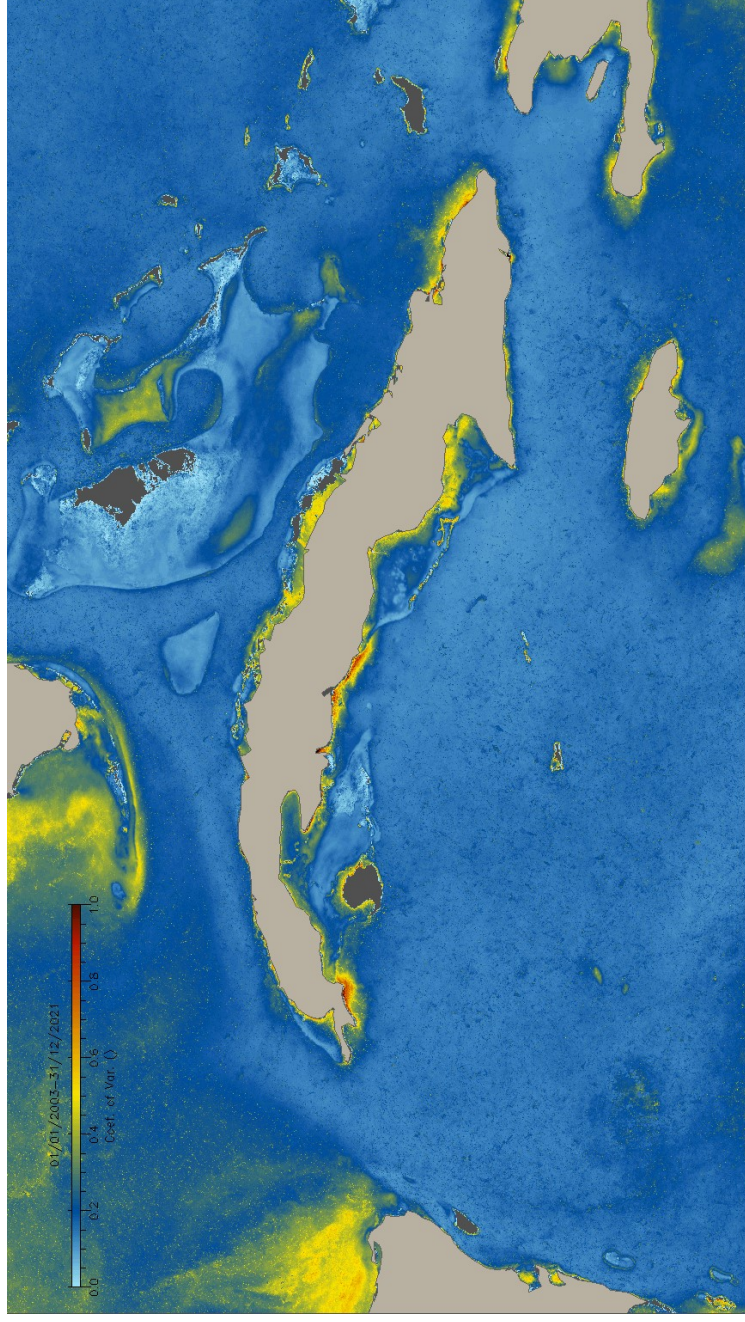
```
v, 'cuba1_modis_cvar_1km_19y_20030101_20211231.AQUA.R2018.0.avg.avg.chla.gz', max=1
```

Seasonal variability (very low)



## Interannual variability (slightly higher than the seasonal var. but rather low anyway...)

(seasonally averaged) from 12 months cvar cuba1\_modis\_cvar\_1km\_1m\_2003\*\_2021\*.AQUA.R2018.0.avg.chla.gz



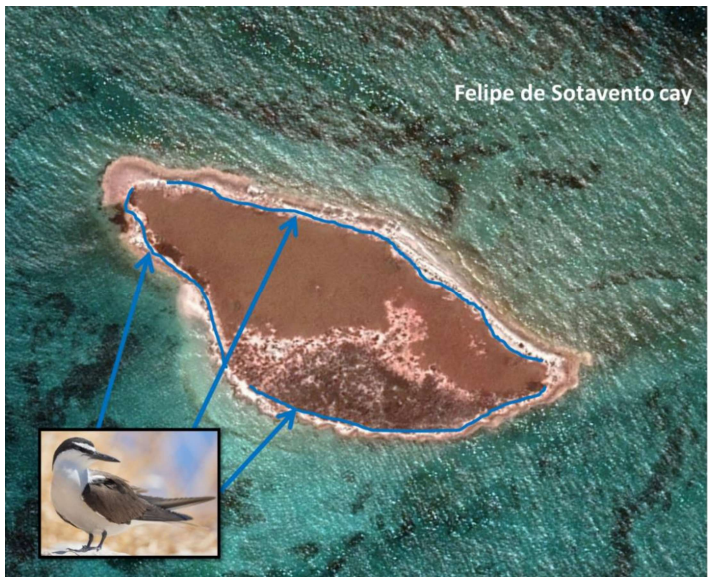
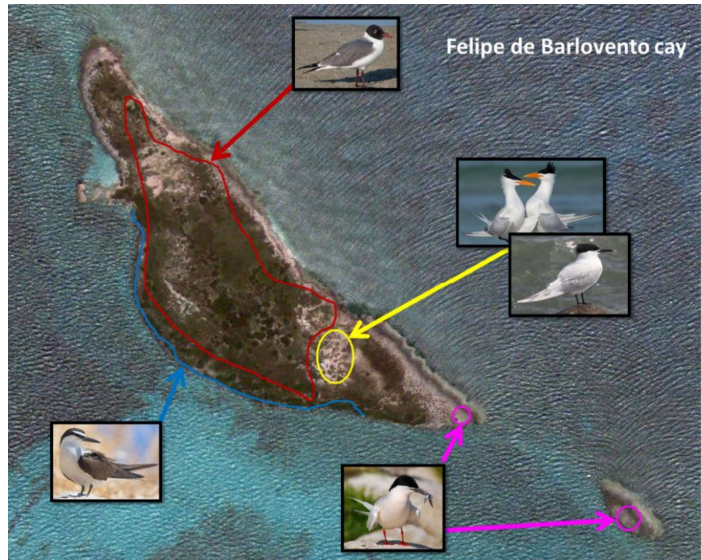


