MULTI-SCALE HABITAT SELECTION OF ANTILLEAN MANATEES (*TRICHECHUS MANATUS MANATUS*) IN SIAN KA'AN BIOSPHERE RESERVE, SOUTHEASTERN MEXICO

ÉMILIE GAGNON

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Department of Biology
Faculty of Science
University of Ottawa

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Abstract

The distribution of organisms across the globe forms non-random patterns that are based on their selection for certain environmental features. Habitat selection is the study of how organisms choose where they live. It is a fundamental behavior shaping several ecological and evolutionary processes. The hierarchical nature of the environment makes it imperative to consider multiple scales in habitat selection studies. Even though there is extensive coverage of scaling in habitat selection literature, most published papers only consider one scale. To our knowledge, habitat selection studies of the Antillean manatee (*Trichechus manatus manatus*) have never included more than one spatial scale. Hence, we modeled Antillean manatee habitat selection in the Sian Ka'an Biosphere Reserve, in Mexico, at two spatial scales: study area and 1 km buffer. We used GPS coordinates of opportunistic encounters (n = 102) recorded since 2009. We randomly generated 500 pseudo-absences per presence point for both scales, and extracted the environmental conditions from each point: seagrass abundance (leaf area index or LAI), water depth, and shortest distance to land, closest river and closest resting hole. We fitted a binomial regression of the probability of presence as a function of the environmental parameters using a Bayesian approach. Our results show that the probability of manatee presence increases in proximity to resting holes for both scales and increases with land proximity at the large-scale. Overall, we showed that proximity to resting holes is the most important feature of habitat selection for Antillean manatees in Sian Ka'an, followed by proximity to land. This study demonstrates the importance of multi-scale designs in habitat selection and highlights the need for more studies looking at the use and ecological implications of manatee resting holes.

Résumé

La distribution des organismes à travers le globe forme des patrons non aléatoires qui sont basés leur sélection de certaines caractéristiques environnementales. La sélection d'habitat étudie le choix de l'habitat des organismes. C'est un comportement fondamental qui façonne plusieurs processus écologiques et évolutifs. La nature hiérarchique de l’environnement marque l’importance de considérer plusieurs échelles de mesure lors de l’étude de la sélection d’habitat. Alors que la littérature scientifique sur la sélection d’habitat à multi échelle est considérable, la majorité des publications se limite à une échelle. À notre connaissance, les études portant sur la sélection d’habitat du lamantin des Antilles (*Trichechus manatus manatus*) n’ont jamais considéré plus qu’une échelle de mesure spatiale. Ainsi, nous avons modélisé la sélection d’habitat du lamantin des Antilles dans la réserve naturelle de Sian Ka’an au Mexique à deux échelles spatiales : l'aire d’étude et un tampon de 1 km. Nous avons utilisé des coordonnées GPS de rencontres opportunistes (*n* = 102) enregistrées depuis 2009. Nous avons généré 500 pseudo-absences par point présence pour chaque échelle et nous avons extrait les conditions environnementales de chaque point : l’abondance d’algues marines, la profondeur d’eau et la distance la plus courte jusqu’à la côte, la rivière la plus près et la doline de repos la plus près pour chaque présence et pseudo-absence générée. Nous avons modélisé la probabilité de présence en fonction de ces effets fixes avec une régression binomiale en utilisant une approche Bayésienne. Nos résultats montrent que la probabilité de présence augmente près des dolines de repos aux deux échelles spatiales, ainsi que près de la côte dans le modèle à grande échelle. Globalement, nous avons démontré que la proximité d’une doline de repos est le facteur de sélection d’habitat prédominant pour les lamantins à Sian Ka’an, suivi de la proximité à la côte. Cette étude démontre l’importance d’une

méthodologie de la sélection d’habitat multi échelle et souligne le besoin d'études sur l’utilisation et l’impact écologique des dolines de repos sur les lamantins.

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Introduction

In theory, given an organism that has no physical constraint in space and no preference in habitat, its population should be uniformly distributed across the available environment. In nature, animals and plants are rarely scattered randomly or uniformly across the globe. It is thus assumed that they select environments based on habitat preferences in areas accessible to them. A selected habitat presumably has at least one abiotic or biotic factor that makes it more suitable than the other available ones. Hence, when a disproportionate use of a specific resource over others is observed, it indicates a preference that allows the fulfillment of fundamental needs. Inhabiting any space coincides with potential costs (predation, stress, failure to defend territory, etc.) and benefits (abundant food, ideal temperatures, protection, etc.), and these considerations are what guide organisms to choose certain areas that will ideally maximize fitness (Fretwell & Lucas, 1969).

Habitat selection describes the organisms' use of their environment, and it has gained lots of interest over the last half century (Hendel et al., 2023; MacArthur & Levins, 1964). This is partly due to recent advances in tracking animal movements (Kays et al., 2015) and statistical techniques (Guisan & Zimmermann, 2000), but mostly because of its versatility and practicality. Within one habitat selection study, it is possible to get insights on the importance of multiple behaviors, such as foraging or threat avoidance, in relation to environmental choices (Boyce & McDonald, 1999; Fretwell & Lucas, 1969). Habitat selection is also intimately linked to multiple other processes of ecology and evolution, such as species distribution and population dynamics (Matthiopoulos et al., 2015), ecological trap (Losier et al., 2015; Weldon & Haddad, 2005), genetic relatedness (Shafer et al., 2012), trophic cascade (Ford et al., 2014), and predator-prey system (Morris, 2003). Hence, exploring habitat selection can help to understand and connect various themes in biology. In terms of implementations, habitat selection can be used to model disease spread (Tardy et al., 2014), provide guidance for conservation management (Cañadas et al., 2005), monitor retention forestry program efficacy (Hendel et al., 2023) and make predictions on, for example, population abundance (Boyce et al., 2016) and the impact of climate and land use changes (Sohl, 2014).

At the individual level, habitat selection is a behavioral consequence for many organisms in response to a stimulus — i.e., perception of the environment and, unconsciously, its effect on fitness (Boyce & McDonald, 1999). Because habitat selection is intrinsically connected to movement and behaviors, it implies a dynamic process that relates to time and space. This hierarchical framework of time and space can be structured into varying scales (Levin, 1992; Wiens, 1989). For example, a coarse-grain scale could pertain to a season at the temporal level, and a continent at the spatial level, while a fine-grain scale could pertain to the time of day at the temporal level and a single food patch at the spatial level. Because the environment is perceived through scales by the animals, they will also make decisions according to those different scales (Dayton & Tegner, 1984; Johnson, 1980; Levin, 1992; Schneider, 2001; Wiens, 1989). For example, Martínez & Zuberogoitia (2010) studied the habitat selection of two owl species (*Asio otus* and *Athene noctua*) in eastern Spain, and found that, for both species, optimal foraging areas were selected at the large spatial scale, while ideal nesting and roosting sites were preferred at the fine spatial scale. It is common for researchers to only consider habitat selection at a large spatial scale (Heisler et al., 2017), in which case the importance of nesting and roosting site would have been overlooked in this study. Hence, because organisms select habitats at different scales, and in order to provide an accurate description of patterns happening in nature, it is crucial that researchers also study habitat selection at multiple scales, each relevant to the perception of the studied system (McGarigal et al., 2016; Paton & Matthiopoulos, 2016; Thompson & McGarigal, 2002).

