SRAS FINAL REPORT:

Occupancy models of two sympatric crocodilian species on the coast of Chiapas

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Abstract.

Occupancy is a relevant indicator of habitat use and the spatial distribution of wildlife species. Few studies in Mexico apply this approach, and none analyze the effect of sympatry between the American crocodile (*Crocodylus acutus*) and Chiapas spectacled caiman (*Caiman crocodilus chiapasius*). In this context, the objective of this study was to evaluate the variables that influence the detection (p) and occupancy (ψ) of *C. acutus* and *C. c. chiapasius* in the La Encrucijada Biosphere Reserve, Chiapas. Occupancy models were employed using the unmarked package in RStudio, considering covariates grouped into three categories: environmental (ambient temperature, precipitation, microhabitat, presence or absence of *C. acutus* nests), anthropogenic (distance to rural human settlements, distance to agricultural soils, and sampling duration per section), and physicochemical (pH and salinity). The analysis was performed for three periods: general, reproductive, and non-reproductive. For *C. acutus*, the models with the strongest support indicated high detection probabilities associated with anthropogenic variables (p = 0.95–0.97) and occupancy probabilities influenced by the presence of nests (ψ = 0.99) and by physicochemical variables (ψ = 0.57–0.67), suggesting high resilience to anthropogenic pressure and the ability to occupy sites with variations in water quality. In contrast, for *C. c. chiapasius*, a sympatry effect during the breeding season, where the presence of *C. acutus* limited its detection, was observed; models showed moderate detection and occupancy probabilities (p = 0.50–0.94; ψ = 0.35–0.75) associated with anthropogenic pressure, precipitation, and microhabitat, indicating greater environmental sensitivity and possible displacement by the American crocodile.

Keywords: habitat use; crocodiles; caimans; distribution; resources.

Introduction.

Three crocodilian species are distributed in Mexico*: Caiman crocodilus chiapasius, Crocodylus acutus,* and *C. moreletii* (Cedeño-Vázquez et al., 2012; Balaguera-Reina & Velasco, 2019; Rainwater et al., 2021) although this study only deals with the first two. These species face various threats, such as habitat destruction and modification (Barrasa, 2013; González-Desales et al., 2016a, 2020, 2021). The state of Chiapas is the only Mexican state where all three species are naturally distributed (Álvarez del Toro, 1974; Lazcano et al., 1988; Casas & Reyna, 1994; Sigler, 1997).

C. c. chiapasius is naturally distributed in Guatemala, El Salvador, and the coastal region of the state of Chiapas in Mexico (Escobedo-Galván et al., 2011, 2015; Venegas-Anaya et al., 2008). It is listed under NOM-059 as a species subject to special protection (SEMARNAT, 2019), while on the International Union for Conservation of Nature (IUCN) Red List it is classified as Least Concern (Balaguera-Reina & Velasco, 2019). *C. acutus* is distributed from the United States to Peru. In Mexico, it is found in the Pacific states of Sinaloa, Nayarit, Jalisco, Colima, Michoacán, Guerrero, Oaxaca, and Chiapas, while in the Gulf of Mexico and the Mexican Caribbean, it is found in the states

of Campeche, Quintana Roo, and Yucatán. This species is listed as Subject to Special Protection under NOM-059 (SEMARNAT, 2019), and as Vulnerable on the IUCN Red List (Rainwater et al., 2021).

Occupation is defined a probability of detection (MacKenzie et al., 2002; Andrade-Ponce et al., 2021). Understanding occupancy involves grasping the ecological niche of species, which consists of three dimensions: spatial (distribution), temporal (activity pattern), and trophic (diet). Occupation models were designed to analyze the spatial distribution of cryptic and low-detectability species (MacKenzie et al., 2002). These models also allow for the identification of variables associated with presence, based on the assumption that species are present at the site but are not always observable (Mackenzie et al., 2002; Andrade-Ponce et al., 2021). The models estimate the probability of occupancy in the area (Ψ), using an Ecological Model: $Zi \sim Bernoulli\ (\psi i)$, and the probability of detection (p), using the Observation Model: $yij|zi \sim Bernoulli\ (zi * pij)$, from detection or non-detection histories (hi), obtained through repetitive sampling (MacKenzie et al., 2002).

As such, the aim of this project was to show how different variables may influence detection and occupation of *C. c. chiapasius* and *C. acutus* on the coast of Chiapas, Mexico.

Methods.

Study Area

The study was conducted in the La Encrucijada Biosphere Reserve, located in the southeastern part of Mexico, within the state of Chiapas, in the coastal area encompassing the municipalities of Pijijiapan, Mapastepec, Acapetahua, Huixtla, Villa Comaltitlán, and Mazatán (Figure 1). It is situated in the Pacific Coast biogeographic province. The climate is warm and humid, with abundant rainfall during the summer (INE-SEMARNAP, 1999).