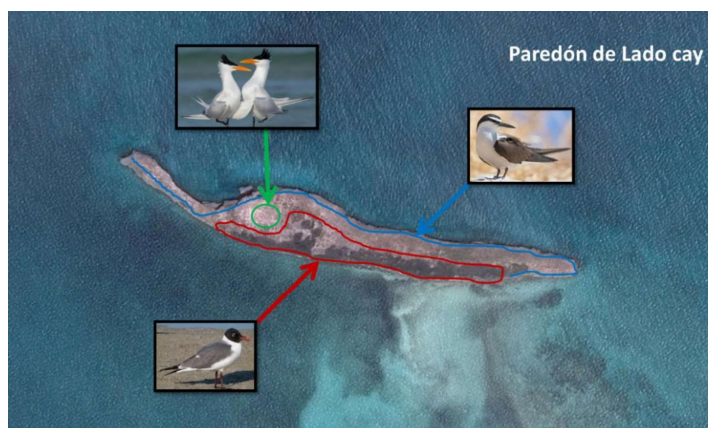
Annex 7





A. Position of the sampling points (in nesting and non-nesting sites) used to assess the breeding microhabitat selection of five Laridae species in three central-northern cays of Cuba during the 2021 breeding season. White = random points (non-nesting sites), red = Laughing Gull nesting sites, blue = Bridled Tern nesting sites, pink = Roseate Tern nesting sites, yellow = mixed Royal and Sandwich terns 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.





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

#### Annex 8

**A.** Characteristics of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopes (mean  $\pm$  SD) in two chicks' tissues of six Laridae species from central-north of Cuba during the 2021 breeding season.

Species	Breeding areas	n	Tissues	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N mass ratio
Laughing Gull ( <i>Leucophaeus atricilla</i> )	Felipes	21	Down	$-16.32 \pm 2.18$	$10.41 \pm 1.46$	$3.16 \pm 0.03$
	Paredón de Lado	15	Down	$-14.87 \pm 2.62$	$10.99 \pm 1.83$	$3.15 \pm 0.02$
	Felipes	16	Feather	$-15.94 \pm 1.77$	$10.32 \pm 1.06$	$3.12 \pm 0.04$
	Paredón de Lado	16	Feather	$-15.09 \pm 1.73$	$10.33 \pm 0.83$	$3.15 \pm 0.11$
Sooty Tern ( <i>Onychoprion fuscatus</i> )	Felipes	2	Down	$-16.38 \pm 0.23$	$9.14 \pm 0.25$	$3.18 \pm 0.01$
	Paredón de Lado	2	Down	$-15.70 \pm 0.97$	$9.14 \pm 0.35$	$3.19 \pm 0.01$
	Felipes	5	Feather	$-15.47 \pm 0.10$	$9.43 \pm 0.26$	$3.16 \pm 0.02$
	Paredón de Lado	1	Feather	-15.38	9.39	3.15
Bridled Tern ( <i>Onychoprion anaethetus</i> )	Felipes	15	Down	$-16.40 \pm 0.34$	$9.05 \pm 0.14$	$3.23 \pm 0.07$
	Paredón de Lado	15	Down	$-16.11 \pm 0.47$	$8.99 \pm 0.14$	$3.20 \pm 0.03$
	Felipes	11	Feather	$-15.75 \pm 0.28$	$9.33 \pm 0.40$	$3.14 \pm 0.06$
	Paredón de Lado	15	Feather	$-15.83 \pm 0.28$	$8.97 \pm 0.31$	$3.17 \pm 0.04$
Roseate Tern ( <i>Sterna dougallii</i> )	Felipes	15	Down	$-14.46 \pm 0.32$	$9.02 \pm 0.16$	$3.23 \pm 0.05$
	Felipes	15	Feather	$-14.44 \pm 0.37$	$8.92 \pm 0.16$	$3.22 \pm 0.06$
Royal Tern ( <i>Thalasseus maximus</i> )	Felipes	16	Down	$-11.60 \pm 1.26$	$11.68 \pm 1.66$	$3.16 \pm 0.02$
	Paredón de Lado	11	Down	$-11.02 \pm 0.95$	$11.28 \pm 1.50$	$3.16 \pm 0.03$
	Felipes	15	Feather	$-10.76 \pm 1.35$	$11.24 \pm 1.57$	$3.14 \pm 0.03$
Sandwich Tern ( <i>Thalasseus sandvicensis</i> )	Paredón de Lado	6	Feather	$-11.09 \pm 1.08$	$10.28 \pm 0.36$	$3.10 \pm 0.02$
	Felipes	15	Down	$-13.27 \pm 1.24$	$10.82 \pm 1.45$	$3.16 \pm 0.02$
	Felipes	17	Feather	$-13.30 \pm 0.76$	$9.93 \pm 0.65$	$3.11 \pm 0.09$

**B.** Intraspecific comparisons based on the Wilcoxon-Mann-Whitney tests of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values among chick tissues (down vs feather) of five Laridae species from central-north of Cuba during the 2021 breeding season. Significant differences are in bold.