In addition, scaling could enable researchers to place the drivers of selection in relative order of importance. In a large-scale, an individual will select a habitat based on the most important feature(s) affecting its survival, called limiting factor(s) (Dussault et al., 2005; Johnson, 1980). At a smaller scale, other less important habitat characteristics are considered for making decisions (Johnson, 1980). Revisiting the prior example of Martínez & Zuberogoitia (2010), the two studied species of owls (*Asio otus* and *Athene noctua*) selected for ideal foraging areas at the large spatial scale and prime roosting sites at the small spatial scale, in which case, food needs are a more immediate priority for the owls than nesting location. If a variable is found to be significantly different from zero in more than one scale, it indicates a higher order of importance than if it was found in one scale only (Rettie & Messier, 2000). This is because the animal considers the variable to be worth selecting for at both large- and small-scale. Since scale is important to consider in ecology, there has been a great interest in multi-scale designs in the past few decades (Schneider, 2001). However according to McGarigal et al. (2016), only about 20% of habitat selection papers published between 2009 and 2014 handled more than one spatial or temporal scale.

Here, we model the habitat selection of the West Indian manatee (*Trichechus manatus*) at two spatial scales, which to our knowledge has never been done before. This species is a slow-moving marine mammal and is subdivided into two subspecies living in different habitats: the Florida manatee (*Trichechus manatus latirostris*) and the Antillean manatee (*Trichechus manatus manatus*). Although both subspecies are in danger of extinction (Self-Sullivan & Mignucci-Giannoni, 2008), the Antillean subspecies is understudied compared to the Florida subspecies. One important knowledge gap of Antillean manatee that must be investigated is its spatial ecology

(Castelblanco-Martínez et al., 2013). Such studies are needed especially in regions incorporating manatee resting holes, as they are thought to represent crucial microhabitats for manatees, and very few studies have investigated their importance (Bacchus et al., 2009; Lacommare et al., 2008). One also cannot protect a species without knowing what the used resources and habitat requirements are (Levin, 1992). We strongly believe that modeling habitat selection of Antillean manatees at multiple spatial scales will enhance our knowledge of the subspecies. This valuable information could then be used to implement appropriate conservation measures with the goal of protecting the current population and providing a safe haven for future generations.

The Antillean manatee lives in the waters of eastern Mexico, Central America, Greater Antilles, and northern and northeastern South America (Lefebvre et al., 2001). Manatees are one of the few marine mammal species that have an herbivorous diet, feeding almost exclusively on seagrass (Allen et al., 2018; Castelblanco-Martínez et al., 2009; Rodrigues et al., 2021). This forces them to rely on sources of fresh water, rather than on their diet, for osmoregulation purposes (Ortiz et al., 1998, 1999). Proximity to fresh water is now a well-known and ubiquitous pattern of manatees' spatial ecology (Auil, 2004; Castelblanco-Martínez et al., 2013; Favero et al., 2020; Haase et al., 2017; Hartman, 1979; L. Lefebvre et al., 2001; Marsh et al., 2011; Olivera-Gómez & Mellink, 2005; Powell et al., 1981; Powell & Rathbun, 1984). Water depth is also an environmental variable strongly associated with manatee presence, with their optimal water depth between 1 and 3 meters (Castelblanco-Martínez et al., 2013; Hartman, 1979; Landero et al., 2014; Lefebvre et al., 2001). It is also more likely to observe manatees closer to land (Castelblanco-Martínez et al., 2013; Landero et al., 2014; Morales-Vela, 2000; Ross, 2007) and in areas of higher seagrass abundance (Lacommare et al., 2008; Lefebvre et al., 2000; Ross, 2007).

The objective of this study was to model habitat selection of Antillean manatees in the Sian Ka'an Biosphere Reserve, Mexico, at a small and large spatial scale. In manatee habitat selection literature, every study uses the entire study area, representing a relatively large spatial scale. Here, we further investigate small scale habitat selection patterns, which has never been done before with manatees. We expected to find different explanatory variables for manatee distribution at the two different scales: whole study area (large-scale) and 1 km buffer (small-scale). Because proximity to fresh water and shallow waters are well documented manatee preferences (Lefebvre et al., 2001), we believed that they would represent the limiting factors of the population distribution. Hence, we predicted that the probability of manatee presence would be greater near resting holes and rivers — potential sources of fresh water —, and in shallower waters at the large-scale. Because the associations between manatee presence and proximity to seagrass and land are not ubiquitous patterns (Lefebvre et al., 2001), we believed that they would represent secondary priorities associated with habitat selection. Furthermore, given that manatees cannot accomplish osmoregulation without fresh water in their diet (Ortiz et al., 1998, 1999), we believed that closeness to fresh water would be that most important factor of selection, therefore linked to selection at both scales. We thus expected that the probability of manatee presence would be higher closer to land, resting holes and rivers, and in areas with abundant seagrass at the small-scale.

Methods

Study Site

The Sian Ka'an Biosphere Reserve is located within the Quintana Roo state of Mexico. The total surface area of the reserve is approximately 4000 km^2, with 1200 km^2 being water (UNESCO, 2023). Sian Ka'an is composed of Ascension Bay, Espiritu Santo Bay, and many lagoons bordering the land (see Figure 1A). Sian Ka'an has a shallow seafloor punctuated with small depressions, which have been termed as resting holes by manatee researchers (Lacommare et al., 2008). Within the study area, some of these resting holes are also sources of fresh water (i.e., artesian springs; Medina-Gómez et al., 2016). In Ascension Bay, there are 4 different species of seagrass (flowering plants growing completely underwater): *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme* and *Ruppia maritima*, in order of abundance (Arellano-Méndez, 2011). *Thalassia testudinum* has been reported to be the preferred species of seagrass to manatees (Castelblanco-Martínez et al., 2009; Landero et al., 2014), while manatees can have a flexible diet (Lefebvre et al., 2001). Ascension Bay has the second highest abundant manatee population in the Mexican Caribbean, with the highest proportion of breeding females (Landero et al., 2014). A single aerial survey of the Ascension Bay revealed a total of 25 individuals (Landero., 2010).

Data Collection

The GPS coordinates of manatee observations were recorded sporadically from 2009 to 2022 (*n* = 102, see Figure 1B). Sightings were either made from a boat or a drone (DJI Phantom 3 Pro, DJI Phantom 4 Pro and DJI Mavic Pro 2). The drone GPS-logged track was overlayed with an orthomosaic map of the region (created with the drone captured images) in QGIS (QGIS

Developmental Team, 2023). The position of the manatee at first detection was located on the drone track, and the GPS coordinates were extracted. For the boat encounters, the boat GPS was used to extract the GPS coordinates.

The water depth at the position of each observation was extracted from a bathymetric map made by the company TCarta (see Figure 1C). The map had a resolution of 10 meters and a calculated uncertainty of 10% (TCarta 2023). In brief, the water depth information was derived from satellite images and processed through a physics-based radiative transfer algorithm. For each pixel, the water depth value was calculated based on water reflectance, while taking into account the properties of the water column and atmospheric corrections (TCarta, 2023).

