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Authors: Hernández, Iván Sandoval, Marín, Mahmood Sasa, Monrós González, Juan S., Bolaños Montero, Juan R., and Ramírez, Juan Sánchez

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# Potential habitat of the American crocodile (*Crocodylus acutus*: Reptilia: Crocodylidae) and identification of areas of interaction with humans in Costa Rica

Iván Sandoval Hernández<sup>1,3,\*</sup>, Mahmood Sasa Marín<sup>2</sup>, Juan S. Monrós González<sup>3</sup>,  
Juan R. Bolaños Montero<sup>4</sup>, Juan Sánchez Ramírez<sup>4</sup>

<sup>1</sup> Escuela de Ciencias Biológicas. Universidad Nacional. Heredia, Costa Rica.

<sup>2</sup> Instituto Clodomiro Picado, Universidad de Costa Rica.

<sup>3</sup> Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, Spain.

<sup>4</sup> Asociación de Profesionales en Crocodílicos, Costa Rica.

\* Corresponding author. Email: ivan.sandoval.hernandez@una.ac.cr

**Abstract.** Crocodylians are known to interact substantially with humans. Conflicts are observed when both species share a habitat and are documented worldwide. In Costa Rica, this conflict has been detected along with increases in human activities. For this reason, we undertook a study to identify potential crocodile habitats and the areas of interaction with humans on the Pacific and Caribbean coasts and the Northern Zone of Costa Rica. This work was performed during 2019 and 2020 in both regions, and determination of the potential habitat of crocodiles was made through analysis of the elevation, topography, drainage net, flooding areas, mangrove areas, and rivers and their outlets. To identify areas of human–crocodile interactions, a map of the potential habitat was used and changes to those habitats were analyzed (e.g., road density, population density, and the density of the populated core). The relationship between species was established to predict interaction hotspots between humans and crocodiles. The habitats with high potential for crocodiles on the Pacific slope correspond to 18% of the study area, and the medium potential habitat to 54%. Within the Central Pacific, there are few areas at higher elevations or with a large index of urbanism; these low potential habitats represent 27% of the study area. In the Central Pacific, the high and medium potential habitats together represent 72% of the study area. On the Caribbean slope, the high potential habitat was identified in areas closer to the coast mainly in the North and Central Caribbean (corresponding to 29% of the study area), while 66% of the study area was labeled as medium potential habitat. In the Northern area, most of the habitat was identified as medium potential, there being only small fragments recognized as high potential habitat. In the Northern Zone and Caribbean Zone, the areas at higher elevation with some land development were identified as low potential habitat (4%). Importantly, 96% of the area of the Caribbean slope and the Northern Zone were identified as high or medium potential habitat.

**Keywords.** Habitat loss; Human activities; Human–crocodile conflict; Urbanism.

**Resumen.** Se sabe que los cocodrilos son un grupo que interactúa intensamente con los humanos. Los conflictos se observan cuando ambas especies comparten el hábitat lo cual está documentado en todo el mundo. En Costa Rica, este conflicto se ha detectado en zonas que presentan actividades humanas. Por esta razón, identificamos el hábitat potencial del cocodrilo, además identificamos las áreas de interacción con humanos en las costas del Pacífico, Caribe y la Zona Norte de Costa Rica. Este trabajo se realizó durante 2019 y 2020 en ambas regiones, y la determinación del hábitat potencial de los cocodrilos se realizó mediante el análisis de la altitud, topografía, red de drenaje, áreas de inundación, áreas de manglares y ríos y sus desembocaduras. Para identificar áreas de interacciones entre humanos y cocodrilos, se utilizó un mapa del hábitat potencial y se analizó la alteración del hábitat (densidad de carreteras, densidad de población y densidad de población). La relación entre especies se estableció para predecir puntos críticos de interacción entre humanos y cocodrilos. Los hábitats con alto potencial para cocodrilos en la vertiente del Pacífico corresponden al 18% del área de estudio, el hábitat de potencial medio (54%). Dentro del Pacífico Central hay pocas áreas de elevada altitud o con un evado índice de urbanismo, estos son hábitats de bajo potencial y representan el 27% (del área de estudio). En el Pacífico Central, los hábitats de potencial alto y medio juntos representan el 72% (del área estudiada). En la vertiente del Caribe, el hábitat potencial alto se identificó en áreas más cercanas a la costa principalmente en el Caribe Norte y Central (29% del área de estudio), mientras que el 66% del área se etiquetó como hábitat de potencial medio. En la Zona Norte, la mayor parte del hábitat se identificó como de potencial medio, habiendo solo pequeños fragmentos reconocidos como hábitat potencial alto. En la Zona Norte y la Zona del Caribe, las áreas de mayor altitud con algún desarrollo territorial fueron identificadas como hábitat de bajo potencial (4%). Es importante destacar que el 96% del área de la vertiente del Caribe y la Zona Norte se identificaron como hábitat de alto o mediano potencial.