Species / Breeding areas	Felipes		Paredón de Lado		General	
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Laughing Gull ( <i>Leucophaeus atricilla</i> )	W = 163.0 p = 0.89	W = 117.5 p = 0.13	W = 139.0 p = 0.47	W = 121.5 p = 0.97	W = 588.5 p = 0.88	W = 495.0 p = 0.32
Bridled Tern ( <i>Onychoprion anaethetus</i> )	W = 39.5 <b>p = 0.03</b>	W = 3.0 <b>p = 0.03</b>	W = 119.5 p = 0.79	W = 27.0 <b>p &lt; 0.01</b>	W = 320.5 p = 0.26	W = 53.5 <b>p &lt; 0.01</b>
Roseate Tern ( <i>Sterna dougallii</i> )	W = 159.0 p = 0.06	W = 104.0 p = 0.74	-	-	W = 159.0 p = 0.06	W = 104.0 p = 0.74
Royal Tern ( <i>Thalasseus maximus</i> )	W = 141.0 p = 0.42	W = 73.0 p = 0.07	W = 45.0 p = 0.25	W = 35.0 p = 0.88	W = 348.0 p = 0.18	W = 206.5 p = 0.11
Sandwich Tern ( <i>Thalasseus sandvicensis</i> )	W = 172.0 p = 0.10	W = 138.5 p = 0.69	-	-	W = 172.0 p = 0.10	W = 138.5 p = 0.69

**C.** Intraspecific comparisons based on the Wilcoxon-Mann-Whitney tests of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values among two breeding areas (Felipes vs Paredón de Lado) of three Laridae species from central-north of Cuba during the 2021 breeding season. Significant differences are in bold.

Species / Chick tissues	Down		Feather	
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Laughing Gull ( <i>Leucophaeus atricilla</i> )	W = 127.5 p = 0.34	W = 97.0 p = 0.05	W = 116.5 p = 0.68	W = 91.0 p = 0.17
Bridled Tern ( <i>Onychoprion anaethetus</i> )	W = 135.5 p = 0.35	W = 79.5 p = 0.18	W = 125.0 <b>p = 0.03</b>	W = 97.5 p = 0.45
Royal Tern ( <i>Thalasseus maximus</i> )	W = 103.0 p = 0.47	W = 66.5 p = 0.30	W = 62.5 p = 0.19	W = 53.0 p = 0.57

**D.** Interspecific paired comparisons based on the Pairwise Wilcoxon Rank Sum tests of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from chick down of five Laridae species from central-north of Cuba during the 2021 breeding season. Laughing Gull (*Leucophaeus atricilla*), Bridled Tern (*Onychoprion anaethetus*), Roseate Tern (*Sterna dougallii*), Royal Tern (*Thalasseus maximus*), Sandwich Tern (*Thalasseus sandvicensis*). Significant differences are in bold.

Breeding areas	Species	Laughing Gull	Bridled Tern	Roseate Tern	Royal Tern	Sandwich Tern
FELIPES	Laughing Gull	-	$\delta^{13}\text{C}$ : p = 0.21	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p = 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>
	Bridled Tern	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	-	$\delta^{13}\text{C}$ : <b>p = 0.02</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p = 0.02</b>
	Roseate Tern	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : p = 0.68	-	$\delta^{13}\text{C}$ : <b>p = 0.02</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>
	Royal Tern	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>
	Sandwich Tern	$\delta^{15}\text{N}$ : p = 0.24	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : p = 0.09	-
	Laughing Gull	-	$\delta^{13}\text{C}$ : p = 0.56	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	-
PAREDÓN DE LADO	Bridled Tern	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	-	-	$\delta^{13}\text{C}$ : <b>p = 0.04</b>	-
	Royal Tern	$\delta^{15}\text{N}$ : p = 0.35	$\delta^{15}\text{N}$ : <b>p = 0.02</b>	-	-	-
	Laughing Gull	-	$\delta^{13}\text{C}$ : p = 0.60	$\delta^{13}\text{C}$ : <b>p = 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>
GENERAL	Bridled Tern	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>
	Roseate Tern	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : p = 1.00	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>
	Royal Tern	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	-	$\delta^{13}\text{C}$ : p = 0.07
	Sandwich Tern	$\delta^{15}\text{N}$ : p = 0.44	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : p = 0.13	-
	Laughing Gull	-	$\delta^{13}\text{C}$ : p = 0.60	$\delta^{13}\text{C}$ : <b>p = 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>

E. Interspecific paired comparisons based on the Pairwise Wilcoxon Rank Sum tests of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from chick feathers of five Laridae species from central-north of Cuba during the 2021 breeding season. Laughing Gull (*Leucophaeus atricilla*), Bridled Tern (*Onychoprion anaethetus*), Roseate Tern (*Sterna dougallii*), Royal Tern (*Thalasseus maximus*), Sandwich Tern (*Thalasseus sandvicensis*). Significant differences are in bold.