The leaf area index (LAI) is the area occupied by vegetation matter per unit of ground surface from a top view. It provides an estimate of the vegetation density, and was used as a proxy for seagrass abundance in the water. We used LAI maps of Sian Ka'an from 2017 to 2021 (resolution: 10m, see Figure 2) provided by Hedley et al. (2021). Their workflow was based on previous work (Hedley et al., 2016), where they developed a method based on the physical properties of water to estimate LAI values from satellite image water reflectance indices. Hedley et al. (2021) evaluated the year-to-year changes in LAI values in Sian Ka'an. They concluded that seagrass abundance remained the same over the years, with the exception of 2018 and 2019. Those years were characterized by lots of *Sargassum* tides, a floating brown macroalgae, which led to inaccurate seagrass abundance indices. To standardize the index, we calculated LAI as the average across the years unaffected by the *Sargassum* tides (i.e., 2017, 2020 and 2021). The map coverage excluded areas of very shallow and turbid waters (see Figure 2), and this limitation resulted in only 38 of the original 102 manatee observations having LAI information available. We thus ran models with and without the LAI variable to maximize the usable sample size and power of the models.

Resting holes and rivers were located by visual inspection of Sentinel-2 satellite imagery (resolution: 10 m; SUHET, 2015) and Google Earth images (resolution up to 30 cm; Google Earth, 2023). The resting holes, being depressions on the seafloor, look like small dark spots in the water when viewed with satellite imagery. Both Google Earth and Sentinel-2 satellite images were used to identify the resting holes. The Google Earth images were also used to locate the rivers.

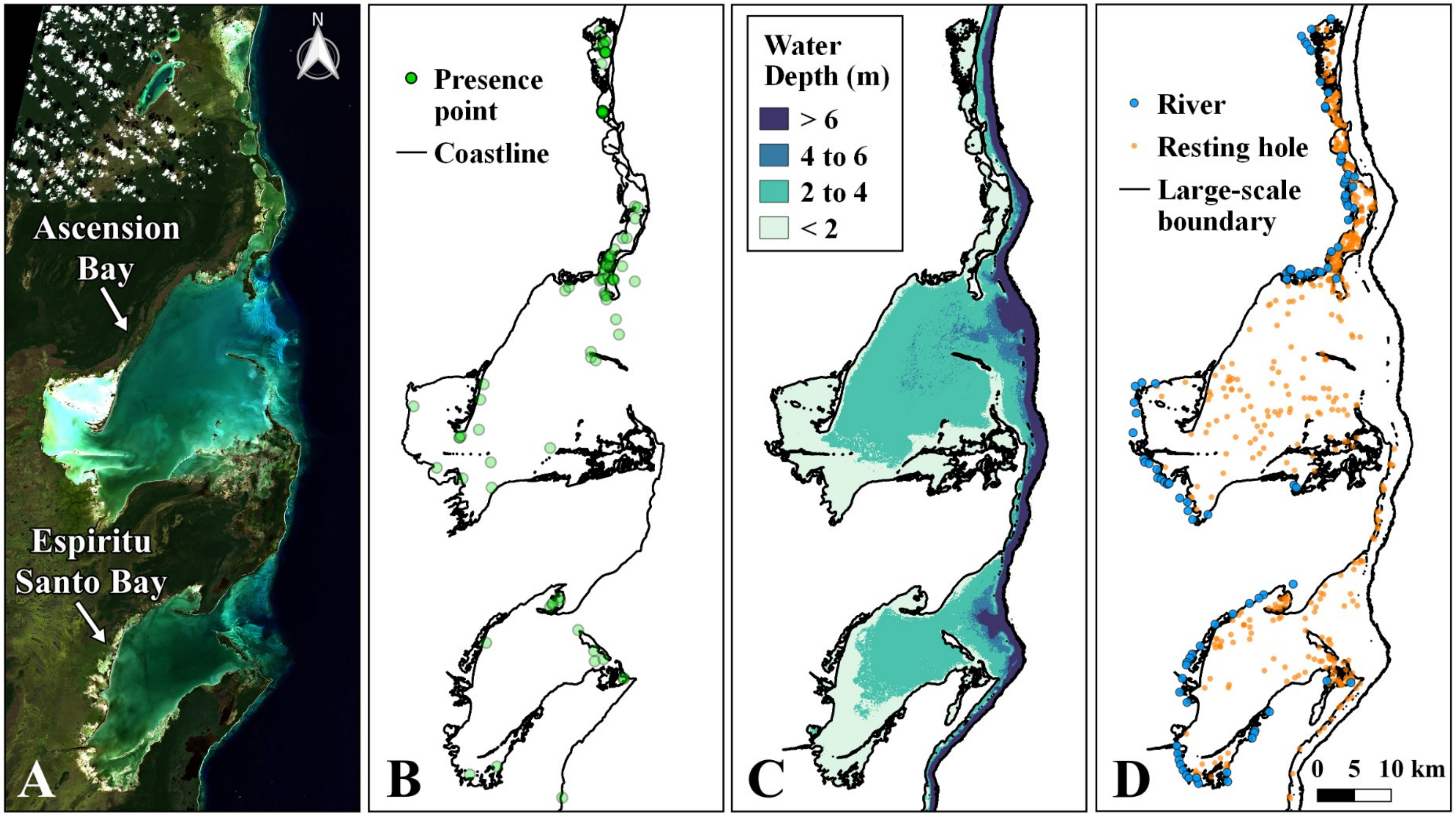

Figure 1. Map of Sian Ka'an Biosphere Reserve, Mexico: A) satellite image (from Sentinel-2 satellite project) with bays labelled, B) coastline and recorded sighting (*n* = 102) locations, C) water depth with black line representing large-scale boundary, and D) distribution of river mouths (*n* = 101) and resting holes (*n* = 409).