## INTRODUCTION

Crocodylia Owen, 1842 is composed of 23 species distributed in the tropical and subtropical zones. Among these species, 14 are crocodylids, 8 are alligatorids, and 1 is a gavialid (Ross, 1998; Leenders, 2019). In the Americas, *Crocodylus Laurenti*, 1768 is represented by four spe-

cies: *Crocodylus acutus* (Cuvier, 1807), *C. moreletii* (Duméril and Bibron, 1851), *C. intermedius* (Graves, 1819), and *C. rhombifer* (Cuvier, 1807) (Franz et al., 1985; Ray et al., 2004). The American crocodile, *Crocodylus acutus*, is broadly distributed in the coastal regions of the continent (Kushlan and Mazzotti, 1989; Thorbjarnarson, 1989), from the southern part of the United States (Florida) to north-

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ern South America (Colombia and Venezuela) on the Caribbean Sea slope, and from Sinaloa in Mexico to Tumbes in Peru on the Pacific Ocean slope; their distribution also reaches the Greater Antilles islands in the Caribbean Sea (Thorbjarnarson, 1989). This species commonly inhabits rivers, lakes, and freshwater or saltwater swamps (Ross, 1998; Leenders, 2001; Savage, 2002).

In Costa Rica, *Crocodylus acutus*, is found along both coasts, as well as inland, with populations concentrated on the Pacific side. Despite the prevalence of this species, few investigations have identified potential crocodile habitats for the entire country, and those that exist are concentrated in the Central Pacific. Crocodiles are simply reported to inhabit rivers, lakes, swamps, estuaries, and mangroves at elevations less than 700 m above sea level (m a.s.l.), as well as coastal waters (Bolaños et al., 1997; Porras Murillo, 2004., Sandoval Murillo et al., 2020; Porras Murillo and Mata Cambroner, 2020).

Woodroffe et al. (2005a) observed that human-wildlife conflicts are a growing problem worldwide, noting that crocodilians are one of the major groups involved (Lamarque et al., 2009; Amarasinghe et al., 2015). Indeed, crocodilians are noted for being a group involved in a large number of interactions with humans worldwide, because humans and crocodiles often share habitats (Vanwersch, 1998; Ferguson, 2004; McGregor, 2005; Woodroffe et al., 2005b; Langley, 2005; Caldicott et al., 2005; Aust et al., 2009; Lamarque et al., 2009; Amarasinghe et al., 2015; Pooley, 2017; Pooley et al., 2021), and conflict can ensue even when changes to habitats by humans result in a reduction in crocodile population size (Mazzotti et al., 2007; Murray et al., 2015).

In Costa Rica, at the beginning of the 1990s, crocodile numbers appeared to have increased along with an increase in attacks against humans. These incidents have been associated with the increase of the interactions between humans and crocodiles, probably because of humans entering/inhabiting crocodile habitats (Bolaños, 2012b). Sandoval Murillo et al. (2019, 2020) performed an analysis of crocodile habitat in Costa Rica's Central Pacific after identifying that in recent years human activities in the zones that were identified as optimal for crocodile presence have increased.

In Costa Rica's Pacific region, interactions between humans and crocodiles occur in areas where there is a wide variety of anthropogenic activities (Porras, 2007; Morales, 2013; Orozco, 2015; Sandoval-Hernández et al., 2017; Sandoval Murillo et al., 2019; 2020; Porras Murillo and Mata Cambroner, 2020) and the crocodile population has recovered successfully (Sánchez-Ramírez, 2001; Bolaños, 2012a, b; Orozco, 2015; Sandoval-Hernández et al., 2017). *Crocodylus acutus* is abundant in zones with a high index of land development, presenting a pattern of coexistence with human populations due to the reduction of forest coverage and the growth of the human population. In several instances, these zones are the locations of important tourism (King et al., 1990; Sánchez et al., 1996; Bolaños et al., 1997; Sánchez-Ramírez, 2001; Escobedo-Galván, 2008; Barrantes, 2010; Bolaños, 2011; Valdelomar et al., 2012; Morales, 2013; Orozco, 2015).

In addition to the protection given to them by law in Costa Rica, because crocodiles are opportunistic, they can benefit from human demographic growth, the advancement of the agricultural frontier, and urban pressure. Crocodiles often feed on domestic animals in areas with many human settlements, a situation that could diminish intraspecific competition in some of the crocodile's habitats (Valdelomar et al., 2012; Carrillo-Rivera, 2013; Morales, 2013; Sandoval-Hernández et al., 2017; Sandoval Murillo et al., 2019; 2020).

The progressive encroachment of humans into multiple environments could be generating increased conflicts between humans and crocodiles as humans change the conditions of those environments inhabited by crocodiles, in turn affecting crocodile behavior (Bolaños, 2012a, b; Valdelomar et al., 2012; Morales, 2013; Peraza, 2015; Sandoval-Hernández et al., 2017; Sandoval Murillo et al., 2019). As such, we have identified the potential habitat of *Crocodylus acutus*, as well as the areas of interaction between crocodiles and humans in the Pacific and Caribbean and the Northern Zone of Costa Rica.

## MATERIALS AND METHODS

The present work was performed during 2019 and 2020 in areas recognized in the literature for being areas of crocodile distribution in and around Costa Rica. To determine the potential habitats of this reptile, including the elevation, topography, drainage net, flooding areas, mangrove areas, rivers and their outlets, and areas of land, we followed the methods described in Sandoval Murillo et al. (2019, 2020).

