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Development of predictive models to explain the distribution of the West Indian manatee *Trichechus manatus* in tropical watercourses

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Abstract

Logistic regressions were used to study the relationship between habitat variables and the use of tropical watercourses by the West Indian manatee *Trichechus manatus* at Northeastern Costa Rica and Southern Nicaragua. Presence of manatees in watercourses was assessed through direct and reported sightings of individuals and feeding signs on aquatic vegetation. Indirect methods provided good approximations to the actual distribution that could not have been achieved through direct observations or aerial surveys. Best multivariate models showed that manatees were most present in watercourses that presented abundant aquatic vegetation, warm, and clear waters, high forest cover, and are wider than those where the species is absent. Although habitat variables that explain habitat use of manatees differed for the two sectors found within the study area, manatees preferred lagoons to other watercourses in both areas. These findings point to forest clearing on the shores as a threat for manatee conservation. Habitat variables are excellent predictors of manatee presence, and predictive models as those developed in this study can help assess potential distribution of manatees in areas where this information is lacking as well as to assist identify potential reintroduction areas.

Keywords: West Indian manatee; *Trichechus manatus*; Habitat selection; Predictive models; Indirect methods for distribution assessment

1. Introduction

Generalized Lineal Models (GLMs) can help us identify the main habitat factors that explain the presence of a particular species. The predictive value of such models can also be used to identify potential areas for the species, outside the region where the model was originally developed. Thus, through the measurement of some habitat variables, GLMs help estimate a species distribution or identify the existence of adequate habitat. The predictive power of these models has been cited as one of their main applications, though this has been seldom tested (Morrison et al., 1992). Most often, the development of a predictive model terminates once it has been tested its predictive power inside the region where the model was developed. There is a lack of studies that validate a model's predictive power in an area that is found outside the place where the model was developed. I describe the development of GLMs – Logistic regressions in this case – that explain the distribution of the West Indian manatee *Trichechus manatus* based on habitat characteristics, and use an indirect approach to test their predictive power on an external area.

The West Indian manatee is an herbivorous and aquatic mammal that inhabits coasts, estuaries, rivers and lagoons from Florida to the central coast of Brazil, including the Greater Antilles (Lefevbre et al., 2001). Manatees are secretive animals that are difficult to observe along most of their range (Reynolds and Odell, 1991). Habitat factors that have been reported to affect

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the species' distribution are: water temperature, though mostly in subtropical areas (Husar, 1977; Irvine, 1983; Deutsch et al., 2003), water depth (Hartman, 1979; Packard and Wetterqvist, 1986; Olivera-Gómez and Mellinck, 2005), salinity (Husar, 1977; Hartman, 1979; Powell et al., 1981; Colmenero-R and Zárate, 1990; Lefevbre et al., 2001; Olivera-Gómez and Mellinck, 2005), currents (Hartman, 1979), tides (Hartman, 1979), abundance of aquatic vegetation (Hartman, 1979; Packard and Wetterqvist, 1986; Deutsch et al., 2003; Olivera-Gómez and Mellinck, 2005), and motorboat traffic (O'Shea, 1995; Smethurst and Nietschmann, 1999). In spite of these references, there is a scarcity of quantitative analyses that test the actual relationship between such factors and the species' distribution. The best studies published on this regard come from Bahía de Chetumal (Axis-Arroyo et al., 1998; Olivera-Gómez and Mellinck, 2005), a large brackish bay whose habitat characteristics differ sharply from Tropical watercourses used by Antillean, Amazonian and West African manatees (Montgomery et al., 1981; Powell, 1996; Lefevbre et al., 2001). Improving our knowledge of habitat needs for manatees seems especially relevant since the species is classified as vulnerable to extinction (Hilton-Taylor, 2000).

I developed GLMs to achieve four objectives: (1) to identify those habitat variables that explain the distribution of the West Indian manatee in tropical watercourses; (2) to compare different methods used to determine the manatee distribution in order to test their potential use in areas where is difficult to observe the species; (3) to test the use of habitats models that predict the presence of manatees; and (4) to identify threats to the species conservation.

2. Materials and methods

2.1. Study area and design

The study area includes 65,000 ha of wetlands on Northeastern Costa Rica and Southern Nicaragua. Three villages delimit the area within a triangular polygon: El Jardín (10°50′N, 84°13′W) in the Northwest, Barra del Colorado in the Northeast (10°46′N, 83°36′W) and Moin in the Southeast (10°00′N, 83°05′W) (Fig. 1). The region belongs to Holdridge's very humid tropical forest life zone with an average annual rainfall near 4500 mm and average temperature of 26 °C (MIRENEM/UICN/ORCA/JAPDEVA, 1991; Bolaños and Watson, 1993). While the study area is essentially aseasonal and does not regularly conform to the customary wet and dry seasons of Costa Rica and Nicaragua (January–April: dry/May–December: wet), heavy rainfall and extensive flooding routinely occur in July–August and November–December (Myers, 1981). Drier months usually fall between January and September although rain is rarely absent for more than two weeks (Myers, 1981). Regular presence of freshwater is large enough to prevent the establishment of mangrove trees even near river mouths. Dense rainforests, *Raphia* palm swamps and grass marshes surround