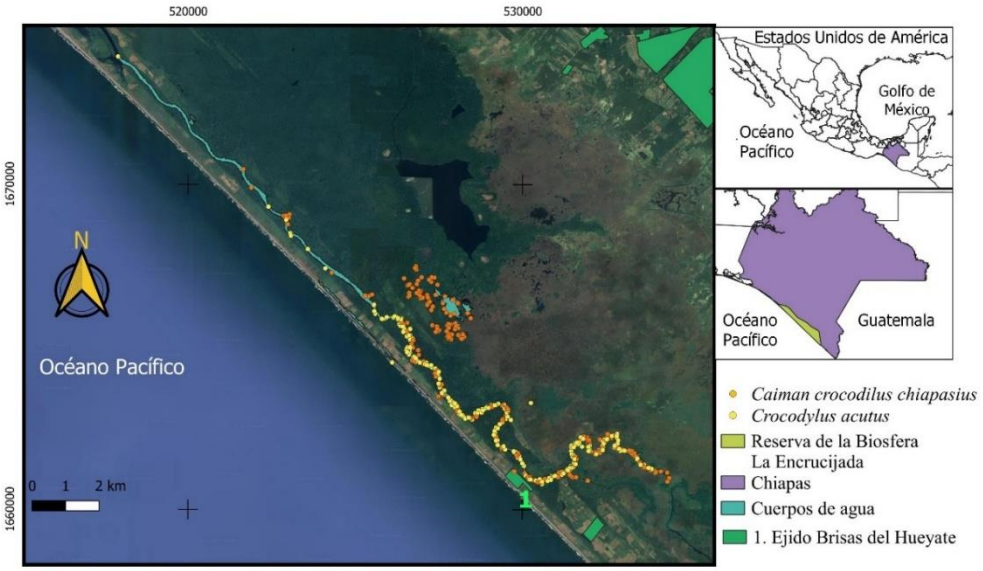


Figure 1. Study area, Estero el Hueyate and surrounding swampy areas, the points represent each observation of an individual of the species *Caiman crocodilus chiapasius* and *Crocodylus acutus.*

Crocodile Monitoring

Sampling consisted of traveling 28 km in a 6 m long boat with a four-stroke outboard motor. Presence and absence were recorded using the Night Visual Detection (NVD) method, in which individuals were located by the reflection of light from lamps (50000 lumens) on the tapetum lucidum membrane present in the eyes of crocodilians (Sigler et al., 2011). We completed eight surveys based on both the rainy and dry seasons that define the reproductive seasons of the species at the study site.

For each individual sighted, the following data were obtained: a) sighting coordinates (longitude and latitude) using Google Maps on a mobile device, b) land use and vegetation cover where the individuals were observed: red mangrove roots, cattail marshes, sapote roots, bodies of water, and floating vegetation, and c) size, based on the classification of Seijas (1983) for *C.c. chiapasius* and Thorbjarnarson (1989) for *C. acutus*. To differentiate the crocodilian species, the bony crests above the eyes and interorbital bridge, which are characteristic of *C.c. chiapasius*, were observed (Álvarez del Toro, 1974). For the proper functioning of the occupancy models, the 28 km² of Estero el Hueyate were divided by species. For *C. acutus*, an average distance of 1,100 m was obtained, resulting in 27 observation segments, while for *C.c. chiapasius*, an average distance of 773 m was obtained, resulting in 35 segments. The database was compiled from the detection histories of each observation segment for each species, incorporating the environmental and spatial values associated with each segment.

Spatial Characterization and Variables to be Evaluated

The variables evaluated were selected based on a literature review on occupancy models for crocodilians (Gardner et al., 2016; Ahizi et al., 2021). They were grouped into three categories: a) environmental, b) anthropogenic, and c) physicochemical. Similarly, they were divided into detection variables and occupancy variables. Finally, the variables were categorized into 3 categories: 1) Environmental variables: precipitation, temperature, microhabitat, light intensity of the moon, presence or absence of *C. acutus* nests, presence of *C. acutus* in the case of the caiman, 2) Anthropogenic variables: distance to rural human settlements, distance to agricultural soils, duration of monitoring at each site, and 3) Physicochemical parameters: pH and salinity (Table 1).

Table 1. Characteristics of the variables evaluated in the occupancy and detection models of the crocodilians of the Hueyate estuary, Chiapas.

Variable category	Variable	Unit of measurement
Environmental	Temperature	Degrees Celsius
	Precipitation	Mm
	Moon intensity	%
	Presence or absence of nests	1 to 0
	Microhabitat	1 to 5
	Presence of *C. acutus*	1 to 0
Anthropogenic	Distance to rural human settlements	Meters
	Distance to agricultural land	Meters
	Sampling duration per section	Minutes
Physicochemical	pH	0 to 14
	Salinity	Psu

Results.