Breeding areas	Species	Laughing Gull	Bridled Tern	Roseate Tern	Royal Tern	Sandwich Tern
FELIPES	Laughing Gull	-	$\delta^{13}\text{C}$ : <b>p = 0.02</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>
	Bridled Tern	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	-	$\delta^{13}\text{C}$ : <b>p = 0.03</b>	$\delta^{13}\text{C}$ : <b>p = 0.03</b>	$\delta^{13}\text{C}$ : <b>p = 0.02</b>
	Roseate Tern	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p = 0.02</b>
	Royal Tern	$\delta^{15}\text{N}$ : p = 0.08	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	-	$\delta^{13}\text{C}$ : <b>p = 0.04</b>
	Sandwich Tern	$\delta^{15}\text{N}$ : p = 0.51	$\delta^{15}\text{N}$ : <b>p = 0.01</b>	$\delta^{15}\text{N}$ : p = 0.06	$\delta^{15}\text{N}$ : <b>p = 0.02</b>	-
PAREDÓN DE LADO	Laughing Gull	-	$\delta^{13}\text{C}$ : p = 0.27	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	-
	Bridled Tern	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	-	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	-
	Royal Tern	$\delta^{15}\text{N}$ : p = 0.91	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	-	-	-
GENERAL	Laughing Gull	-	$\delta^{13}\text{C}$ : p = 0.36	$\delta^{13}\text{C}$ : <b>p = 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : p = 0.05
	Bridled Tern	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>
	Roseate Tern	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	$\delta^{15}\text{N}$ : p = 0.07	-	$\delta^{13}\text{C}$ : <b>p &lt; 0.01</b>	$\delta^{13}\text{C}$ : <b>p = 0.01</b>
	Royal Tern	$\delta^{15}\text{N}$ : p = 0.11	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	-	$\delta^{13}\text{C}$ : <b>p = 0.01</b>
	Sandwich Tern	$\delta^{15}\text{N}$ : p = 0.20	$\delta^{15}\text{N}$ : <b>p &lt; 0.01</b>	$\delta^{15}\text{N}$ : <b>p = 0.04</b>	$\delta^{15}\text{N}$ : <b>p = 0.04</b>	-

**F.** Percentage of  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  overlap of corrected Bayesian standard ellipses areas of chicks' down of five Laridae species from central-north of Cuba during the 2021 breeding season. Laughing Gull (*Leucophaeus atricilla*), Bridled Tern (*Onychoprion anaethetus*), Roseate Tern (*Sterna dougallii*), Royal Tern (*Thalasseus maximus*), Sandwich Tern (*Thalasseus sandvicensis*). Note that two overlap values per species comparison are given, e.g. Laughing Gull vs. Bridled Tern and vice versa.

	Laughing Gull	Bridled Tern	Felipes area		
			Roseate Tern	Royal Tern	Sandwich Tern
<b>Laughing Gull</b>	-	2.71	0.03	32.46	45.30
<b>Bridled Tern</b>	97.83	-	0.00	0.00	51.09
<b>Roseate Tern</b>	1.01	0.00	-	21.21	100
<b>Royal Tern</b>	23.83	0.00	0.46	-	50.48
<b>Sandwich Tern</b>	46.92	1.47	3.09	71.21	-
Paredón area					
<b>Laughing Gull</b>	-	3.98	-	30.72	-
<b>Bridled Tern</b>	96.30	-	-	0.00	-
<b>Roseate Tern</b>	-	-	-	-	-
<b>Royal Tern</b>	43.07	0.00	-	-	-
<b>Sandwich Tern</b>	-	-	-	-	-
General area					
<b>Laughing Gull</b>	-	3.43	0.28	34.45	50.23
<b>Bridled Tern</b>	94.53	-	2.34	0.00	59.38
<b>Roseate Tern</b>	10.10	3.03	-	1.01	100
<b>Royal Tern</b>	32.66	0.00	0.03	-	53.91
<b>Sandwich Tern</b>	55.26	2.37	3.09	62.57	-



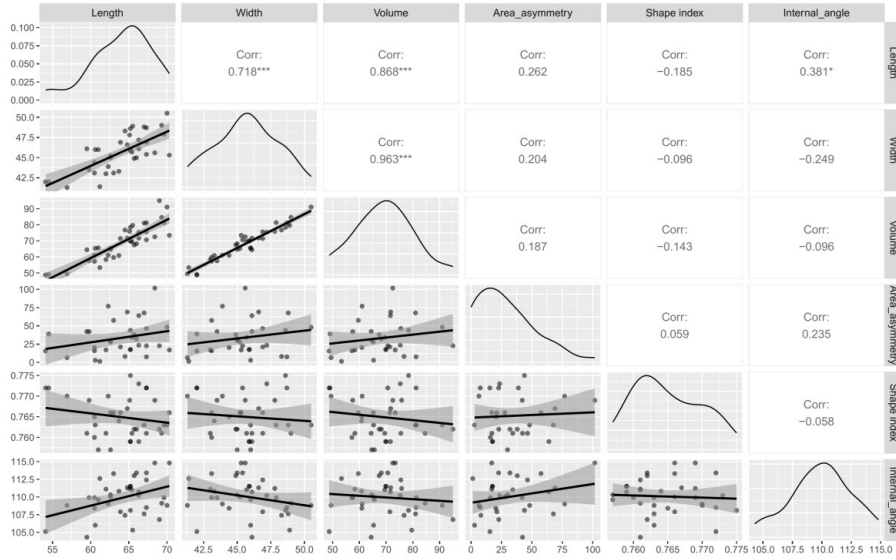
G. Percentage of  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  overlap of corrected Bayesian standard ellipses areas of chick feathers of five Laridae species from central-north of Cuba during the 2021 breeding season. Laughing Gull (*Leucophaeus atricilla*), Bridled Tern (*Onychoprion anaethetus*), Roseate Tern (*Sterna dougallii*), Royal Tern (*Thalasseus maximus*), Sandwich Tern (*Thalasseus sandvicensis*). Note that two overlap values per species comparison are given, e.g. Laughing Gull vs. Bridled Tern and vice versa.