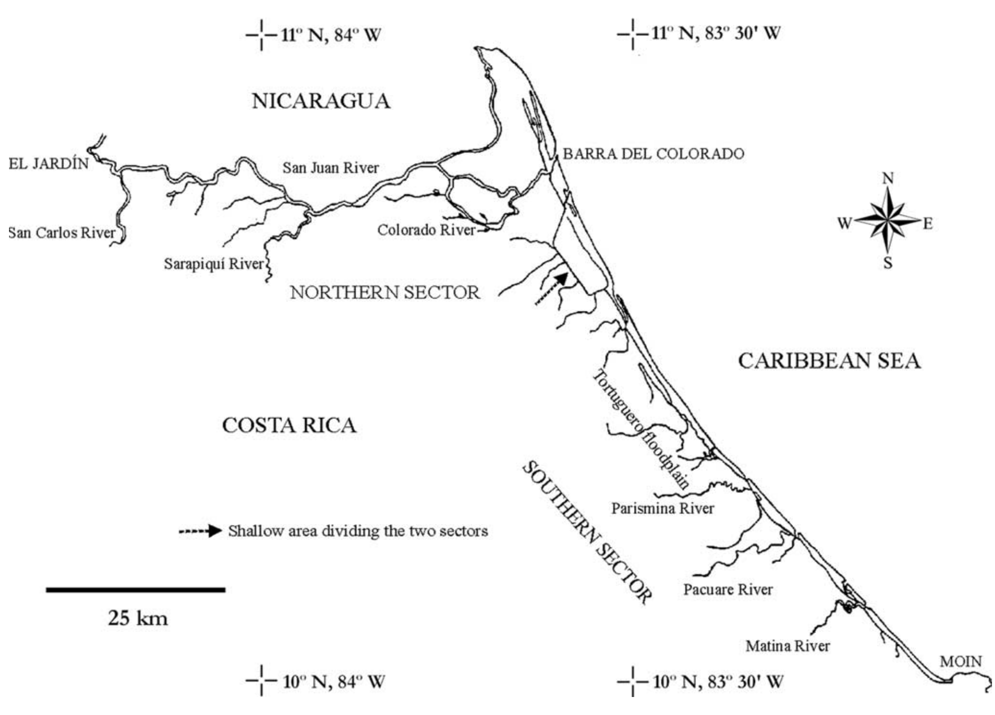

Fig. 1. Study area with its two study sectors and their limit.

watercourses along the whole study area. Due to low water visibility, local wetlands are poor on submerged vegetation while they harbor abundant emergent and floating vegetation near their edges.

In spite of sharing these general traits, the area is compromised of two sectors with some habitat differences, which are set apart by a tract of very shallow water (i.e., less than 50 cm of depth) that may constrain continuous interchange of manatees between both sectors (Fig. 1). The northern sector includes the southern half of the San Juan river basin. The main rivers of the northern area (i.e., San Juan, Colorado, Sarapiquí and San Carlos) contain fast moving turbid waters that flow in a West to East direction. In the eastern side of this sector there is a network of lagoons surrounded by grass marshes and black-water creeks that carry their slow waters to the Colorado River. The second and southern sector lies on the Tortuguero floodplain and it is characterized by coastal lagoons, creeks, rivers and artificial canals that contain mostly slow moving black tinted waters that run parallel to the coastline. Several fast moving rivers (i.e., Pacuare, Parismina and Matina) carry their turbid and silt-rich waters from the western volcanic range to the Tortuguero floodplains.

Manatee hunting was not considered a significant factor affecting the species' distribution since local law enforcement is high and manatee poaching is minimal (Jiménez, 1999). Therefore, manatees were assumed to be free to use all watercourses they could access. Coastal waters are highly turbid and seagrass beds seem to be either absent or extremely scarce (MIRENEM/UICN/ORCA/JAPDEVA, 1991).

Sampling units (i.e., watercourses) were identified using both a qualitative and quantitative approach. First, each unit was primarily delimited through 1:50,000 maps from the Instituto Geográfico Nacional, based on its shape and the presence of intersections with other watercourses (Fig. 2). The adequacy of this cartographic delimitation was tested in the field while measuring habitat variables, merging adjacent wetlands when they showed similar habitat characteristics and separating tracts when there were sectors of at least 200 m that showed distinct habitat differences. Thus the study area was finally delimited in 111 units of which 87 were used for analysis: 38 on the northern sector and 49 on the southern one. Field data were collected between June 1996 and August 1997.

2.2. Habitat variables

For each watercourse, I measured the following habitat variables that were presumed to influence presence of manatees: (1) water depth, (2) water visibility, (3) water temperature, (4) water current, (5) watercourse width, (6) total abundance of aquatic vegetation, (7) abundance of emergent vegetation, (8) abundance of floating vegetation, (9) forest cover on the shore, and (10) boat traffic. To detect a spatial aggregation pattern in the species' distribution I also included geographic coordinates for each watercourse as variables. Given that environmental variables included within aquatic ecosystems are highly dynamic and show significant fluctuations through time, measures obtained during the study were not considered as actual mean values but as approximations to overall environmental conditions during the study. Habitat variables were measured during two field seasons – November 1996 and May 1997 – and measures were averaged for analysis.

Each watercourse was transected along its central area, except for those areas that presented shallow banks and that were crossed through their deepest portions. Surface water temperature and watercourse depth were measured with a sonar (model 570, APELCO, USA), taking measurements every 80 m on watercourses longer than 500 m and every 40 m on shorter ones. Water visibility was estimated with a Secci disc in two to five random points per unit, and the same sites were used to measure water current with a speedometer (model 6645, Weathertronics, USA) at 40 and 100 cm of depth. I took 16 water samples from the surface of 14 watercourses adjacent to the coast and river-mouths and measured salinity with a salinometer (model 33, YSI, USA) without detecting any salinity in them. Therefore, salinity was excluded as a variable for analysis and all watercourses were considered as freshwater wetlands, though some of the rivers and lagoons that lay close to the sea contain salt water near their bottom. Average width for each unit was measured through 1:60,000 aerial photographs and 1:50,000 cartographic maps, except on watercourses narrower than 30 m where distance between shores was measured in situ.