### Elevation

A digital elevation model (DEM) was generated from a curved vectorial layer on a scale of 1:50,000 of the topographic sheets from the Instituto Geográfico Nacional de Costa Rica (IGN; Ortiz, 2014). Subsequently, an interpolation was performed to obtain the DEM with the interpolation tool Topo to Raster (ArcGIS), which is based on the program ANUDEM (Hutchinson, 1988, 2011). The DEM was reclassified to obtain the range of elevations encompassing the optimal topographic conditions for *Crocodylus acutus*, which inhabits the coasts of both slopes, including the North Zone, at 0–700 m a.s.l. (King et al., 1990; Sánchez et al., 1996; Bolaños et al., 1997; Sánchez-Ramírez, 2001; Bolaños, 2011; 2012a, b; Orozco, 2015; Sandoval-Hernández et al., 2017; Sandoval Murillo et al., 2019; 2020). In the Caribbean and Northern Zone, we worked between 0–200 m a.s.l. because it is a flat area with no high elevations. For the landscape analysis, it was necessary to reclassify this variable into categories. Based on the probability of a crocodile encounter, the following classes were established: 0–233 m a.s.l. (high), 234–466 m a.s.l. (medium), and 467–700 m a.s.l. (low) for the Pacific coast; 0–87.1 m a.s.l. and 87.2–200 m a.s.l. for the Caribbean coast and the Northern Zone (Table 1).

### Drainage network

The drainage network was calculated for the study area using the river vectorial layer at a scale of 1:50,000 on the topographic sheets of the IGN (Ortiz, 2014). Subsequently, the sectors with the largest density of drainage per km<sup>2</sup> in the study area were determined using the Density/Kernel tool. Next, they were reclassified as: low (with a range between 0.074–1.195), medium (1.196–1.861), and high (1.862–3.053; Table 2).

### Flooding areas

Using the drainage network, we assigned the value 3 to sites susceptible to flooding and 1 to areas not exposed to this kind of event in the study area, according to the official demarcation carried out by the National Emergency Commission of Costa Rica and systematized in the database of flooding risk of the Atlas de Costa Rica (Ortiz, 2014; Table 2).

### Delimitation of areas with forest, mangrove, rivers, and their outlets

To perform the delimitation of areas with forest cover, bodies of water, mangrove, and swamped vegetation, rapid eye satellite images (2000–2015) were used at a scale of 1:25,000, followed by photointerpretation using the editing tools of the software ArcGIS 10.5 (ESRI, 2011).

**Table 1.** Digital elevation model classification for the potential habitats of the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

Caribbean elevation			
Clasifi_mdt	Weight_mdt	mdt_norm	Category
10–87.1	3	1	High
87.2–200	2	0.666667	Medium
Pacific elevation			
Clasifi_mdt	Weigh_mdt	mdt_norm	Category
1–233 m a.s.l.	3	1	High
234–466 m a.s.l.	2	0.666667	Medium
469–600 m a.s.l.	1	0.333337	Low

**Table 2.** Drainage network density (km<sup>2</sup>) and flooding areas of potential habitats for the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

Caribbean		
Classification	Weight	Normalization
0.074–1.195 low density	1	0.33
1.196–1.861 medium density	2	0.66
1.862–3.053 high density	3	1
Pacific		
Classification	Weight	Normalization
0.074–1.195 low density	1	0.33
1.196–1.861 medium density	2	0.66
1.862–3.053 high density	3	1
Flooding areas		
Classification	Weight	Normalization
No flood-prone	1	0.33
Flood prone	3	1

### Classification of land-use categories

The land-use layer comprised several categories of forest: in low descent, mangroves, swamped vegetation, bodies of water. They were assigned a weight according to the optimal conditions for the presence of crocodiles. The mangrove coating and swamped vegetation were given heavier weight. These land-use layers were utilized in the elaboration of a model of the potential habitat for crocodiles, while the categories pasture, farming, and urban had lower weights in the map of changing crocodile habitats (Table 3).

### Classification of potential habitat

With the classification performed, the summary of variables was used in ArcGIS 10.5 utilizing the normalized weights of each variable. With the field calculator, their values were added and divided by the number of variables, and then they were classified into three groups (via an equalitarian hierarchy between values) to obtain the potential habitat of each category inhabited by crocodiles (Table 4).

### Identification of human activities in crocodile habitat (potential habitat alteration)

For the identification of human activities within crocodile habitat, socio-environmental factors were analyzed: density of communication routes, population density, population density by district, and land use ‘coating’ (settlements, farming, and pastures). For the estimation of the degree of ground alteration, elements such as behavior in a timeline of different land-use coatings between 2000 and 2015 were analyzed, along with landscape indexes (see below), to determine the degree of fragmentation of the crocodile habitat.

**Table 3.** Classification of the land use categories for potential habitat of the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

Classification	Weight	Normalization	Category
High descent forest	1	0.33	High
Low descent forest	3	1	High
Mangrove	3	1	High
Swamped vegetation	3	1	High
Low descent pasture	2	0.66	Medium
High descent pasture	1	0.33	Low
Farming	1	0.33	Low
Urban	1	0.33	Low

**Table 4.** Classification of potential habitat for the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

ID	Sum Range	Categories
1	1–1.5	Low
2	1.51–2.24	Medium
3	2.25–3	High

**Land use**

Landsat satellite images at a resolution of 30 m were used for 2000 and 2015. A radiometric and atmospheric correction was applied to the images, according to Blondeau-Patissier et al. (2004). The processing of Landsat images was considered at two stages. The first was centered on the identification of the coating (urban

areas, bodies of water, farming, and mangroves), which was delimited by photointerpretation. For the second stage, the samples on the image were taken from each spectral firm of the missing classification coatings of some of land-use categories (forests on high descent, forests on low descent, pastures on high descent, and pastures on low descent), according to Sandoval et al. (2020; Table 5).