	Laughing Gull	Bridled Tern	Felipes area		
			Roseate Tern	Royal Tern	Sandwich Tern
<b>Laughing Gull</b>	-	6.17	1.93	25.32	10.14
<b>Bridled Tern</b>	99.64	-	6.42	0.00	0.00
<b>Roseate Tern</b>	60.18	12.39	-	30.09	84.07
<b>Royal Tern</b>	19.77	0.00	0.75	-	8.03
<b>Sandwich Tern</b>	71.89	0.00	19.08	72.89	-
			Paredón area		
<b>Laughing Gull</b>	-	2.62	-	4.82	-
<b>Bridled Tern</b>	12.76	-	-	0.00	-
<b>Roseate Tern</b>	-	-	-	-	-
<b>Royal Tern</b>	4.96	0.00	-	-	-
<b>Sandwich Tern</b>	-	-	-	-	-
			General area		
<b>Laughing Gull</b>	-	8.05	1.42	25.05	10.78
<b>Bridled Tern</b>	88.84	-	7.44	0.00	0.41
<b>Roseate Tern</b>	33.63	15.93	-	21.24	84.07
<b>Royal Tern</b>	19.59	0.00	0.70	-	9.81
<b>Sandwich Tern</b>	57.83	0.20	19.08	67.27	-

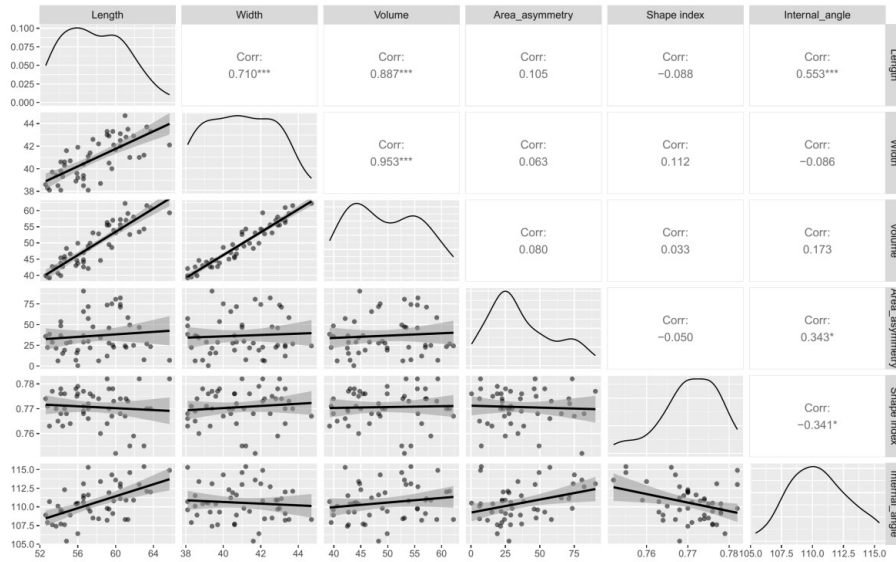
**Annex 9** Stable isotope values (mean  $\pm$  SD) in adults and chicks' tissues of Bridled Tern (*Onychoprion anaethetus*) from central-north of Cuba during the 2021 breeding season.

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

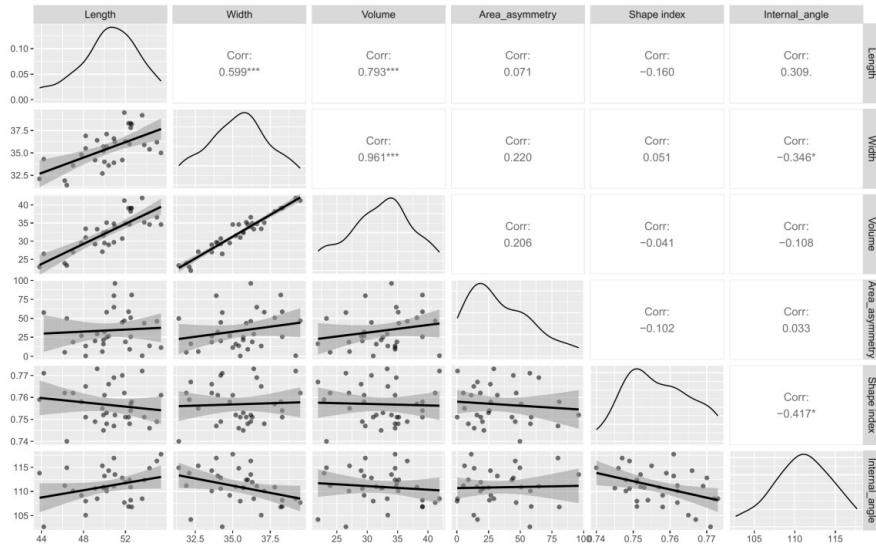
**Annex 10**  
**Laughing Gull (*Leucophaeus atricilla*)**



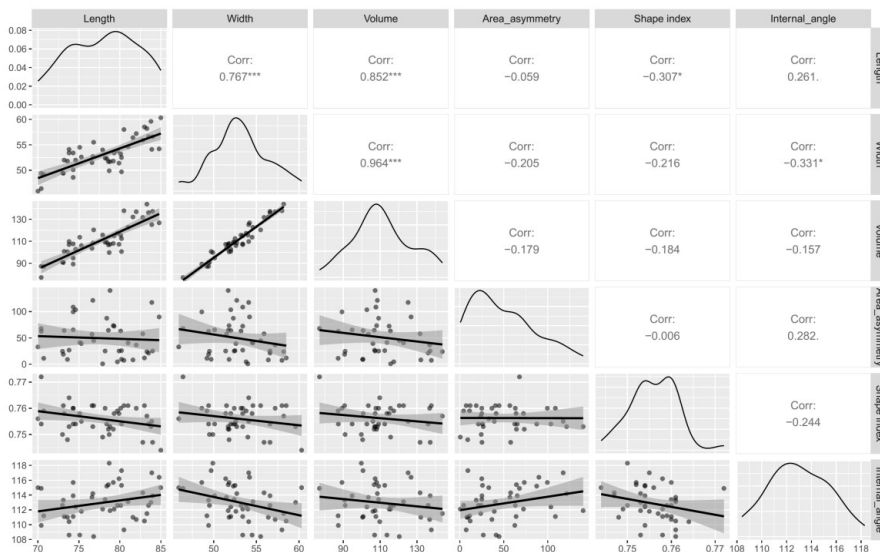
**Bridled Tern (*Onychoprion anaethetus*)**