Presence and bank width for aquatic plants that serve as food for manatees were measured every 40 m along both shores for the entire length of each watercourse. Such plants were considered part of the species' diet after finding feeding signs on them and interviewing local experts (i.e., former manatee hunters). These plants were classified in two groups: (1) *emergent vegetation*, composed of aquatic grasses such as *Panicum maximum*, *Oryza latifolia*, *Hymenochne amplexicaulis* and *Brachiaria* sp., plus terrestrial grasses that grew on the shores; and (2) *floating vegetation* or water hyacinth (*Eichhornia crassipes*). Two measures of relative abundance were obtained for each group: (1) *presence of vegetation*: the proportion of points with presence of vegetation along a transect; and (2) *vegetation cover*: the product of the previous measure by the average width of vegetation banks found within each unit. Estimates of presence and cover for each group of aquatic vegetation were added to obtain total values of *aquatic vegetation* on each watercourse.

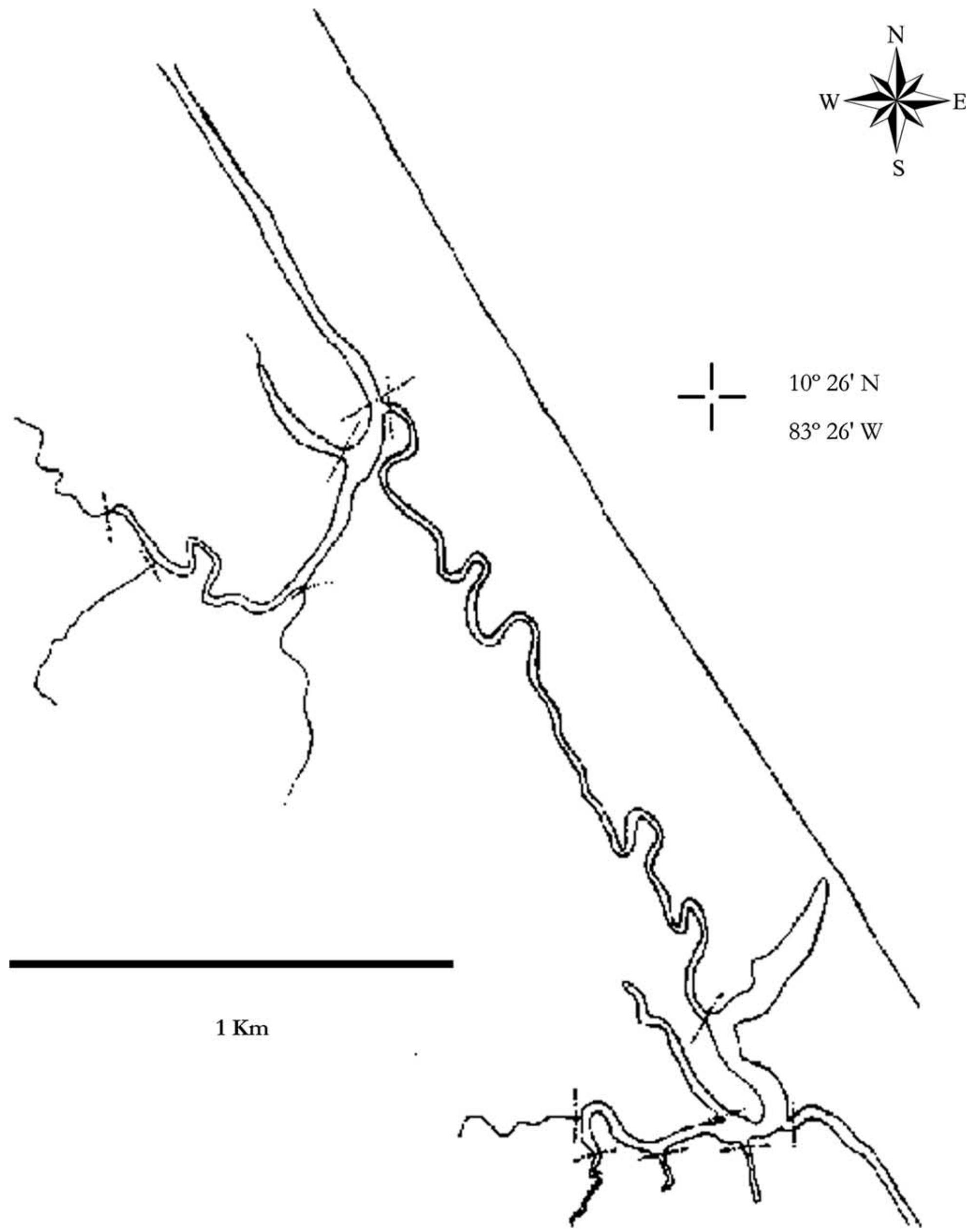

Fig. 2. Detailed section of the study area showing limits between sample units (i.e., watercourses).

Presence or absence of forest cover on the shore was measured every 40 m. In the case of lagoons surrounded by grass marshes, forest presence was considered positive when the forest line was closer than 50 m from open water. Boat traffic was assessed through interviews to local boaters and field observations. I used this information to classify each watercourse within each of the following categories: (1) *low traffic*: areas inaccessible to boats or very seldom visited, (2) *medium traffic*: marginal routes and fishing spots for motorboats, and (3) *high traffic*: main routes for aquatic transportation. Coordinates of the central point for each unit were obtained through a GIS database made with ArcView software.