**Table 5.** Definition of the land use categories for potential habitat of the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

Category	Description
<b>High descent forest</b>	Vegetal cover dominated by trees with wide, almost continuous, canopies, on descents higher than 30%.
<b>Low descent forest</b>	Vegetal cover with the presence of trees and bushes creating less continuous canopies. These areas are regenerating and are on descends lower than 30%.
<b>High descent pasture</b>	Suppression of the forest by human perturbations and substitution with grass for intensive livestock farming, on descents higher than 30%
<b>Low descent pasture</b>	Suppression of the forest by human perturbations and substitution with grass for intensive livestock farming, on descents lower than 30%
<b>Mangrove</b>	Swamp forests occupy spaces with high sedimentation where the sea habitat mixes with the terrestrial habitat.
<b>Swamped vegetation</b>	Vegetal cover that remains underwater most of the year.
<b>Bodies of water</b>	Areas with lakes, lagoons, and watercourses (main rivers and their affluents).
<b>Farming</b>	Areas that are permanently farmed.
<b>Human settlements</b>	Represented by the dispersed urban-residential occupation, accompanied by public, institutional, industrial and commercial services

Source: Adapted from Sandoval et al. (2020).

**Table 6.** Evaluation of the landscape structure of the potential habitat for the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

PACIFIC										
Categories, year 2015										
	High descent forest	Low descent forest	Body of water	Farming	Mangrove	High descent pasture	Low descent pasture	Urban	Swamped vegetation	Clouds
Peso	100	200	300	400	500	600	700	800	900	1000
Use year 2000 Pacific										
High descent forest	1 101	201	301	401	501	601	701	801	901	1001
Low descent forest	2 102	202	302	402	502	602	702	802	902	1002
Body of water	3 103	203	303	403	503	603	703	803	903	1003
Farming	4 104	204	304	404	504	604	704	804	904	1004
Mangrove	5 105	205	305	405	505	605	705	805	905	1005
High descent pasture	6 106	206	306	406	506	606	706	806	906	1006
Low descent pasture	7 107	207	307	407	507	607	707	807	907	1007
Urban	8 108	208	308	408	508	608	708	808	908	1008
Swamped vegetation	9 109	209	309	409	509	609	709	809	909	1009
Clouds	10 110	210	310	410	510	610	710	810	910	1010
CARIBBEAN										
	High descent forest	Low descent forest	Body of water	Farming	High descent pasture	Low descent pasture	Urban	Swamped vegetation		
Peso	10	20	30	40	50	60	70	80		
Use, year 2000										
High descent forest	1 11	21	31	41	51	61	71	81		
Low descent forest	2 12	22	32	42	52	62	72	82		
Body of water	3 13	23	33	43	53	63	73	83		
Farming	4 14	24	34	44	54	64	74	84		
High descent pasture	5 15	25	35	45	55	65	75	85		
Low descent pasture	6 16	26	36	46	56	66	76	86		
Urban	7 17	27	37	47	57	67	77	87		
Swamped vegetation	8 18	28	38	48	58	68	78	88		
Clouds	9 19	29	39	49	59	69	79	89		
		No change		Change						

### Evaluation of the landscape structure

The tool Patch Analysis in ArcGIS 10.5 was used, selecting the following landscape indexes: a) surface: the coating area (ha), b) number of fragments: the total number of fragments of each category, c) average size of the fragments: the sum of the areas of each coating divided by the number of fragments, and d) standard deviation of the fragments: a measurement of the dispersion of the fragment size, according to each coating. To establish the change of coating in terms of land use, an algebraic sum was taken for the maps of the land use in the years 2000 and 2015, moving from the matrix interpretation (Table 6). This enabled us to identify the areas that represented changes in the coating on land use in the potential crocodile habitat.

### Road network density and crocodile incidents attended by the Costa Rican Fire Department

With regards to road network density, we applied the method used by Ramírez et al. (2005), defined as the average of the total longitude of roads per unit area (km/km<sup>2</sup>). The ArcGis extension (Density > Line density): determined the density of roads in the areas close to the crocodile habitat and their relationship with the incidence of inci-

**Table 7.** Road network density of the potential habitat of the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

Classification	Weight	Normalization	Category
0–0.77	1	0.33	Low
0.78–1.55	2	0.66	Medium
1.56–2.33	3	1	High

**Table 8.** Population density of the potential habitat of the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

Classification	Weight	Normalization	Category
0–0.1	1	0.33	Low
0.11–0.25	2	0.66	Medium
0.26–0.4	3	1	High

**Table 9.** Population size by district for the American crocodile (*Crocodylus acutus*) potential habitat in Costa Rica, 2021.