### Roseate Tern (*Sterna dougallii*)



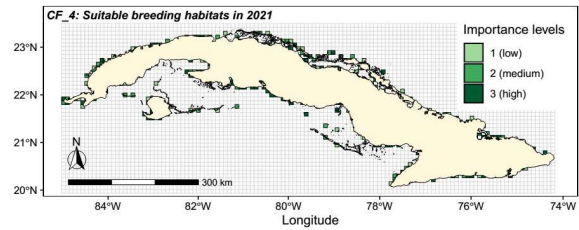
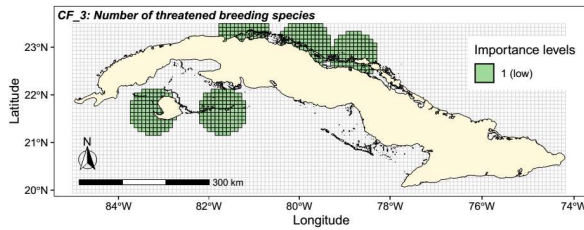
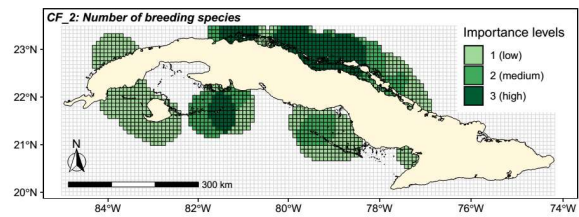
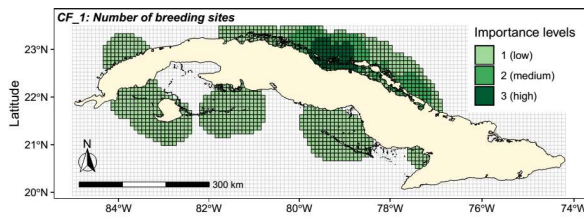
### Royal Tern (*Thalasseus maximus*)

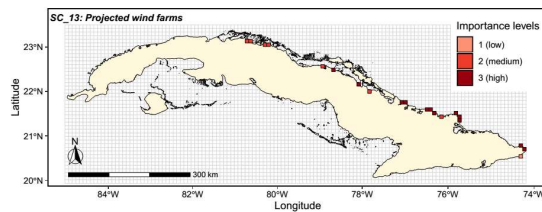
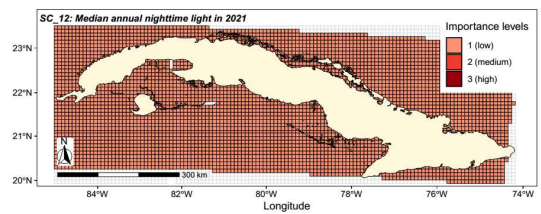
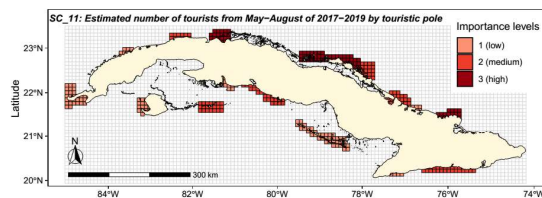
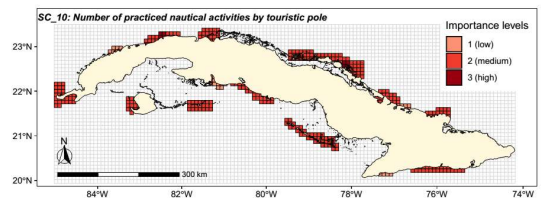
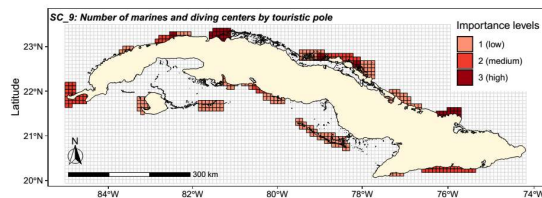
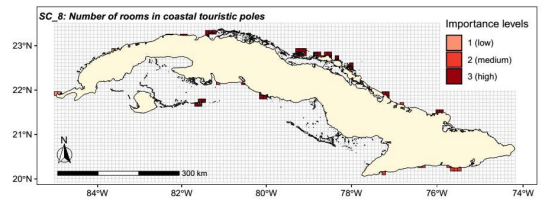
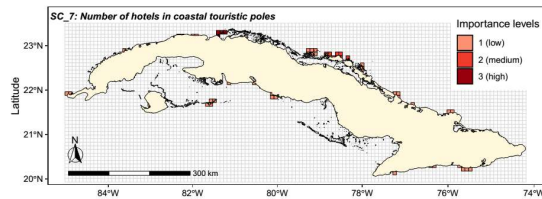
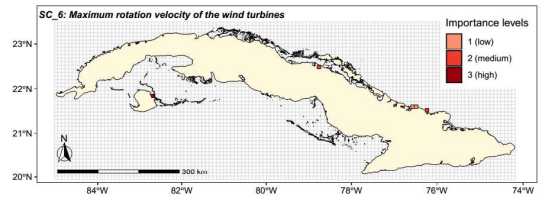
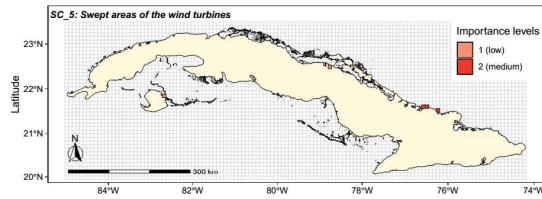
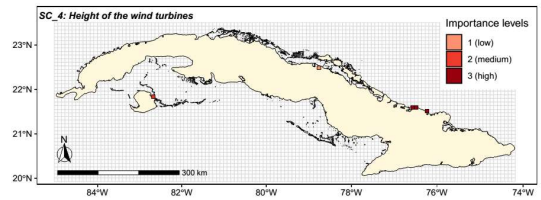
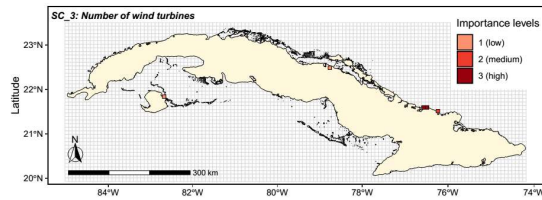
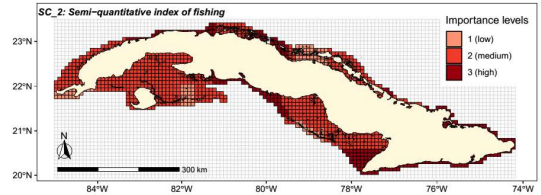
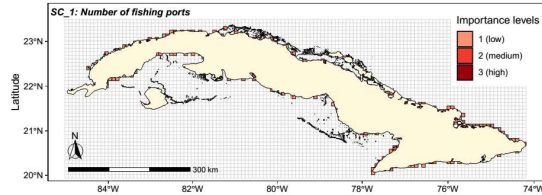