2.3. Use of watercourses by manatees

Three sources of information were used to determine the presence of manatees in watercourses: direct sightings, feeding signs, and reported sightings. To observe manatees, I carried out silent stalks on a fiberglass canoe throughout their potential feeding areas early in the morning (5:00–8:00 h), late afternoon (16:00–18:00 h), or during clear nights. Such method was suggested by local former manatee hunters as the optimum way to see these animals. I carried out 49 silent stalks during 96 h, visiting all watercourses reported as being the most used by manatees. The number of sightings achieved with this technique was insufficient to assess the actual distribution of the species within the study area, and these data were pooled with the reported sightings as explained below.

Feeding signs left by manatees on emergent and floating vegetation are typical, with no other species leaving similar ones. Each watercourse was surveyed at least twice after feeding signs with at least one month lag between surveys. Based on this method, a watercourse was considered to be used by manatees if feeding signs were found there.

To compile reports of manatee sightings, 257 short interviews were conducted among boaters, fishermen, tourist guides, peasants, park rangers, hotel managers and border guards. Human presence in the study area is high enough to assume that these interviews could detect potential sightings through all of it. In spite of differences in the availability of informants throughout the study area, interview effort was directed to avoid sharp biases among places and villages. Questions asked in each interview included if they had seen a manatee, location, date, hour and a short description of what they had seen to assess report credibility. Combining information from interviews with direct sightings, a unit was classified as positive for manatees if there was a direct sighting or more than one report. Watercourses with no reports were assigned a negative value for manatee use, and units with only one report were considered as dubious and excluded from the analysis.

Three final classifications of watercourses regarding the presence of manatees were obtained: one based on feeding signs, another based on direct and reported sightings, and a last one that considered a watercourse as containing manatees if it had a positive value in any of the two previous systems. Those watercourses that were so remote as to preclude visits from local people or where feeding signs were impossible to observe because of a lack of aquatic vegetation were excluded from the analysis since it was considered that sampling intensity was insufficient to assign them an appropriate value. Therefore, from the 111 units in which the study area was originally divided, 87 had values assigned regarding habitat variables and presence of manatees.

2.4. Statistical analysis

Data analysis was carried out in three steps: (1) environmental characterization of the study area and its two corresponding sectors, (2) development of GLMs for all the study area, (3) development of GLMs for the two sectors, and (4) testing the predictive power of these models and their potential for extrapolation into other areas.

Pearson correlation tests were developed to study relations between habitat variables. Correlations were obtained for the entire area and both sectors. To verify that habitat conditions differed between the two sectors that comprised the study are, median values for each environmental variable were compared between both areas using Mann–Whitney tests (Siegel and Castellan, 1988). To assess differences in relations between variables for the two sectors, coefficients of correlation were normalized to z, and differences in z values between areas were compared with T tests (Sokal and Rohlf, 1981).

To relate the presence of manatees with habitat variables, I developed Generalized Linear Models with program GLIM 3.77 (McCullagh and Nelder, 1983; Payne, 1985). Given that data on manatee presence behave as a binary variable (i.e., presence vs. absence), I chose Logistic regression models with a binomial error and a logistic link function (Crawley, 1993).

To improve our understanding of relations between predictor variables (i.e., habitat factors) and the dependent variable (i.e., use of watercourses by manatees), I developed univariate Logistic regression models for the whole study area before developing multivariate ones. Univariate models had the same structure as explained above though their lineal predictor included only one variable. Each predictor variable was divided into six classes and bivariate graphs were plotted with each of these variables and data on manatee presence. If these graphs suggested a curved response a quadratic function was tested initially, and a cubic term was then tested to ensure that a higher order polynomial was not necessary to improve the model. Square root and logarithmic transformations of all predictor variables were also tested to improve lineal relationships.

Multivariate model fitting followed the branching forward stepwise procedure used by Donázar et al. (1993). Each variable was tested for significance in turn and the one that contributed the largest significant change in deviance from the null model was selected and fitted. This procedure was used to fit other variables to the model until the inclusion of no further variables caused a significant change in residual deviance using a 5% level of significance. Alternative models were also built fitting the second and third most significant variables over the null model. This branching procedure could eventually produce a set of different models, but in this study they all converged in the same final model or in alternative models with the same biological meaning. Three different multivariate models for the whole study area were developed depending on the method used to assign values to the response variable (i.e., feeding signs, sightings or both combined).

A residual analysis was undertaken for the final models (Nicholls, 1989). Standardized residuals were plotted against fitted values for possible deviations from initial model assumptions. Observations with high influence were re-examined for potential data errors and outliers. Thus, I found that the value of manatee use given by informants to one highly influential watercourse could have been mistaken due to confusion in how it was named locally. Exclusion of this unit from models caused a significant improvement, and therefore it was removed from all final models.

Fitted values for the Logistic regression models were interpreted as the probability (p) that manatees were using a watercourse. Units with $p > 0.5$ were classified as used and those with $p < 0.5$ were classified as absent (Donázar et al., 1993). Comparing model predictions with actual results, I tested the potential for the three models to predict presence of manatees using habitat data. The percentage of improvement from a random classification was obtained and tested using Kappa values (Siegel and Castellan, 1988; Wilkinson et al., 1992, p. 667). Through this method, I identified which of the three final habitat models – each using a different method to assess presence of manatees – predicted their presence with the highest accuracy.