Classification	Weight	Normalization	Category
635–2997	1	0.33	Low
2997.1–7741	2	0.66	Medium
Mayor a 7741.1	3	1	High

**Table 10.** Concentration of human activities in the potential habitat of the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

ID	Sum range	Categories
1	1–1.5	Low
2	1.51–2.24	Medium
3	2.25–3	High

dents involving crocodiles recorded by the Costa Rican Fire Department. Thus, the classification of the road network density serves as an indicator of alteration of the crocodile’s habitat (Table 7).

### Population size and density by district

The human population of each district was analyzed for the periods studied (2011–2025). Population data were acquired from the Instituto Nacional de Estadísticas y Censos for the census year of 2011 and for projected estimates for the years 2017 and 2025. Euclidian measures provided the distance from each cell in the raster to the closest origin, which is a common method for creating a layer of adequation, where the date represents the distance from a specified object (ESRI, 2015; Tables 8–9).

### Human activities concentration (mentioned previously)

The same procedure used to assess the generation of potential habitats was used here (Table 10).

### Human–crocodile interaction zones

With the map of potential habitat (topography, drainage network, and land use cover) and the map of human activities in crocodile habitat (habitat alteration based on road density, population density, and distance to populated cores), a relationship between them was established to detect the zones of interaction between humans and crocodiles (Table 11).

### Variable classification to determine zones of interaction between crocodiles and humans

The same procedure used create the potential habitat was used to create layers of the zones of interaction between crocodiles and humans (Table 12).

### Crocodile incident registry

The database of incidents with crocodiles attended by the national fire department (2017) was used in the analysis (road network density and zones of interaction between crocodiles and humans).

### Classification of values process, weight, and normalization of each variable

With the elevation variables, drainage network, mangrove areas, flooding areas, use of a land coating, road density, population density, and settlements density, the weight assigned to each variable,  $x_i$ , was standardized

**Table 11.** Human–crocodile interaction zones in Costa Rica, 2021.

Potential habitat		
Classification	Weight	Normalization
High	3	1
Medium	2	0.66
Low	1	0.33

Habitat alteration		
Classification	Weight	Normalization
High	3	1
Medium	2	0.66
Low	1	0.33

and normalized through the method of ‘highest on the list’ (Sandoval Murillo et al., 2019, 2020), which involves dividing the weight of each value by the highest value recorded for that variable (the resulting values consequently within the range of 0 to 1):

$$X_i = X_i / X_{max}$$

Three groups of categories by value were established according to the normalized weights assigned to each variable and classified into three ranges defined as high, moderate, and low. Once the ranges were determined, they were related via an algebraic relation of maps (sum), utilizing the corresponding mean of all the punctuations of the variable divided by the number of cases. The po-

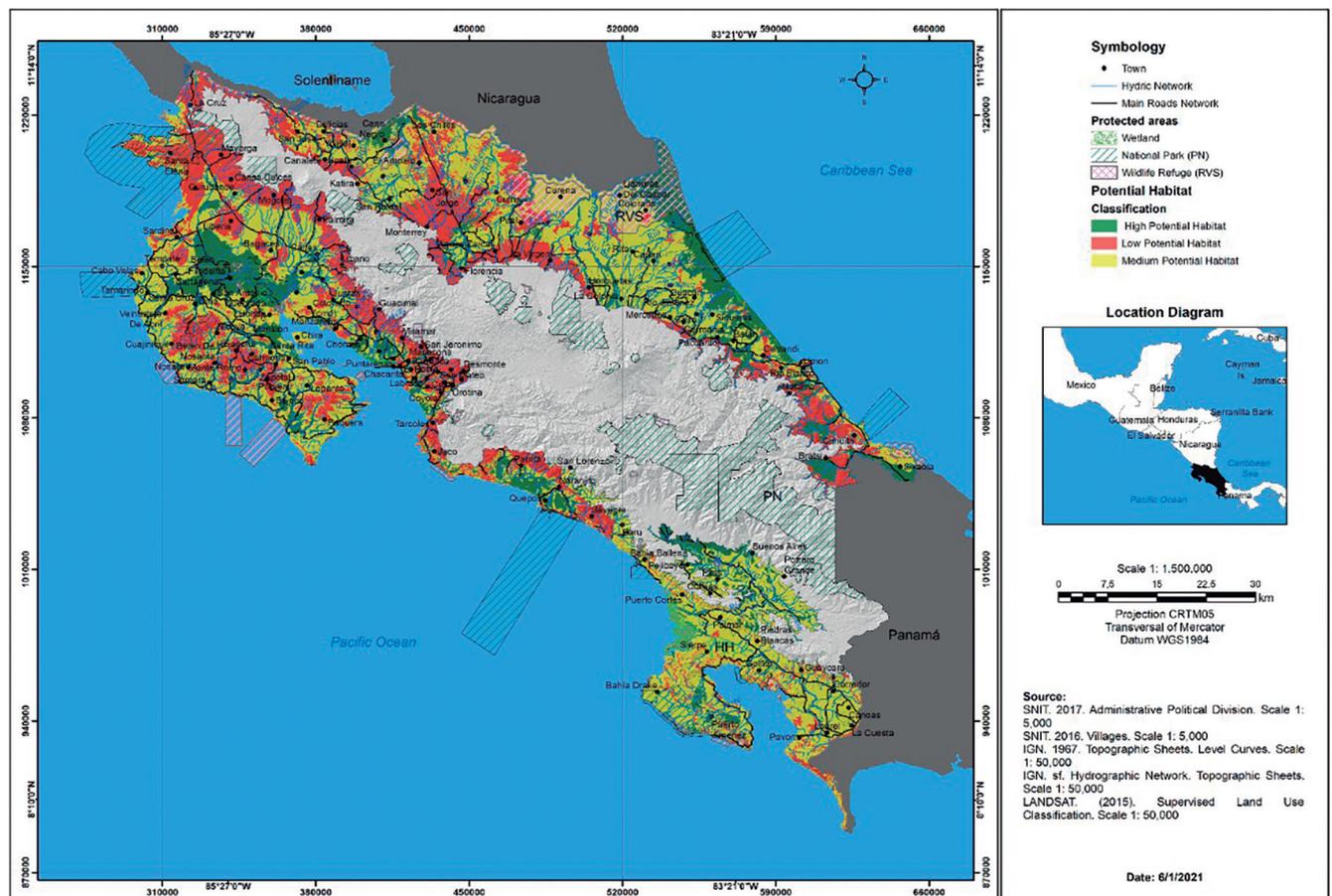
**Table 12.** Areas of interaction between crocodiles and humans in the potential habitat of the American crocodile (*Crocodylus acutus*) Costa Rica, 2021.