For both species, three analyses were performed: a general single-season analyses and then separate reproductive and non-reproductive analyses.

Crocodylus acutus

469 individuals were recorded along the 28 km study area, including individuals of all age classes. *C. acutus* is the most prevalent species throughout the sampling area.

Detection. This species was present in 22 of the 27 observation sections. The best detection model for the overall analysis indicates that the presence of *C. acutus* is influenced by the distance to rural human settlements (Table 2). The shorter the distance, the greater the probability of detecting the species.

The reproductive season for this species in the area is from March to June (González-Desales et al., 2016b). Detection was influenced by two anthropogenic variables (Table 2): distance to rural human settlements and to agricultural land.

The non-reproductive season encompasses the months of August to February (González-Desales et al., 2016b). The detection of *C. acutus* during this season was determined by two environmental variables: temperature and precipitation (Table 2). Higher temperatures resulted in a lower probability of detection. Precipitation levels indicate a higher probability of detection.

Occupancy. In the overall analysis, we observed that occupancy is influenced by the presence of *C. acutus* nests (Table 2). As the presence of *C. acutus* nests increases, crocodile occupancy also increases.

During the reproductive season, which includes several months of rainfall in the area (INSE-SEMARNAP, 1999), pH also determines occupancy (Table 2), keeping in mind that rainfall can alter the range of this physicochemical variable. For the non-reproductive season, the combination of the two physicochemical variables, pH and salinity, determines occupancy (Table 2).

Table 2. Best models for detecting and occupancy of the American crocodile, by season, in the La Encrucijada Biosphere Reserve, Chiapas, Mexico. nPars = number of parameters estimated in the model, AIC = Aikake Information Criterion value, and p = value to determine if there is significance. Sal is salinity

Occupancy and detection models		nPars	AIC	p
General analysis	p(hum)psi(nests)	4	135.59	0.03
Reproductive season	p(humans+agriculture)psi(pH)	5	91.09	0.04
Non-reproductive season	p(temperature+precipitation)psi(pH+sal)	6	85.32	0.04

Caiman crocodilus chiapaisus

Detection. 389 individuals were observed during the surveys. For this species, the presence of the *C. acutus* was added as a variable for detection and occupancy, given its greater abundance.

For the general analysis, the variables that determine the detection of the *C.c. chiapasius* are anthropogenic variables: distance to rural human settlements and agricultural area (Table 3).

For the reproductive season (June to October; González-Desales et al., 2016a), detection is determined by two variables of different categories: agricultural area (anthropogenic) and the presence of the *C. acutus* (environmental) (Table 3). The greater the percentage of agricultural areas, the greater the probability of detection. The greater the presence of the *C. acutus*, the lower the detection of the *C.c. chiapasius*.

During the non-reproductive season (November to May; González-Desales et al., 2016a), detection is influenced by the distance to rural human settlements (Table 3). The closer to these areas, the greater the probability of detection.

Occupation. Occupation during the overall analysis was influenced by precipitation. It shows a positive relationship with the higher the level of precipitation, the greater the probability of occupancy by the *C.c. chiapasius*.

For the reproductive season, occupancy is also influenced by precipitation, but in this case, lower precipitation is associated with a higher probability of occupancy.

Occupation is determined by the microhabitat, using the following scale: 1) bodies of water, 2) floating vegetation, 3) cattail marsh, 4) red mangrove, 5) sapote roots. The trend indicates that the presence of sapote increases the probability of occupancy.

Table 3: Best detection and occupancy models of the Chiapas spectacled caiman, by seasons, in the La Encrucijada Biosphere Reserve, Chiapas, Mexico.

Occupancy and detection models		nPars	AIC	P
General analysis	p(humans+agriculture) psi(precipitation)	5	274	0.04
Reproductive season	p(agriculture+crocs) psi(precipitation)	5	98.48	0.03
Non-reproductive season	p(humans)psi(microhabitat)	4	164.86	0.04

Discussion.

This study analyzes, for the first time, the occupancy and detection of two crocodilian species in the state of Chiapas, using occupancy models. Furthermore, it describes, for the first time, the effect of sympatry in Mexico between *C. acutus* and *C. c. chiapasius*. The results indicate the need to propose conservation and sustainable management strategies for these species in the REBIEN (Regional Biosphere Reserve of Chiapas), in collaboration with local communities.

C. acutus

The detection rate of *C. acutus* in the general analysis was influenced by the anthropogenic variable: distance to rural human settlements, with more crocodiles present closer to settlements. Communities are present in the El Hueyate estuary. These communities engage in fishing, agriculture, and livestock farming. Human presence has been reported to limit the distribution of crocodiles in their natural range (Ahizi et al., 2021) but our results do not support this hypothesis.