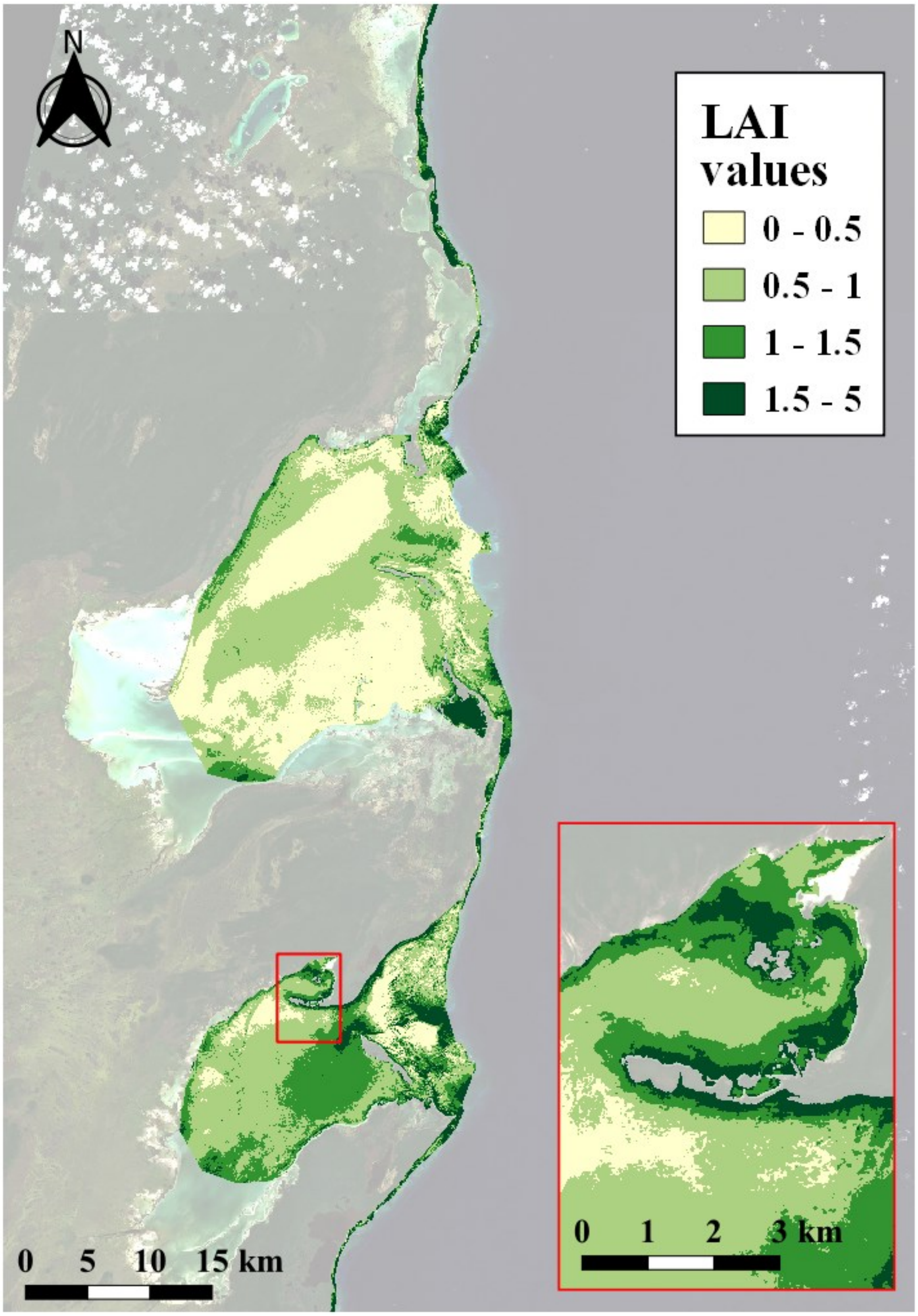

Figure 2. LAI (leaf area index) map of Sian Ka'an layered over Sentinel-2 satellite images, using Hedley and colleagues (2021) data. The LAI data used for this map was the calculated average of the year 2020.

Statistical Analyses

Statistical tests and models were run on the open-source R software (v4.2.2; R Developmental Core Team, 2023). Geographic manipulations and mapping were done with the open-source software QGIS (v3.28 Firenze; QGIS Developmental Team, 2023).

Given that we only had opportunistic observations, we used a pseudo-absence ("pseudo" because they are not true absence points, i.e., recorded absences on the field) approach to model habitat selection at two spatial scales. The large spatial scale represented the whole area of Sian Ka'an thus, for each observation, a pseudo-absence location was randomly generated within the entire area (see boundary on Figure 1C, D). Pairing presence points with closely located pseudo-absence points was also suggested to be an appropriate method for low mobility species that have a large home range or species without a well-defined home range, such as manatees (Compton et al., 2002). Hence, for the small spatial scale, the pseudo-absence points were randomly generated 400 m to 1,000 m away from each manatee observation (see Figure 3). The reason for excluding a 400 m radius was twofold. First, the daily travel rate of manatees was estimated to be 0.4 to 0.5 km (Castelblanco-Martínez et al., 2013). This exclusion zone would thus encompass all the space the observed manatee could have occupied for the day it was sighted. The donut shape itself, where pseudo-absences were generated, would represent all the other possibilities of occupancy for a day's worth of space by the individual. Second, this exclusion zone ensured that the pseudo-absence points would be far enough from the presence points to capture environmental conditions that were different from the presence points. This is an especially important consideration in the water biodome as it is much more homogeneous than the terrestrial biodome (Grosberg et al., 2012). This would also lead to more accurate results (Zaniewski et al., 2002) and there would be no pseudo-absence points at the exact same location as or close to a presence point (Pearce & Boyce, 2006; Wisz & Guisan, 2009). To confirm the validity of this spatial scale, we also ran analyses with a circle of a 1 km radius, without exclusion zones. From the donut and circle shapes, we excluded area of land and any water behind land, which would not have been directly accessible to the individuals (see Figure 3).

We generated 500 pseudo-absence points per presence point — per spatial scale —, and fitted a model for each set of 102 pseudo-absence points. In other words, we ran a total of 500 iterations of each model and for each iteration, 102 unique pseudo-absence points were generated (one for each presence point), while the same 102 presence points were used for all 500 iterations of a model. This randomization technique was used to avoid potential biases due to generation of pseudo-absences and to represent a wider range of available resources to manatees. To describe habitat selection of manatees, we used generalized linear (mixed) models (GLMMs). Other methods, such as tree-based, are highly sensitive to sample collection biases (Hastie et al., 2009). There are also fewer risks of overfitting or biased predictions using a GLM rather than a presence-only method, such as Ecological Niche Factor Analysis (ENFA; Phillips et al., 2008) and Maximum Entropy (MaxEnt; Phillips et al., 2006). Both ENFA and MaxEnt have ill-defined outputs and generate predictions of habitat similarity rather than probability of presence (Brotons et al., 2004; Elith et al., 2011; Royle et al., 2012).

All variables were standardized prior to modeling, and Euclidean distances were transformed using an exponential decay function ($e^{-\alpha/d}$; Carpenter et al., 2010; Nielsen et al., 2009). Effectively, decay functions decrease the effect of large distances between resources and presence or pseudo-absence points, distances for which the individual is unlikely to know the existence of the resource. The α term dictates the maximum distance of potential knowledge for the resource, which was set to 1,000 m.

We used a Bayesian approach for our analyses to better incorporate the variation between and within models. We used the *brm* function in R (from *brms* package version 2.19.0; Bürkner, 2017) with the family Bernoulli: 4 chains, each with iter = 2,000; warmup = 1,000; thin = 1; total post-warmup draws = 4,000. We modeled the presence-absence (coded as 1 and 0, respectively) as a function of the fixed effects: LAI, water depth, and distance to land, resting hole and river. Two-way interactions between all variables were also added to the models to test for all possible outcomes, but removed if they were deemed not different from zero. For the fine-spatial scale model only, we also included the observation number as a random effect to account for spatial autocorrelation (see Figure 3). Each presence and their 500 pseudo-absence points were numbered form 1 to 102, and including a random effect of this number in the models essentially paired all presence points with their respective pseudo-absence points.