ID	Sum range	Categories
1	0.33–0.495	High
2	0.4951–0.665	Medium
3	0.6651–1	Low

tential habitat integrates the variables elevation, drainage network, mangrove areas, flooding areas, and land use coating. The alteration and loss of habitat links the following related variables: road density, population density, the distance between populated cores, and use of a land coating that generates an alteration of habitat.

## RESULTS

We determined that the habitat with high potential on the Pacific slope corresponds to an area of 317,743.3 ha (18% of the total Pacific slope study area). This joins the zone of the Northern Pacific with the Great Tempisque Wetlands in the Central Pacific and the zones closer to the cities of Puntarenas, Parrita, and Quepos in the zone of the South Pacific, in Sierpe. Also, some insular zones associated with the Sierpe-Térraba Wetlands and areas of the Osa Peninsula presented high habitat potential values. The habitat with medium potential, totaling 485,845.9 ha



**Figure 1.** Potential habitat of the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

(54% of the total), was widely identified in the North and South Pacific. The Central Pacific presented few areas with medium potential habitat (only towards the South of the same area, close to Bahía Ballena), and those locations that are slightly higher or with higher urban indexes such as Tárcoles, Jacó, had values of low potential habitat (27% of the total study area). In the Pacific slope, the high and medium potential habitat corresponded to 72% of the study area (632,715.2 ha; Fig. 1).

On the Caribbean slope and north zone, the habitat with high potential was identified in areas closer to the coastal zones mainly in the Central and North Caribbean (269,475.3 ha, corresponding to 29% of the total study area). Because this slope is flat, it has proper conditions for water bodies and 67% of the study area was recognized as medium potential habitat (614,628.7 ha), mainly in the lower zones such as Siquirres and Cariari in the Caribbean (Fig. 1).

In the northern zone, most of the habitat was identified as medium (for example, in Horquetas), and there were only small fragments, close to Caño Negro, identified as high potential habitat. In both regions (the north zone and the Caribbean), zones at higher elevations and with some urbanization were identified as low potential habitat, totaling 35,114.7 ha (close to 4% of the total study area). A total of 96% (884,104.0 ha) of the area on the Caribbean slope and the Northern Zone was identified as high or medium potential habitat.

Regarding the identification of the interactions between humans and crocodiles, in the North Pacific the zones of high interaction were identified as those influenced by the Tempisque River, mainly in areas such as Belén, Filadelfia, Ortega, Bolsón, and some other areas in the Peninsula closer to Nicoya, such as Quebrada Honda, Mansión, and Santa Rosa. In the continental zone, the areas of Cañas and Bebedero were identified as zones of high interaction between humans and crocodiles, similar to some other coastal zones close to Chomes, Punta Morales, and Santa Teresa and Malpaís. The zones of medium interaction in the Northern Pacific region were identified towards the outlet of the Tempisque River as well as the area closer to Quebrada Honda and Puerto Thiel. In the Central Pacific, the zones of Pitahaya, El Roble, Barranca, Labrador, Tárcoles, Jacó, Parrita, and Quepos were identified as areas with high and medium interactions between humans and crocodiles. On the South Pacific, zones closer to Palmar, Sierpe, Ciudad Cortés, and Puerto Jiménez had small areas identified as zones of high and medium interaction. In the continental zone, there were zones closer to the Térraba river such as Buenos Aires and Pilas that were classed as high interaction (Fig. 2).