**Annex 10** Correlograms for six egg morphometric variables of four Laridae species during the 2021 breeding season at three northern-central cays of Cuba. Area\_asymmetry = Area of side asymmetry, Internal\_angle = Internal angle of a side. Significance is represented by asterisks: \* <0.05, \*\* <0.01, \*\*\* <0.001.

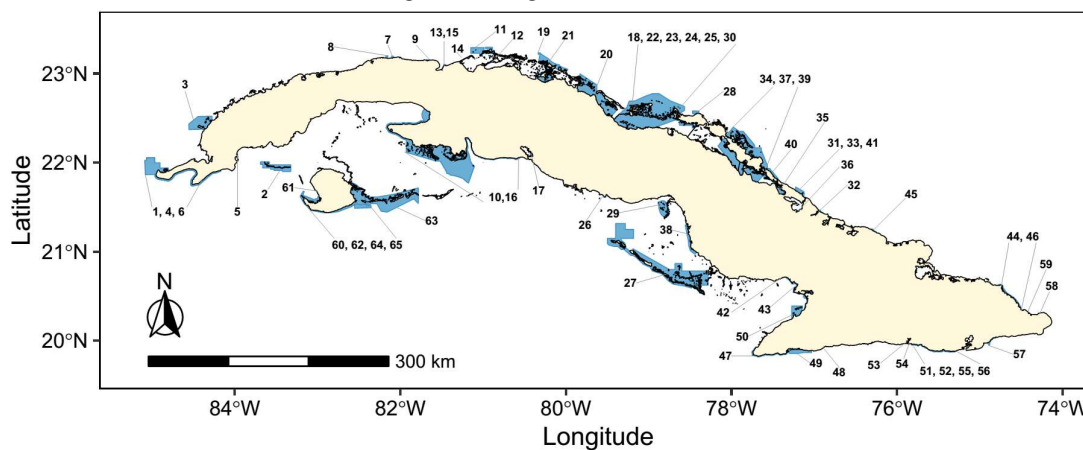
**Annex 11** Spatial ranking of the conservation features (CF) and socioeconomic costs (SC) in three importance levels related with the conservation of breeding larids in Cuba. Notice the complementarity among the table and maps.

ID	Unit	Range	Low	Medium	High
CF_1	-	1 - 16	1 - 5	6 - 10	$\geq 11$
CF_2	-	1 - 8	1 - 3	4 - 6	$\geq 7$
CF_3	-	0 - 1	1 - 2	3 - 4	$\geq 5$
CF_4	p-value	0.51 - 1.00	0.51 - 0.67	0.68 - 0.84	0.85 - 1.00
SC_1	-	1 - 8	1 - 3	4 - 6	$\geq 7$
SC_2	-	1 - 6	1 - 2	3 - 4	5 - 6
SC_3	-	1 - 34	1 - 10	11 - 20	$\geq 21$
SC_4	m	1 - 100	1 - 30	31 - 60	$\geq 61$
SC_5	m <sup>2</sup>	1 - 4 644.5	1 - 1 000.0	1 001 - 2 000	$\geq 2 001$
SC_6	rad/min	1 - 46	1 - 20	21 - 40	$\geq 41$
SC_7	-	1 - 62	1 - 20	21 - 40	$\geq 41$
SC_8	-	1 - 21 895	1 - 200	201 - 400	$\geq 401$
SC_9	-	1 - 7	1 - 2	3 - 4	$\geq 5$
SC_10	-	1 - 5	1 - 2	3 - 4	$\geq 5$
SC_11	-	1 - 720 730	1 - 9 999	10 000 - 99 999	$\geq 100 000$
SC_12	nW/cm <sup>2</sup> /sr	0.01 - 20.18	0.01 - 6.73	6.74 - 13.46	$\geq 13.47$
SC_13	MW	15 - 51	15 - 29	30 - 45	$\geq 46$





**Annex 12** Map and list of the approved Marine Protected Areas of Cuba. Mapped areas (blue) correspond to the marine-coastal surfaces of the Cuban Protected Areas. Some of them are nested inside others with less restrictive management categories.