The posterior distribution of all 500 models was combined into one for each variable, and the estimate was calculated as the posterior mode. Predictor variables were deemed to be different from zero if the 95% highest posterior distribution interval (HPDI) excluded zero. To test the performance of our models, we calculated the area under the curve (AUC) of the receiver operating characteristic (ROC) curve (using the R package *pROC* v1.18.2; Robin et al., 2011). Correlation matrices between variables were generated for each scale to flag any correlation issues.

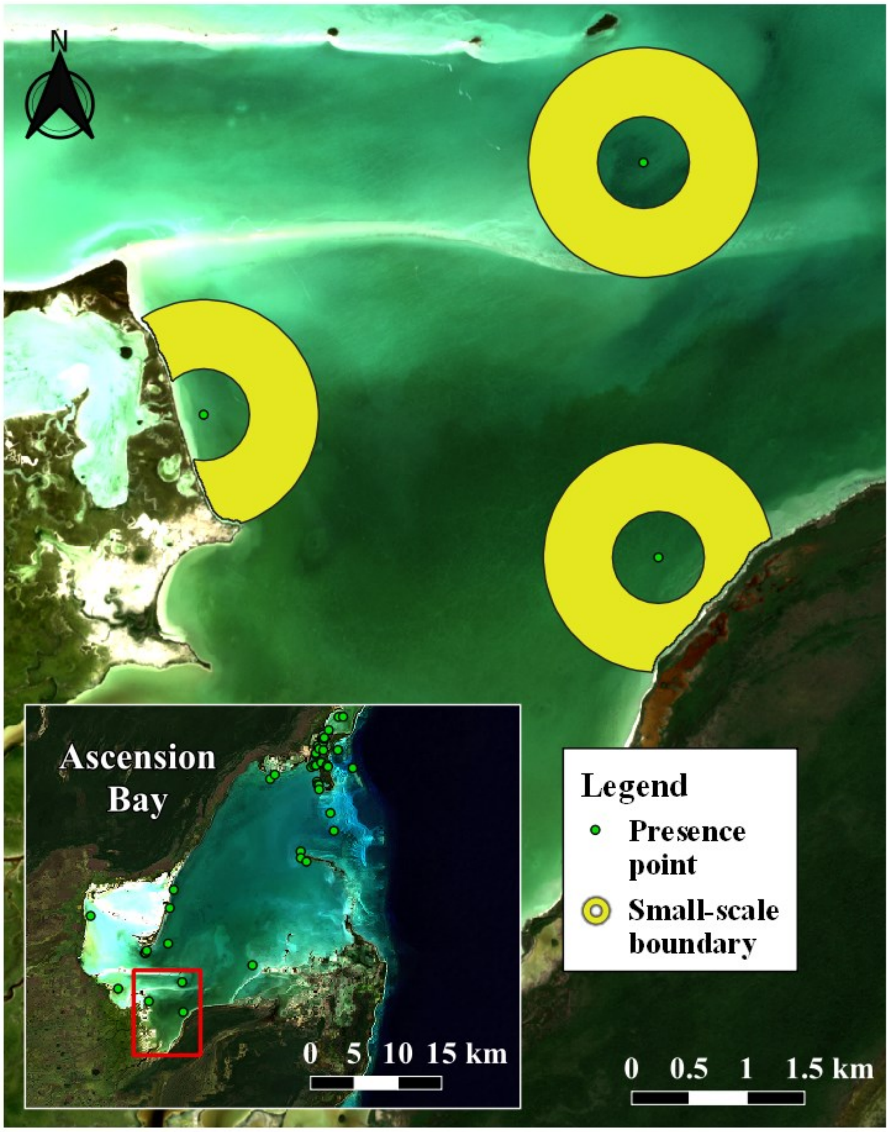

Figure 3. Visual representation of small-scale availability zone for manatee presence points in Sian Ka’an. Each buffer was positioned 400 to 1,000 m away from a presence point. Areas of land and water behind a slit of land, blocking manatee access, were excluded from the buffer zone (e.g., the leftmost small-scale boundary).

Results

A total of 102 manatee observations were made in the Sian Ka'an Biosphere Reserve (see Figure 1B). 409 resting holes and 101 rivers were detected in the study area (see Figure 1D).

The highest calculated values from the correlation matrix of the small- and large-scale variables were 0.694 and 0.463 (respectively for each scale; see S1 and S2), showing no correlation issues between variables. None of the two-way interactions were found to be significantly different from zero at either spatial scale (see S3) and were therefore removed from the models.

For models without LAI, at both scales, all variables had a negative effect on manatee presence, but some had small effects or large errors. At the large-scale, both the distance to resting hole (estimate of -1.648 and 95% HPDI of [-2.382, -1.005]) and distance to land (estimate of -0.826 and 95% HPDI of [-1.618, -0.113]) showed a strong negative effect different from zero (see Table 1 and Figure 4). At the small-scale, only the effect of distance to resting hole (estimate of -0.642 and 95% HPDI of [-1.131, -0.192]) was different from zero (see Table 1 and Figure 5). The models fitted well the data, especially the large-scale, with AUC values of 92% and 73% (large- and small-scale, respectively).

Table 1. Posterior mode and 95% HPD interval of environmental variables in the habitat selection models at the large- and small-scale (GLMM; *brms* function in R). Variables that have 95% HPD interval excluding zero were considered significantly different from zero (highlighted in bold).

	Posterior mode	Lower 95% HPDI	Upper 95% HPDI
Large scale			
Water Depth	-0.108	-0.815	0.898
Distance to river	-0.427	-1.292	0.342
Distance to resting hole	**-1.648**	**-2.382**	**-1.005**
Distance to land	**-0.826**	**-1.618**	**-0.113**
Small scale			
Water Depth	-0.477	-0.975	0.011
Distance to river	-0.087	-0.497	0.307
Distance to resting hole	**-0.642**	**-1.131**	**-0.192**
Distance to land	-0.067	-0.596	0.446

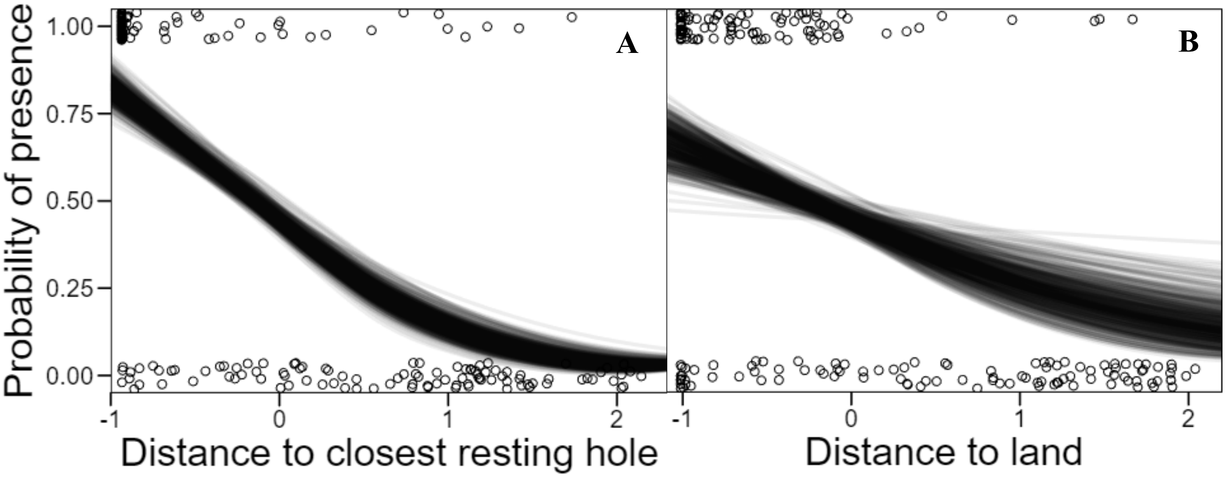

Figure 4. Large-scale habitat selection of Antillean manatees in Sian Ka'an as a function of decay distance to the closest resting hole (A) and decay distance to land (B), both standardized. The model included distance to resting hole, river and land, and water depth as fixed effects. Each line (*n* = 500 per graph) represents the predicted values for one of the 500 models, each having a different set of pseudo-absence points. For ease of visualization, the presence and pseudo absence points are jittered around their y value, and only 102 pseudo-absence points are represented in each graph.