In the Northern Zone, there were a few zones identified as high and medium interaction. Some of them are small areas close to Los Chiles, the territory near Caño Negro, Aguas Zarcas, Florencia, Pital, and Horquetas. In the Caribbean slope, most of the coastal zone was iden-

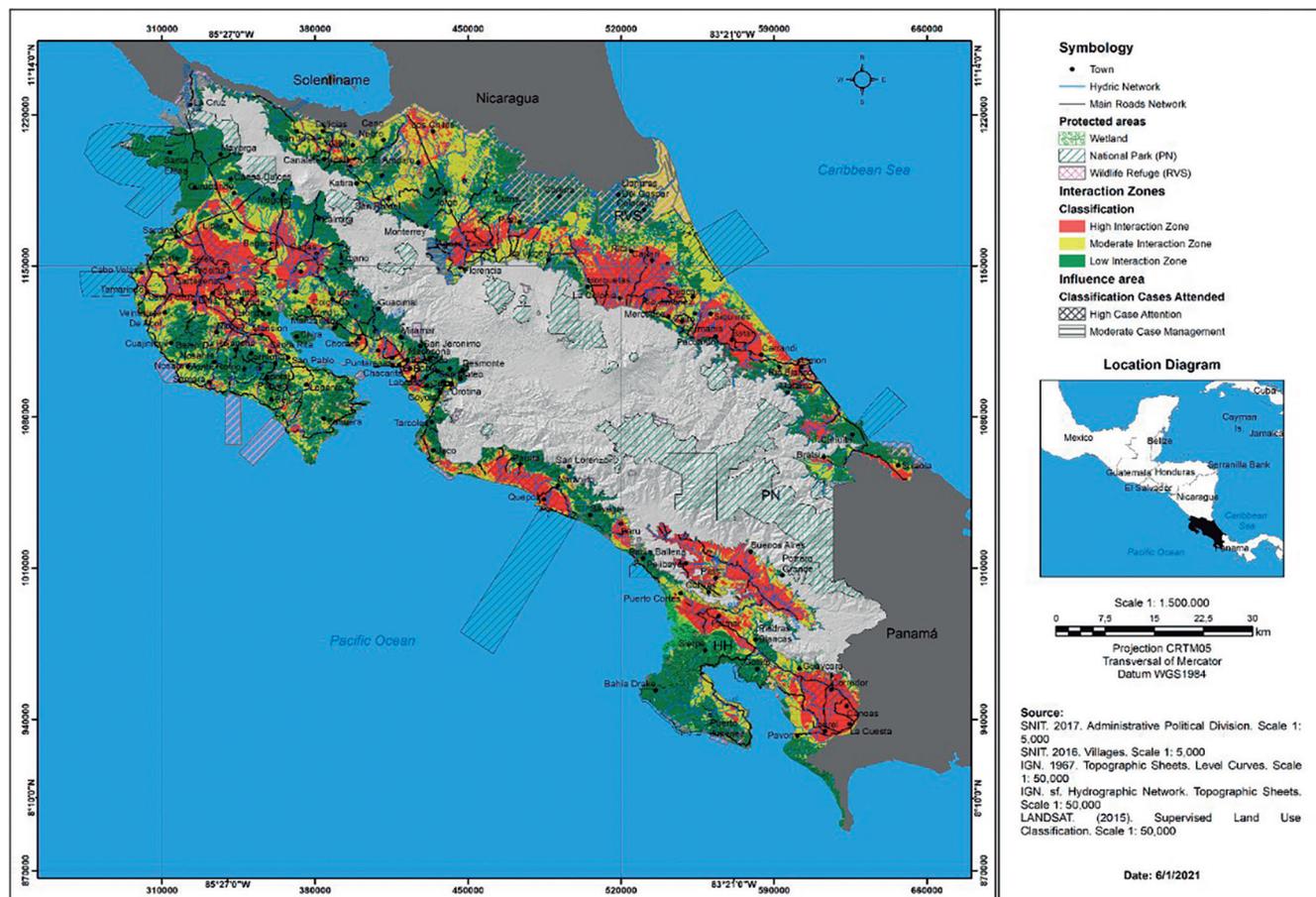


Figure 2. Areas of interaction between humans and the American crocodile (*Crocodylus acutus*) in Costa Rica, 2021.

tified as a medium interaction zone (Barra del Colorado, Tortuguero, Parismina, Pacuare). In the coastal zone of the South Caribbean, there were zones of high interaction identified towards Matama and Cahuita. In the continental zone, the same thing happened in zones with higher urban density (Jiménez river, Siquirres, Germania, Matina, and Bataan), because these were identified as high interaction areas (Fig. 2).

## DISCUSSION

The areas identified as habitats with high and medium potential for crocodiles in the Pacific coincide in the North with the Great Tempisque Wetlands, an area that has been recognized as harboring one of the most important populations of crocodiles in Costa Rica (Sánchez-Ramírez, 2001; Bolaños, 2012a, b; Valdelomar et al., 2012; Murray et al., 2015; Orozco, 2015; Peraza, 2015; Sandoval-Hernández et al., 2017). This area also encompasses a high density of wetlands and areas favorable for crocodiles and their prey (Menacho, 2001; Ramírez, 2008). In the Central and South Pacific both the high and medium potential habitats coincide with areas of mangrove (Puntarenas and Sierpe-Térraba) and river outlets (e.g., Jesús María and Tárcoles), areas considered important for the species, however, with important amounts of human activities including tourism (Sánchez et al., 1996; Bolaños et al., 1997; Sánchez-Ramírez, 2001; Escobedo-Galván, 2003; Porras, 2007; Barrantes, 2008; Bolaños, 2011; Orozco, 2015; Valdelomar et al., 2012; Morales, 2013; Sandoval-Hernández et al., 2017; Sandoval Murillo et al., 2019; 2020; Porras Murillo and Mata Cambronero, 2020).