Once a best model was identified, I wanted to validate its predictive power in other areas. Due to a lack of data from other regions I used an indirect method to achieve this validation. I used the same model-fitting procedure explained above to develop multivariate models for each one of the two different sectors. A habitat model developed in each sector was used to predict the presence of manatees in the other and this was tested using Kappa values. At this stage the response variable that produced the best model for the whole area and that made the most biological sense was chosen for model fitting. Through this method I tested the assumption that a GLM developed in a region could be used to predict the presence of manatees in another area.

3. Results

Table 1 shows basic statistics for habitat variables measured in the study, excluding boat traffic, which was measured in three ranks. Many habitat variables were correlated in the study area, as it is typical of aquatic ecosystems (Table 2). Emergent and floating vegetation were not distributed in a similar manner and there was a negative correlation between both kinds of aquatic vegetation. Water temperature and visibility, floating vegetation, and forest cover were positively correlated, while water current, emergent vegetation, watercourse width and boat traffic were also positively correlated among them, but negatively to the previous group. The variable that showed the lowest correlation with all other variables was the abundance of aquatic vegetation (i.e., total manatee food).

Both sectors of the study area showed different patterns regarding mean habitat values and relationships among variables. The northern sector contains wider watercourses with more turbid and faster flowing waters, and less forest cover than the southern sector (Table 3). The former sector harbored almost no floating vegetation while floating plants predominated over emergent ones in the south (Table 3). Relationships among habitat factors were similar in the south area compared to the whole study area, but the northern sector showed some differences regarding these relationships. Northern watercourses tended to be shallower ($T = 2.15$, $p < 0.05$) and to have less aquatic vegetation ($T = 2.179$, $p < 0.05$) in forested areas, while the opposite happened in the south. Due to the presence of semi-still lagoons, water tended to be warmer in the wider wetlands of the North than in the South, where the wider watercourses were large rivers with fast flowing and, therefore, cooler waters ($T = 2.19$, $p < 0.05$).

I saw manatees in seven occasions and heard them breathing at night twice. This data served to verify the presence of the species in only five watercourses, not providing a good estimate of the species' distribution. Data gathered through reports and feeding signs gave a much more complete picture of manatee distribution. Even though local fishermen often labor in coastal waters, they never reported seeing manatees in them. I compiled 305 reports of sightings and found feeding signs in 112 occasions in 37 different watercourses. Table

Table 1
Basic statistics for habitat variables measured in the study, excluding boat traffic, which was measured in three ranks

Habitat variable (measuring unit)	Minimum average observed value	Maximum average observed value	Average value	SD
Watercourse depth (m)	0.93	7.80	3.03	1.22
Water visibility (cm)	20	240	92.77	59.3
Temperature (°C)	24.6	29.9	27.1	1.08
Water current (m/min)	0.0	162	22.7	25.6
Watercourse width	10	473	90.8	99.4
Presence of emergent vegetation	0.0	100	30.1	30.5
Cover of emergent vegetation	0.0	400	50.6	73.8
Presence of floating vegetation	0.0	100	19.3	30.2
Cover of floating vegetation	0.0	3000	103	364.6
Presence of aquatic vegetation	0.0	165	47.9	35.9
Cover of aquatic vegetation	0.0	3000	151.9	363.7
Forest cover	0.0	100	65.2	37.6

Table 2
Correlation matrix for the habitat variables used in the study ($n = 87$)

	Water depth	Water visibility	Temperature	Water current	Watercourse width	Presence of emergent vegetation	Cover of emergent vegetation	Presence of floating vegetation	Cover of floating vegetation	Presence of aquatic vegetation	Cover of aquatic vegetation	Forest cover	East coordinates	North coordinates	Motorboat traffic
Water depth	1.000														
Water visibility	0.345**	1.000													
Temperature	0.234*	0.482***	1.000												
Water current	−0.097	−0.416***	−0.444***	1.000											
Watercourse width	0.207	−0.253*	0.046	0.249*	1.000										
Presence of emergent vegetation	−0.149	−0.161	−0.141	0.157	−0.068	1.000									
Cover of emergent vegetation	−0.084	−0.344**	−0.171	0.221*	0.314**	0.601***	1.000								
Presence of floating vegetation	0.213*	0.498***	0.301**	−0.497***	−0.218*	−0.243*	−0.330**	1. 000							
Cover of floating vegetation	0.221*	0.480***	0.318**	−0.362**	−0.076	−0.253*	−0.203	0.811***	1.000						
Presence of aquatic vegetation	0.043	0.002	0.033	−0.126	0.139	0.411***	0.597***	0.332**	0.378***	1.000					
Cover of aquatic vegetation	0.113	0.134	0.089	−0.183	0.094	0.336**	0.490***	0.480***	0.492***	0.970***	1.000				
Forest cover	0.204	0.686***	0.470***	−0.297**	−0.410***	−0.367***	−0.462***	0.343**	0.355**	−0.168	−0.053	1.000			
East coordinates	−0.093	0.204	−0.085	−0.206	−0.231*	−0.254*	−0.142	0.359**	0.447***	−0.006	0.05	0.143	1.000		
North coordinates	0.031	−0.070	0.209	0.179	0.278**	0.201	0.108	−0.376***	−0.434***	−0.072	−0.104	−0.007	0.000	1.000	
Motorboat traffic[a]	−0.240	−0.47	−0.133	0.378	0.373	0.026	0.039	−0.233	−0.242	−0.296	−0.344	−0.418	−0.072	0.142	1.000

All correlations measured through Pearson tests, except those including boat traffic, which were measured through Spearman tests.
[a] Spearman correlations do not include level of significance.
* $p < 0.05$.
** $p < 0.01$.