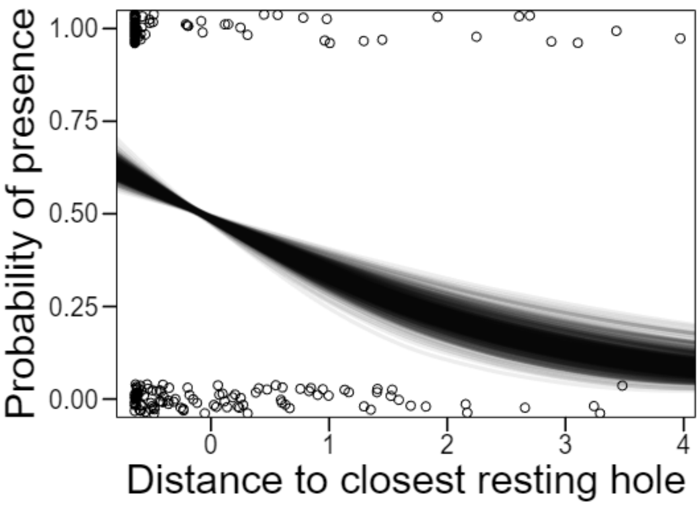

Figure 5. Small-scale habitat selection of Antillean manatees in Sian Ka'an as a function of decay distance to the closest resting hole, which was standardized. The model included distance to resting hole, river and land, and water depth as fixed effects. Each line (n = 500 per graph) represents the predicted values for one of the 500 models, each having a different set of pseudo-absence points. For ease of visualization, the presence and pseudo absence points are jittered around their y value, and only 102 pseudo-absence points are represented in each graph.

The results of the models with LAI (see Table 2 and Figure 6) were similar to the ones without LAI. All variables had a negative relationship with probability of presence, with the exception of distance to river for the small-scale model, which had a positive effect. None of the variables were deemed different from zero for the small-scale model, while in the large-scale model, both distance to closest resting hole (estimate of -1.197 and 95% HPDI of [-2.594, -0.112]) and distance to land (estimate of -1.654 and 95% HPDI of [-3.825, -0.380]) were deemed to be different from zero. The AUC values for the large- and small-scale models were 91% and 67%, respectively.

Table 2. Posterior mode and 95% HPD interval of environmental variables in the habitat selection models–with the LAI variable–at the large- and small-scale (GLMM; *brms* function in R). Variables that have 95% HPD interval excluding zero were considered significantly different from zero (highlighted in bold).

	Posterior mode	Lower 95% HPDI	Upper 95% HPDI
Large scale			
Water Depth	-0.714	-2.342	0.650
Distance to river	-0.496	-2.500	0.982
Distance to resting hole	**-1.197**	**-2.594**	**-0.112**
Distance to land	**-1.654**	**-3.825**	**-0.380**
LAI value	-0.394	-1.493	0.649
Small scale			
Water Depth	-0.093	-0.958	0.711
Distance to river	0.088	-0.608	0.747
Distance to resting hole	-0.451	-1.233	0.263
Distance to land	-0.271	-1.119	0.551
LAI value	-0.224	-0.924	0.413

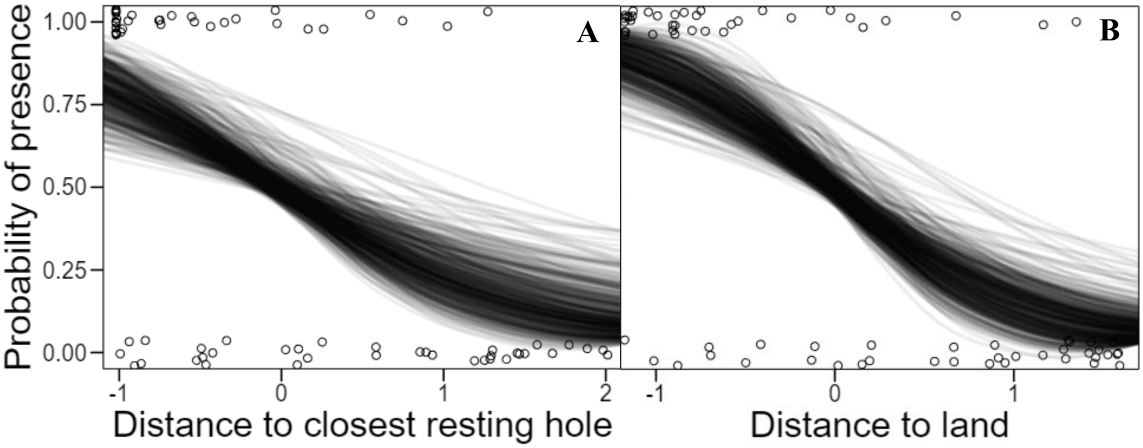

Figure 6. Large-scale habitat selection of Antillean manatees in Sian Ka'an as a function of decay distance to the closest resting hole (A) and decay distance to land (B), both standardized. The model included distance to resting hole, river and land, water depth and LAI, as fixed effects. Each line (*n* = 500 per graph) represents the predicted values for one of the 500 models, each having a different set of pseudo-absence points. For ease of visualization, the presence and pseudo absence points were jittered around their y value, and only 36 pseudo-absence points are represented in each graph.

Discussion

The goal of this study was to model habitat selection at different spatial scales to gain insight into the Antillean manatee's spatial ecology — especially at a small spatial scale. As expected, we observed different explanatory variables for the two scales, showcasing the need for multi-scale designs in habitat selection studies. In the large spatial scale model, covering the entirety of Sian Ka'an Biosphere Reserve, the probability of presence increased closer to resting holes and to land. In the small spatial scale model, characterized by an availability zone situated between 400 m and 1,000 m away from presence points, the probability of presence was also greater closer to resting holes. The most important feature of habitat selection for Antillean manatees in Sian Ka'an was the only variable significantly different from zero at both spatial scales — i.e., the closeness to resting hole. According to our results, distance to river, water depth and LAI were not good predictors for manatee sighting probability at either spatial scale.