Areas that have both high or medium habitat potential for crocodiles and also harbor human activities pose an important challenge to the management of possible human–crocodile conflicts. Because the Pacific slope of Costa Rica is being recognized as an important area for national and international tourism (Bartels Villanueva, 2012), the human–crocodile conflicts have been documented by multiple research groups in the North Pacific zone (Valdelomar et al., 2012; Morales, 2013; Sandoval-Hernández et al., 2017). Sandoval Murillo et al. (2019; 2020) have determined similar conflicts in the Central Pacific part of the country.

In the Caribbean slope, the zones identified as high and medium potential habitat coincide with the coastal regions and the areas closer to the cores of major populations, situation that coincides with that mentioned by Bolaños et al. (2019). On the Caribbean slope, the level of infrastructure development is lower than on the Pacific slope, and there are fewer human–crocodile incidents reported. This difference may also be explained by the geographic conditions in the two slopes being different in terms of the slopes, land heights, and climate.

The identification of areas in the Northern Zone that have crocodile populations has also been mentioned by Allsteadt and Vaughan-Dickhaut (1992). On the Caribbean slope, crocodiles tend to avoid interaction with humans

and their behaviors are evasive (Bolaños et al., 2019), thus less conflicts are generated. The same authors also identified an important number of crocodiles in the zone represented by Matina, Pacuare, Reventazón, and Parismina, in addition to the coastal region of the Central Caribbean and up to Tortuguero. Bolaños et al. (2019) also reported that the habitat in the Caribbean brings important conditions for the establishment of crocodiles in the zone, and also that their densities tend to increase in the zones closer to human populations; therefore, identifying the zones of interaction becomes important for informing the management of conflicts, especially in zones like Matina and Siquirres. Balaguera-Reina and González-Maya (2010) identified that, in Colombia, the level of interaction can define the degree of conflict between humans and crocodiles. When the human densities are low and the economic conditions of the villagers are poor, there can be exploitation of the crocodile population.

In this matter, Aust et al. (2009) recommend the effective control of potentially problematic animals, improved education of local communities about crocodile ecology, and conflict avoidance measures. They state that it is important to know more about the social, political, and cultural contexts which have led to the human–crocodile conflict (Pooley, 2017). As seen in Africa, the expansion of human settlements and activities into crocodile habitats and the increasing demands on tourism and supplies of products by the market are resulting in escalating conflicts (Pooley, 2016), mirroring what we are experiencing in Costa Rica (Carrillo-Rivera, 2013; Porras Murillo and Mata Cambronero, 2020).

In this regard, Carrillo-Rivera (2013) reported conflicts in the North Pacific of Costa Rica between humans and crocodiles related to attacks, loss of domestic animals, and impacts on economic and recreational activities and fisheries. In general, Carrillo-Rivera (2013) describes a low tolerance by people to the presence of crocodiles in the area. For the Central Pacific, the conflicts are similar, and disinformation plays against both species—a situation that could drive an increase in human–crocodile interactions (Chavarria, 2020; Madrigal Vargas, 2020).

In the zones inhabited by crocodiles in which human activities are extensive, such as tourism, aquaculture, or even poor waste management, the interactions between these species increase (Amarasinghe et al., 2015; Pooley, 2017; Pooley et al., 2017; 2021). According to these authors, the interactions with humans are driven by the presence of possible prey for the crocodiles such as rats, birds, and dogs that are attracted to the waste, which draws the crocodiles closer to the human inhabitants. This situation is present in most of the zones identified in the present study.

The conflict and interaction between humans and crocodiles can increase when the crocodiles are hunted, perhaps because they are perceived to be mystical animals, or their meat or fat is attributed healing or aphrodisiac properties. This serves to again reduce the distance between the species (Valdelomar et al., 2012; Morales, 2013; Amarasinghe et al., 2015; Pooley, 2017; Pooley

et al., 2017; 2021; Sandoval-Hernández et al., 2017; Porras Murillo and Mata Cambroner, 2020).

In summary, this paper identifies potential crocodile habitat and areas of interaction with humans, giving important outlooks for the Costa Rican Ministry of Environment, the National System of Protected Areas, the Ministry of Public Education, and the Tourism Ministry to take measures to diminish human–crocodiles conflicts. The evidence of the association between crocodiles and anthropic areas is clear and gives us the opportunity for the first time in Costa Rica to address management policies and education strategies in specific areas, to ensure human safety and the conservation of this reptile. Human usage of wildlife areas is increasing; therefore, encounters between humans and crocodiles are likely to rise. The generalist and opportunistic characteristics of *Crocodylus acutus* made them a “threat” in the anthropic and touristic areas identified in this paper, and it has become a challenge in terms of conservation and development for Costa Rica.

The knowledge provided through this study allows some decisions to be made that have historically been postponed, partly due to the fact that there was no knowledge related to the state of crocodile populations and their population dynamics in the country, and in part because this information had not yet been integrated with the information on the evolution of human populations in the shared habitat, as well as the environmental conditions that our study provides.

We hope the information generated will fuel future research and consequent policy directives to identify and minimize human–crocodile interactions and their adverse effects. Such an approach would help develop a new line of thinking about conservation problems, tolerance, outreach, and effective management in areas dominated by wildlife and with anthropic activities within them.

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