Table 3
Habitat variables that showed the most significant differences between the two sectors that compose the study area

Habitat variable (measurement unit)	Mean value for south sector (n = 49)	Mean value for north sector (n = 38)	p
Water visibility (cm)	107.1	72.4	<0.01
Water current (m/min)	29.6	42.4	0.061
Watercourse width (m)	54.9	141.7	<0.01
Presence of emergent vegetation (%)	19.1	45.7	<0.001
Cover of emergent vegetation (% × m)	34.2	73.9	<0.001
Presence of floating vegetation (%)	32	1.4	<0.001
Cover of floating vegetation (% × m)	174.8	3.1	<0.001
Forest cover (%)	72.2	55.3	<0.05

Differences tested through Mann–Whitney tests.

4 compiles data on manatee presence by method and area. There was a high level of agreement between classifications based on sightings and feeding signs. Seventy six percent of the watercourses gave the same value of manatee presence through both methods, other 19.5% were classified as positive areas based on sightings but as negative based on signs, and the last 4.5% were watercourses classified as positive based on signs but where the presence of manatees could not be confirmed through interviews or direct sightings. Jiménez (1999, 2000) gave detailed information on the species distribution in the study area.

Table 4
Data summary regarding presence of manatees in the study area

Method	Area					
	Study area (n = 87)		Southern sector (n = 49)		Northern sector (n = 38)	
	Present	Absent	Present	Absent	Present	Absent
Feeding signs	37	50	18	31	19	19
Sightings	50	37	25	24	25	13
Both	54	33	27	22	29	9

Presence of the species was determined through feeding signs, reported and direct sightings, and a combination of both methods.

Table 5
Univariate GLMs that relate presence of manatees with habitat variables

Habitat variable	Study area (n = 86)	Southern sector (n = 49)	Northern sector (n = 37)
	Slope	Slope	Slope
Water depth	0.51[a*]	0.616[*]	n.s.
Water visibility (ln)	1.35[***]	2.303[***]	n.s.
Temperature	1.377[***]	1.481[***]	0.93[*]
Water current	−0.019[***]	0.05[***]	n.s.
Watercourse width	0.012[***]	n.s.	0.015[**]
Presence of emergent vegetation	n.s.	−2.966[*]	3.9[**]
Cover of emergent vegetation	n.s.	n.s.	4.01[**]
Presence of floating vegetation	1.72[*]	3.26[**]	n.s.
Cover of floating vegetation	0.7[**]	1.091[***]	n.s.
Presence of aquatic vegetation	1.7[*]	1.14[*]	3.865[**]
Cover of aquatic vegetation	0.79[***]	0.64[**]	3.88[**]
Forest cover	1.89[***]	5.51[***]	n.s.
Motorboat traffic	n.s.	$k_a = 1.792$[*b] $k_2 = -1.792$[*] $k_3 = -2.033$[*]	n.s.
East coordinates	n.s.	-7.8×10^{-5}[**]	n.s.
North coordinates	2.7×10^{-5}	6×10^{-5}[**]	2×10^{-5}[*]

Error structure is binomial and link function is logistic. Presence of manatees was determined through feeding signs and sightings combined.

[a] GLM is a regression with structure: $\ln[p/(1-p)] = a + bx$.

[b] GLM is an ANOVA with structure: $\ln[p/(1-p)] = k_1x_1 + k_2x_2 + k_3x_3$, where $x_1 = 1$ in low traffic and $x_1 = 0$ in other kind of traffic, $x_2 = 1$ in medium traffic and $x_2 = 0$ in other kinds, and $x_3 = 1$ in high traffic and $x_3 = 0$ in other kinds.

[*] $p < 0.5$.

[**] $p < 0.01$.

[***] $p < 0.001$.

Univariate GLMs identified relations between each habitat variable and the presence of manatees (Table 5). The chances for a watercourse being used by manatees in the study area increased with water depth, temperature and visibility, watercourse width, and cover of floating and aquatic vegetation, while chances decreased with water current. Univariate models developed in the southern sector showed a similar pattern than those developed for the whole study area, but GLMs for the northern sector only detected water temperature, watercourse width and abundance of emergent and aquatic vegetation as significant variables. It is noteworthy that boat traffic is associated with a decrease in the presence of manatees only in the southern sector.

I developed three final multivariate GLMs that related significant habitat variables with presence of manatees based on sightings, signs and both methods combined (Table 6). Models based on sightings or sightings combined with signs produced the best results regarding the percentage of explained residual deviance and their predictive power. These two models showed that manatees tend to use wide watercourses with clean and warm waters – though not the warmest –, abundant emergent vegetation and forest cover (Table 6). Models based on sightings included a negative selection towards the East (i.e., the coastline), while models based on sightings and signs included a quadratic term of the East variable indicating that manatees tended to be close to the coast but not on the coastline. The GLM based on feeding signs shows a positive relation between water depth, cover of aquatic vegetation, latitude, and presence of manatees (Table 6).