As expected, the distance to resting hole was significantly different from zero at both scales, highlighting the importance of resting holes for manatees in Sian Ka'an. A few studies from Belize (Bacchus et al., 2009; Lacommare et al., 2008) showed a strong preference by manatees to stay closer to resting holes. Bacchus and collaborators (2009) found that resting holes had a significantly lower surface water velocity, which would explain their preference to stay in resting holes. This would enable the animals to rest in a resting hole without spending lots of energy fighting the water movement to stay in the same location. While resting holes were probably mostly used for the purpose of resting behavior, there is also the possibility for them to drink fresh water there. On few occasions, manatees were also seen drinking fresh water at resting hole locations in Sian Ka'an (N. Castelblanco-Martínez, personal communication). Furthermore, while we expected for the distance to river variable to be correlated to manatee presence, it was deemed not different from zero. Water salinity at a river mouth increases when the flow of the river is slower because the marine water mixes with the incoming fresh water higher up the river (Matsoukis et al., 2023). It is thus possible that the rivers’ current in Sian Ka’an was not strong enough to carry fresh water to the mouth of the rivers, making it less accessible to manatees. Another plausible explanation is that the water is not deep enough at the river mouths for manatees to have access to the incoming fresh water. We argue that manatees in the study area most likely use the resting holes for both resting and drinking purposes. We know that multiple resting holes in the study area are sources of fresh water, although the exact freshwater input locations would need to be confirmed in future studies.

Distance to land was different from zero and negative in the large-scale model only. We expected this variable to have a negative relationship with probability of presence (Castelblanco-Martínez et al., 2013; Landero et al., 2014; Morales-Vela, 2000; Ross, 2007), but in the small-scale rather than the large-scale. In 2013, Castelblanco-Martínez and collaborators observed that manatees spent most of their time close to land, and explained that closeness to land also generally entailed a combination of favorable habitat characteristics for manatees: shallower water (between 1 to 3 m deep; Castelblanco-Martínez et al., 2013; Hartman, 1979; Landero et al., 2014; Lefebvre et al., 2001) and lots of vegetation to eat (Hedley et al., 2021; Lefebvre et al., 2000). Additionally, there is a greater proportion of resting holes positioned near land than further away, especially in the lagoonal areas north of Ascension Bay (see Figure 1D). While, based on the information available to us, it is impossible to distinguish which specific environmental factors are responsible for the preference of manatees to be closer to land, it remains true that areas in proximity to land seem to be prime microhabitats for manatees.

While we predicted manatees to select shallower water in the large-scale model, our results show that the effect was not different from zero in either scale. It is possible that since most of Sian Ka'an is quite shallow, there would be no need for manatees to select areas of shallow water at the large-scale as most of the area would already be shallow enough for them. Indeed, the proportion of deep water (> 4 m) in the study area was very small compared to shallow waters (< 4 m; see Figure 1D). This could explain the absence of water depth's effect on probability of presence at the large-scale. For the small-scale results, the 95% HPD interval of water depth almost excluded zero (see Table 1). The overall effect of water depth on manatee presence was negative, meaning that individuals were selecting for deeper waters at the small-scale. In most studies on manatee habitat selection, results indicate that they prefer shallower waters (Landero et al., 2014; Lefebvre et al., 2000). However, the spatial scale of these studies is large (e.g., whole study area), and we implemented a fine-scale method that could explain the difference in the observed trend (i.e., preference for deeper rather than shallower water). Hartman (1979) also noticed that manatees tend to dislike or look uncomfortable in very shallow water conditions, partly because of spatial constraints and because of the stress posed by human presence. Hence, manatees would have selected the deeper parts of shallow waters for space advantages and ease of navigation. It was also reported that when manatees encounter boats or drones from too close, they flee the area and go to swim in deeper water for protection (Ramos et al., 2018, Lefebvre et al., 2001). It is therefore possible that the preference for deeper water was artificially created by the presence of our team scanning the area. The number of individuals reacting to the presence of a boat or drone remains impossible to know, as most behaviors were not noted and closeness to manatees varied from sighting to sighting. More studies would be needed to confirm or infirm this potential deeper water preference.

We predicted LAI to be positively correlated with manatee presence in the small-scale model. While the LAI variable in both models was negative and not deemed different from zero (see Table 2), the estimates were not far from being different from zero, especially in the large-scale model. Most studies of manatee habitat selection demonstrate a positive correlation between probability of presence and seagrass abundance (Lacommare et al., 2008; Lefebvre et al., 2000; Ross, 2007). However, two studies (Favero et al., 2020; Landero et al., 2014) found a significant negative effect of seagrass quantity on manatee abundance. Landero and collaborators (2014) justified that since manatees could eat the nutritious roots and rhizomes of vascular plants and seagrass by digging in the mud, they did not need a large amount of seagrass stems or leaves, represented by a large above-ground seagrass quantity or high LAI. This foraging behavior had previously been recognized through the observation of manatee feeding scars and marks (Bacchus et al., 2009) and could explain the negative correlation of LAI with probability of manatee presence. Alternatively, manatees could have adjusted their diet by eating more shoreline emergent plants or other plant matter, such as floating leaves (Castelblanco-Martínez et al., 2009). Among all the coastal waters of the Yucatan peninsula, Sian Ka'an has the lowest seagrass abundance (Hedley et al., 2021), which would be an incentive for manatees to rely more on vascular plants as a source of food. The non-significance of LAI could also be due to the low sample size of these models. This reduced statistical power however also implies that our LAI model results should be interpreted with caution. Regardless, this pattern requires further investigating.

It is important to keep in mind that there are limitations of the LAI to represent seagrass quantity. Debris or other vegetation matter, which appear identical to seagrass on 10m resolution satellite maps, could have led to an erroneous overestimation of LAI (Hedley et al., 2021). Overall, this index roughly represents the abundance of above-ground seagrass. It is possible that an individual was observed more than once, especially given the population estimate of the area. While some of our observations were done using drone videos, which could have helped us identify the different individuals, other observations were done through a visual survey from boats without any recording equipment. It was therefore impossible for us to identify the individuals, and there might be a disproportionate representation of a few individuals within our sample. While this would decrease the generalization of the pattern detected for the population, given the sporadic nature of the collected observations, the probability of a few individuals being observed repeatedly in a short period of time is low.

In the small-scale availability zone, we added a zone of exclusion extending to 400 m away from each presence point (see Figure 3). To confirm the robustness of our geographical design, we tested the same model with pseudo-absence points generated up to 1,000 m away from the presence points without zones of exclusion and effectively obtained the same results (see S4). It was estimated that Antillean manatees travel between 400 and 500 m within a day (Castelblanco-Martínez et al., 2013). Therefore, this 400 m zone of exclusion would incorporate the hypothetical space occupied by the manatee for the day it was observed, while the 400 to 1,000 m availability zone would represent all the possible space that could have been — but was not — used by the manatee on that same day. This implies that our small-scale model informs us of the day-to-day habitat selection decisions made by manatees in Sian Ka'an. Hence, we are confident that the delimitation of our small-scale availability zone is sound and informative.