ID	Management categories	Name of the Marine Protected Areas	Provinces	Marine-coastal surfaces (ha)	Nested area
1	National Park	Guanahacabibes	Pinar del Río	16685.83	yes
2	National Park	Cayos de San Felipe	Pinar del Río	23996.89	no
3	Ecological Reserve	Los Pretils	Pinar del Río	34016.63	no
4	Highlighted Natural Element	Banco San Antonio	Pinar del Río	7392.28	yes
5	Managed Floristic Reserve	San Ubaldo-Sabanalamar	Pinar del Río	88.10	no
6	Protected Area of Managed Resources	Península de Guanahacabibes	Pinar del Río	58705.99	no
7	Protected Natural Landscape	Rincón de Guanabo	La Habana	513.49	no
8	Protected Natural Landscape	Laguna del Cobre-Itabo	La Habana	573.76	no
9	Ecological Reserve	Bacunayagua	Mayabeque - Matanzas	428.73	no
10	National Park	Ciénaga de Zapata	Matanzas	133385.05	yes
11	Ecological Reserve	Cayo Mono-Galindo	Matanzas	15966.09	no
12	Fauna Refuge	Cayos de las Cinco Leguas	Matanzas	177.20	no
13	Fauna Refuge	Laguna de Maya	Matanzas	356.44	no
14	Protected Natural Landscape	Varahicacos	Matanzas	4.71	no
15	Protected Natural Landscape	Valle del Río Canimar	Matanzas	4.29	no

16	Protected Area of Managed Resources	Península de Zapata	Matanzas	207490.92	no
17	Fauna Refuge	Guanaroca-Punta Gavilán	Cienfuegos	1001.36	no
18	National Park	Los Caimanes	Villa Clara -Ciego de Ávila	28639.33	yes
19	Highlighted Natural Element	Ojo del Mégano	Villa Clara	445.97	no
20	Fauna Refuge	Lanzanillo-Pajonal-Fragoso	Villa Clara	72876.70	no
21	Fauna Refuge	Las Picúas-Cayo Cristo	Villa Clara	37400.45	no
22	Fauna Refuge	Cayo Santa María	Villa Clara	24062.39	yes
23	Fauna Refuge	Las Loras	Villa Clara	3544.72	yes
24	Protected Area of Managed Resources	Buenavista	Villa Clara – Sancti Spiritus – Ciego de Ávila	223411.85	no
25	National Park	Caguanes	Sancti Spiritus	11859.08	yes
26	Fauna Refuge	Tunas de Zaza	Sancti Spiritus	275.47	no
27	National Park	Jardines de la Reina	Ciego de Ávila - Camagüey	191357.67	no
28	Ecological Reserve	Centro y Oeste de Cayo Coco	Ciego de Ávila	12955.58	no
29	Fauna Refuge	Cayos de Ana María	Ciego de Ávila	17963.47	no
30	Highlighted Natural Element	Dunas de Playa Pilar	Ciego de Ávila	4.06	yes
31	Ecological Reserve	Maternillos-Tortuguilla	Camagüey	4855.95	yes
32	Ecological Reserve	Bahía de Nuevas Grandes-La Isleta	Camagüey – Las Tunas	1398.10	no
33	Managed Floristic Reserve	Laguna Larga	Camagüey	2.50	yes
34	Fauna Refuge	Correa	Camagüey	5234.72	yes
35	Fauna Refuge	Río Máximo	Camagüey	8925.75	no
36	Fauna Refuge	Cayos Los Ballenatos y manglares de la bahía de Nuevitas	Camagüey	347.81	no
37	Fauna Refuge	Cayo Cruz	Camagüey	4178.41	yes
38	Fauna Refuge	Macurije-Santa María	Camagüey	11235.12	no
39	Protected Area of Managed Resources	Humedales de Cayo Romano	Camagüey	140659.81	no
40	Protected Area of Managed Resources	Cayo Guajaba	Camagüey	7253.05	no
41	Protected Area of Managed Resources	Cayo Sabinal	Camagüey	5060.10	no
42	Fauna Refuge	Ojo de Agua	Las Tunas	6.73	no
43	Fauna Refuge	Delta del Cauto	Las Tunas - Granma	8512.35	no

44	National Park	Alejandro de Humboldt	Holguín - Guantánamo	2143.43	yes
45	Ecological Reserve	Caletones	Holguín	590.63	no
46	Protected Area of Managed Resources	Cuchillas del Toa	Holguín - Guantánamo	5187.05	no
47	National Park	Desembarco del Granma	Granma	6096.04	no
48	National Park	Turquino	Granma – Santiago de Cuba	8.82	no
49	Ecological Reserve	El Macío	Granma	12482.94	no
50	Fauna Refuge	Ensenada del Gua y Cayos de Manzanillo	Granma	14860.31	no
51	Natural Reserve	El Retiro	Santiago de Cuba	298.70	yes
52	Ecological Reserve	Siboney-Juticí	Santiago de Cuba	804.79	yes
53	Fauna Refuge	San Miguel de Parada	Santiago de Cuba	75.33	no
54	Protected Natural Landscape	Estrella-Aguadores	Santiago de Cuba	13.64	no
55	Protected Area of Managed Resources	Reserva de Biosfera Baconao	Santiago de Cuba - Guantánamo	5493.51	no
56	Ecological Reserve	Hatibonico	Guantánamo	618.57	yes
57	Ecological Reserve	Baitiquirí	Guantánamo	1452.11	no
58	Highlighted Natural Element	Cañón del Yumurí	Guantánamo	0.53	no
59	Highlighted Natural Element	Yara-Majayara	Guantánamo	8.18	no
60	National Park	Punta Francés	Isla de la Juventud	2973.08	yes
61	Ecological Reserve	Los Indios	Isla de la Juventud	50.45	no
62	Highlighted Natural Element	Punta del Este	Isla de la Juventud	25142.76	yes
63	Fauna Refuge	Cayo Campos-Cayo Rosario	Isla de la Juventud	87698.59	no
64	Fauna Refuge	Ciénaga de Lanier	Isla de la Juventud	6024.39	yes
65	Protected Area of Managed Resources	Sur de la Isla de la Juventud	Isla de la Juventud	60577.88	no