For *C. acutus*, in Mexico, it is reported that they avoid areas with anthropogenic activities and human settlements, preferring less disturbed environments (Marín-Enríquez et al., 2023). This was not the case in this study. One of the areas with the highest percentage and frequency of nesting is "Isla La Concepción", in which anthropogenic activities are carried out (González-Desales et al., 2016b). Occupancy during the general analysis was influenced by the presence of nests; that is, a greater presence of nests increased occupancy. This can be explained by this land area being suitable for *C. acutus* regardless of season whereby in the nesting season it provides ideal nesting substrate and hatchability and in the non-reproductive season, it provides suitable cover for nurseries tend to form and parental care by the mother. Furthermore, crocodiles often reuse nesting areas (Charruau & Hénaut, 2012; Brien et al., 2014).

Considering these results, we could infer that human-modified environments offer ideal resources for nesting in these areas of the REBIEN. The breeding season of this species varies according to the geographic zone (Casas-Andreu, 2003; Charruau et al., 2010; Charruau et al., 2017). These results do not coincide with what has been reported for this species in other areas of its distribution, where it is mentioned that it prefers less disturbed habitats for nesting (Enríquez-Marín et al., 2023). This may be due to nest destruction and the limited space available for nest construction (Enríquez-Marín et al., 2023). However, there are other studies that mention that disturbance caused by human activities can benefit suitable habitats (Charruau et al., 2010; González-Desales et al., 2016b).

In the REBIEN, it was found that temperature has a negative relationship with the detection of *C. acutus* during the non-reproductive season, while precipitation has a positive relationship. These variables directly influence detection, as crocodiles regulate their body temperature and spend most of their lives in the water (Grigg & Kirshner, 2015).

The non-reproductive season coincides with the summer months, with the highest temperatures recorded in the REBIEN (INE-Semarnap, 1999). High ambient temperatures in crocodilians may represent periods of inactivity or a search for thermal refuge, or areas with high water levels and dense vegetation, thus reducing their visibility during sampling (Barham et al., 2025). The presence of *C. acutus* in the REBIEN is predominant in areas with dense vegetation such as red mangroves and bodies of water, consistent with previous reports.

Caiman crocodilus chiapasius

The variables that influenced the detection of the *C. c. chiapasius* were anthropogenic. Distance to rural human settlements had a positive correlation, while distance to agricultural lands increased the probability of detection as the distance to these areas grew. The correlation with distance to agricultural lands is due to the use of satellite imagery from 2022 as input for the models in this study (Gebhardt et al., 2014). Currently, these areas are being reforested with native vegetation such as red mangrove and cattails, which provide ideal resources for the optimal development of the *C. c. chiapasius* (Mañon-González, 2022; Pereira et al., 2023).

The breeding season represents a critical stage in the life cycle of caimans throughout their range (Staton & Dixon, 1975). During this stage, females have been reported to seek out nesting sites and resources, while males seek out sites where females are present but avoid human presence (Mascarenhas Junior et al., 2023; Mascarenhas Junior et al., 2024).

Caimans throughout their range have faced niche overlap with anthropogenic activities, primarily fishing and agriculture (Pereira et al., 2023). Similarly, in the REBIEN (Regional Biosphere Reserve of Chiapas), there is an overlap of human settlements with the distribution of the *C. c. chiapasius*

(Aguilar-Galindo, 2015; Mañon-González, 2022). The importance of reforestation with native species in previously exploited areas creates ideal environments (Marques et al., 2020; Pereira et al., 2023). It is important to continue these programs because they can generate conservation strategies for these species.

The variable influencing detection during the non-reproductive season was the distance from rural human settlements, the shorter the distance, the greater the probability of detection. During these months, rainfall is scarce in the REBIEN (INE-SEMARNAP, 1999). During the dry season, caimans tend to seek out sites with available resources and seasonal water bodies (Pereira et al., 2023; Mascarenhas-Junior et al., 2024). These sites may be disturbed and close to human settlements, but they serve as refuges during certain seasons and do not directly impact on the caimans' body condition (Pereira et al., 2023; Mascarenhas-Junior et al., 2024).

In the REBIEN, the *C. c. chiapasius* is subject to environmental, anthropogenic, physicochemical, and *C. acutus* pressures. One strategy to mitigate these pressures is ranching, which has helped stabilize some crocodilian populations around the world (Biodiversa, 2004; Velasco, 2017). Furthermore, the *C. acutus* can be sustainably harvested through ranching or wild harvesting, as it has a greater number of nests and a higher nesting index (RI) than the *C. c. chiapasius* (Velasco and De Sola 1997; Martínez-Ibarra, 1996; Peña, 2011; Velasco, 2017).

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