There are many variables that could be added to a future model of manatee habitat selection in Sian Ka'an. The most valuable additions would be related to temporal scales: season and time of day. In this study, our sample size was not large enough to include season as a factor, which could influence the calculated estimates of variables. Indeed, in the study area, the seasons affect the water salinity (Medina-Gómez et al., 2014), water temperature (Varela et al., 2018), seagrass distribution (Dawes, 1986) and water level (Medellín & Torres-Freyermuth, 2019), which would change the access to bank vegetation. During the dry season, the increased water salinity could force manatees to show a stronger preference for closeness to fresh water (Favero et al., 2020) and the reduced access to bank plants could oblige them to stay closer to seagrass patches. We would recommend including wet and dry seasons as a factor in future studies if provided with a sufficient sample size. As for the time of day, all our sightings were done during the day, and this could have further influenced our results. Studies showed that manatees have a diel activity pattern and seem to be nocturnal, with more foraging and traveling behaviors at night and more resting behaviors during the day (Bacchus et al., 2009; Jiménez, 2002; Rathbun et al., 1983). This is a potential major explanation for our results going against our predictions for the estimates of distance to river, water depth and seagrass. The strong association to resting holes found in this study could also be due to the time frame of our observations, which would mainly be associated with a resting behavior. Performing manatee sightings at night would be a difficult task, imply complex logistics, and probably lower the reliability of the data. We thus recommend using the combination of both a telemetry method on tagged individuals, to comment on diel activity patterns, and day observations, to have a greater sample size and a better represented population.

Another variable that could add information to habitat selection is the sex of the individuals. While there is a lot of unknown regarding sex-specific behaviors, it was previously shown that females tend to reside in a single bay and males travel much greater distances in Chetumal Bay, Mexico (Castelblanco-Martínez et al., 2013). Incorporating the sex of the manatee in a habitat selection model would most likely help unveil space use sexual dimorphism. However, sexing manatees could be difficult to achieve, since visual sighting from a boat or even a drone is not a reliable method (Yauri et al., 2020). An alternative would be to include in the model whether the observed manatee was with or without a calf (Gannon et al., 2007). There are also other variables that would benefit the model: salinity, temperature and boat traffic (Lefebvre et al., 2000). The lack of environmental condition monitoring in that Sian Ka'an Biosphere Reserve and our limited sample size prevented us from including these variables. While we may have faced some limitations, this study informed us on our understanding of the habitat use of the endangered Antillean manatee in one of its most used regions, Sian Ka'an which has only been home to one other published paper on manatee.

Conclusion

To our knowledge, this is the first study looking at habitat selection of manatees at more than one spatial scale and, consequently, offers a unique look into their space use preferences. Habitat selection is contextual, meaning that it varies as a function of both time and space, as well as the environmental factors of each specific study area (Gannon et al., 2007; Paton & Matthiopoulos, 2016; Thompson & McGarigal, 2002). This complicates the task of implementing conservation measures for the protection of the endangered Antillean manatee (Self-Sullivan & Mignucci-Giannoni, 2008). Each regional population of manatees will be faced to a different set of habitat characteristics, and therefore each will be confronted to its own set of challenges. This also implies that the results of our study are intimately linked with the manatee population specific to Sian Ka'an (Matthiopoulos et al., 2011). Since, to this day, there has been only one paper published regarding manatee habitat selection in Sian Ka'an Biosphere Reserve (in Ascencion Bay only: Landero et al., 2014), this study adds valuable information. Finally, given the understudied nature of the Antillean manatee (especially compared to the other subspecies, the Florida manatee), this study represents an important piece of the manatee literature. We hope that by combining already published data on manatees with the present findings, we can better understand the needs of Antillean manatees and implement appropriate conservation measures for the sake of the subspecies' survival.

Appendices

APPENDIX I – Correlation matrices

S1. Correlation matrix of large- and small-scale (final) model variables.

	Water depth	Distance river	Distance resting hole	Distance land
Large scale				
Water Depth	-			
Distance river	-0.336	-		
Distance resting hole	-0.355	0.220	-	
Distance land	-0.358	0.463	0.126	-
Small scale				
Water Depth	-			
Distance river	-0.502	-		
Distance resting hole	-0.401	0.352	-	
Distance land	-0.694	0.444	0.497	-

S2. Correlation matrix of large- and small-scale (LAI) model variables.

	Water depth	Distance river	Distance resting hole	Distance land	LAI
Large scale					
Water Depth	-				
Distance river	-0.289	-			
Distance resting hole	-0.064	0.112	-		
Distance land	-0.587	0.383	0.047	-	
LAI	0.248	-0.320	0.078	-0.335	-
Small scale					
Water Depth	-				
Distance river	-0.376	-			
Distance resting hole	-0.365	0.349	-		
Distance land	-0.652	0.324	0.387	-	
LAI	0.401	-0.033	-0.172	-0.330	-

APPENDIX II – Results of models with two-way interactions

S3. Posterior mode and 95% HPD interval of environmental variables in the habitat selection models at the large- and small-scale (GLMM; *brms* function in R). Variables that have 95% HPD interval excluding zero were considered significantly different from zero (highlighted in bold).

	Posterior mode	Lower 95% HPDI	Upper 95% HPDI
Large scale			
Water Depth	-1.116	-5.351	1.353
Distance to river	-1.160	-3.532	0.372
Distance to resting hole	**-2.084**	**-3.532**	**-1.084**
Distance to land	-0.775	-2.444	1.193
Depth:River	1.134	-2.145	5.144
Depth:Hole	1.022	-0.890	4.045
Depth:Land	-0.016	-1.947	2.091
River:Hole	0.476	-0.864	1.900
River:Land	-0.432	-2.780	1.536
Hole:Land	0.630	-0.466	1.865
Small scale			
Water Depth	**-0.724**	**-1.516**	**-0.031**
Distance to river	0.096	-0.453	0.669
Distance to resting hole	**-1.169**	**-2.102**	**-0.405**
Distance to land	-0.078	-0.992	0.863
Depth:River	-0.026	-0.783	0.712
Depth:Hole	0.115	-0.518	0.797
Depth:Land	0.185	-0.294	0.694
River:Hole	0.661	-0.192	1.533
River:Land	0.124	-0.910	1.114
Hole:Land	0.140	-0.452	0.737

APPENDIX III – Results small-scale models without exclusion zones

S4. Posterior mode and 95% HPD interval of environmental variables in the habitat selection models at the small-scale–with and without two-way interactions (GLMM; *brms* function in R). Variables that have 95% HPD interval excluding zero were considered significantly different from zero (highlighted in bold).

	Posterior mode	Lower 95% HPDI	Upper 95% HPDI
Small scale			
Water Depth	-0.609	-1.375	0.071
Distance to river	0.057	-0.518	0.611
Distance to resting hole	**-1.017**	**-1.900**	**-0.251**
Distance to land	-0.078	-0.928	0.970
Depth:River	-0.034	-0.802	0.634
Depth:Hole	0.078	-0.480	0.731
Depth:Land	0.151	-0.298	0.628
River:Hole	0.558	-0.271	1.407
River:Land	0.041	-1.020	1.022
Hole:Land	0.129	-0.433	0.704
Small scale no interactions			
Water Depth	-0.403	-0.911	0.058
Distance to river	-0.075	-0.496	0.306
Distance to resting hole	**-0.511**	**-1.009**	**-0.119**
Distance to land	-0.045	-0.562	0.458

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