In spite of the fact that the GLM based on sightings predicted a slightly higher percentage of watercourses with presence of manatees than the model based on both sightings and signs (Table 6), it can be seen in Table 4 that this method classified as negatives four of the watercourses where the presence of manatees was confirmed through signs. Therefore, I determined that a combination of sightings and signs was the measure of manatee presence that made both the most statistical and biological sense and it was chosen to develop GLMs for the two sectors of the study area. Thus, manatees selected mildly warm and wide watercourses with abundant emergent vegetation in the northern sector while in the south they preferred slow moving wide watercourses with abundant forest on their shores (Table 7). Models developed for each of the two sectors of the study area showed a degree of adjustment and a predictive power similar to GLMs developed for the whole area (Table 7). When each of these two models was used in the other sector to predict presence of manatees it produced better results than just by random classification (Table 7). However, they resulted in a decrease in explained deviance and predictive power compared to when they were used in the sector where they were developed.

Table 6
Description and assessment of GLMs (logistic regressions) that relate habitat variables with the presence of manatees in the study area

	Presence assessed through sightings ($n = 86$)			Presence assessed through feeding signs ($n = 87$)			Presence assessed through sightings and feeding signs ($n = 86$)		
		Parameter estimate	Standard error		Parameter estimate	Standard error		Parameter estimate	Standard error
Model structure	Constant	−1663	672.3	Constant	−9.61	3.37	Constant	−2856	1140
	Water temperature	120	48.78	Water depth (ln)	1.63	0.79	Water temperature	142	59
	Water temperature (quadratic)	−2.156	0.884	Cover of aquatic vegetation (ln)	1.15	0.29	Water temperature (quadratic)	−2.562	1.1
	Watercourse width (ln)	6.183	2.04	North coordinates	2.9×10^{-5}	1.1×10^{-5}	Watercourse width (ln)	7.91	2.8
	Presence of emergent vegetation	11.47	4.671				Presence of emergent vegetation	15.9	6.35
	Forest cover	9	3.74				Forest cover	9.7	4.1
	Water visibility (ln)	4.28	1.73				Water visibility (ln)	4.73	2.19
	East coordinates	-9.22×10^{-5}	3.3×10^{-5}				East coordinates	2.9×10^{-3}	1.7×10^{-3}
							East coordinates (quadratic)	-2.6×10^{-9}	1.5×10^{-9}
% of explained deviance	73			28			79		
% of correct classification	96			75			93		
Kappa	0.903^{***}			0.48^{***}			0.85^{***}		

Error structure is binomial and the link function is logistic.
*** $p < 0.001$.

Table 7
Description and assessment of GLMs (logistic regressions) that relate habitat variables and presence of manatees for the two sectors of the study area

	South sector ($n = 49$)			Northern sector ($n = 37$)		
		Parameter estimate	Standard error		Parameter estimate	Standard error
Model structure	Constant	−10.97	5.26	Constant	−1266	786
	Water current	−0.07	0.03	Water temperature	91.06	57.5
	Watercourse width	0.077	0.04	Water temperature (quadratic)	−1.64	1.05
	Forest cover	11.7	4.93	Cover of emergent vegetation	8.37	3.75
				Watercourse width	0.046	0.03
Assessment of GLM predictive power inside its sector	$n = 49$			$n = 37$		
% of explained deviance	71			73		
% of correct classification	94			92		
Kappa	0.874***			0.803***		
Assessment of GLM predictive power for the other sector	$n = 37$			$n = 49$		
% of explained deviance	36			35		
% of correct classification	78			83		
Kappa	0.38*			0.57***		

Presence was assessed through sightings and feeding signs combined. Error structure is binomial and link function is logistic.
* $p < 0.05$.
*** $p < 0.001$.

4. Discussion

Low water visibility and a shy behavior confirmed by local informants made extremely difficult to determine the distribution of manatees in the study area based on direct observations. Prior to this research and related ones (Jiménez, 1999, 2000), Reynolds et al. (1995) unsuccessfully used aerial surveys to determine manatee distribution in the same region. Similar problems occur when trying to assess the conservation status of other threatened species and, therefore, it is important to find methods that provide both reliable and feasible estimates of the distribution of certain secretive species. In this study we have seen how the combination of extensive interviews and surveys of manatee feeding signs provided a good assessment of the species' distribution in Northern Costa Rica and Southern Nicaragua. Two facts support that the estimated distribution is a good approximation to the real distribution. First, there is a high degree of agreement on the distributions obtained through both methods in spite that they came from very different sources: one method was based on what local people transmitted and the other was based on signs left by the animals' activity. A priory, the first method was less objective and subject to more errors than the second. Second, models developed in this study showed that habitat variables could predict – with an excellent degree of adjustment – distributions that were estimated through both methods. The fact that habitat variables are good predictors of estimated distributions also indicate that these estimates were good approximations to the actual distribution.

A general pattern explaining the relationship between habitat and manatee distribution comes out from the final GLMs developed for the study area and its two sectors (Tables 6 and 7). First, almost every model identified the abundance of aquatic vegetation or, in this case, food availability – expressed as emergent or overall aquatic vegetation, or measured as lineal presence or bidimensional cover – as a significant factor explaining presence of the species. Second, manatees are selecting watercourses with warm waters (though not the warmest), high depths, and slow currents, all factors being positively correlated among them and with water visibility (Tables 3, 6 and 7). Other factors that explain presence of the species are watercourse width and forest cover, although this variable did not turn out significant in the northern area. Water salinity is a factor that could affect the distribution of manatees (Husar, 1977; Hartman, 1979; Powell et al., 1981; Colmenero-R and Zárate, 1990; Lefevbre et al., 2001; Olivera-Gómez and Mellinck, 2005) but it was not included in the models because local watercourses in the study area were mostly freshwater wetlands.

Differences in watercourses present in the two sectors of the study area explain why sectorial GLMs identified different habitat variables that explain manatee presence. The southern sector is comprised mostly of elongated lagoons, and slow-moving rivers, and creeks surrounded by rainforest. All of them are covered by abundant banks of floating vegetation and some patches of thin emergent grasses that give shape to a landscape similar to the black-water wetlands described as optimum habitat for the Amazonian manatee (*Trichechus inunguis*) during the dry season (Montgomery et al., 1981; Timm et al., 1986; Montenegro, 1994; Weber Rosas, 1994). Within the southern sector of the study area those watercourses that best fitted the characteristics included in its model were lagoons since they are wide, with minimum current and abundant forest cover (Table 7).

In the northern sector, besides the presence of watercourses that are very similar to those of the south, there is another type of wetland that consists of open lagoons surrounded by grass marshes instead of rainforest. In these lagoons, thick grasses (i.e., *Panicum maximum* and *Paspalum repens*) replace floating vegetation and thin grasses (i.e., *Brachiaria* sp.) that dominate in the south. Such open lagoons show those characteristics identified in the northern GLM as determinant for manatee presence: warm and wide watercourses with abundant emergent vegetation (Table 7). Therefore, manatees are selecting lagoons over other watercourses in both sectors. These are elongated and surrounded by rainforest in the south, and wide and surrounded by open marshes in the north.

GLMs relating habitat variables with presence of manatees were robust both for all the study area and its two sectors, and percentages of original deviance explained by them (71–79%) were higher than what it is usually found in other habitat-use models, which typically range below or around 50% of this deviance (Morrison et al., 1992, p. 260). Models developed in this study showed a very high predictive power, which allowed them to accurately classify more than 90% of local watercourses. A similar study achieved another high, though slightly lower (i.e., 77%), capability to predict presence of manatees using habitat variables (Olivera-Gómez and Mellinck, 2005).

The fact that the distribution of manatees is so well explained by habitat variables implies that there is a low incidence from other ecological factors such as intra- and interespecific competition and predation. This result concurs with studies that describe an absence of defined social structure and territorial behavior for the species and the existence of very few competitors and natural predators (Hartman, 1979; Reynolds, 1981; Reynolds and Odell, 1991). It is also noteworthy an absence of present significant hunting pressure on the species that would deter manatees from colonizing all available habitats in the study area (Jiménez, 1999, 2000). The facts that manatees are well distributed throughout the region and they are present in the same places where they were seen several decades ago (Reynolds et al., 1995; Jiménez, 2000; O'Donnell, 1981), do not support the assumption that present distribution, although not abundance, might be affected by former hunting.

Positive selection of watercourses with abundant forest cover on their shores points at deforestation as a possible threat on the species survival in tropical rainforest habitats. During the study, I noticed how the absence of trees near the shores of fast flowing rivers produced high walls on the edges that precluded manatees from feeding on them. Forest cover was not detected as a significant habitat variable in the northern area and this was due to the existence of open lagoons surrounded by grass marshes. Forests surrounding these lagoons tended to be more than 50 m away from the water and therefore they passed undetected with the criteria used in this study. However, this does not mean that forests are not necessary for the long-term existence of the open lagoons preferred by manatees. Historical data support the fact that forest clearing in the river shores might destroy manatee habitat: two large rivers were manatees were seen in the late XIX century (i.e., Sarapiquí and San Carlos) showed an equal absence of trees and manatees in the next century (O'Donnell, 1981).

Loss of depth in local watercourses from increasing sedimentation might become another possible threat for the species conservation, taking in account that they are selecting deep wetlands over shallow ones. Smethurst and Nietschmann (1999) and Jiménez (2000) described how local watercourses have been loosing depth during the last decades. However, shallow areas are still rare in the region and mostly centered around river mouths. Such effect of sedimentation might explain the present absence of manatees in the Parismina river where manatees were seen some decades ago and shoals have become much more common and larger in size during the last 10 years (Jiménez, 2000).

Smethurst and Nietschmann (1999) also cited boat traffic as another threat for the species, describing a "strong correlation" between the species' presence and the absence of boat traffic, though they did not carry an statistical analysis that could support such statement. The results of the models developed in this study do not support this point. Boat traffic only resulted as a significant variable when left by itself in a univariate model for the southern sector (Table 5). Whenever traffic was included with other habitat variables in a GLM, it lacked any significant effect on manatee presence. Though local informants repeatedly pointed boat traffic as one of the causes of the decline of manatees in previous decades, I found frequent signs of manatees feeding in areas with the highest traffic (i.e., village surroundings). This fact and the results of the GLMs indicate that boat traffic is not displacing manatees from their feeding areas, although it could be affecting the species at a level of habitat selection that has not been detected in this study (Johnson, 1980; O'Shea, 1995). For example, Jiménez (1999) noted that local manatees tend to develop nocturnal activity in areas with high human presence, and other authors report a similar strategy in other areas (Rathbun et al., 1983; Reynolds and Odell, 1991; Powell, 1996). However, recent increase in manatee mortality within the Tortuguero National Park points to boat traffic as the single biggest threat to manatee conservation in the area (Jiménez, unpublished data).

It has been argued that a habitat use model developed in any region has limited predictive power in other areas (Morrison et al., 1992). Results of this study show that models developed in one area can help us classify potential manatee habitat in other regions. However, there is a loss of predictive power when models are used outside the area where they were developed, which highlights the caveats of using "imported models" (Morrison et al., 1992). Models like those developed for the study area could improve our ability to identify areas used by manatees or areas that could host the species for potential reintroductions or translocations. The utility of such models would increase if they were matched with remote sensing methods that could assign relevant habitat values to wetlands in large regions with difficult access.

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