

Population status of the American crocodile, *Crocodylus acutus* (Reptilia: Crocodylidae) and the spectacled caiman, *Caiman crocodilus* (Reptilia: Alligatoridae) in the Costa Rican North Caribbean

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Abstract: Along the Costa Rican Caribbean shoreline, it is possible to find two species of crocodilians, the American crocodile (Crocodylus acutus) and the spectacled caiman (Caiman crocodilus). This region can be divided geographically into three subregions: North, Central, and South Caribbean. We conducted this research in the North Caribbean, between October 6, 2018 and August 31, 2019. Specifically, we worked in the area lying between the Jalova Station of the Tortugero National Park (TNP) and Agua Dulce Lake situated in the northern tip of Machuca Island, at the mouth of the Colorado River inside the Barra del Colorado National Wildlife Refuge (BACORE), which includes other connecting wetlands as well (Sierpe River, Samay Lake). Overall, this study area had an approximate extension of 408 km² characterized by large, wide and deep canals, as well as wetlands, meanders, and adjacent lakes. The sampling was performed along 10 segments that varied in length from 7.5 km up to 29.49 km, located in the nearby zones of TNP and BACORE. In these zones, nightly counts were carried out using dazzling lamps. Individuals of C. acutus and C. crocodilus were classified into eight and six body size classes, respectively (both with 50 cm intervals). A relative abundance of 0.55 crocodiles and 1.37 caimans per linear kilometer was estimated during these spotlight surveys. The capture of 39 caimans let us to estimate a ratio of 30 males to 9 females (3.3:1 M:F). In stark contrast, only 1 male and 1 female crocodile were captured. A total of 85 C. acutus and 205 C. crocodilus were observed. Regarding the number of caiman sightings in the TNP, a statistically significant difference was found ($X^2=5.62$, $p\le0.05$) for the distribution by sizes between the zones of BACORE and TNP, whereas no such difference was found for C. crocodilus sightings (Z=-1.22, p ≥ 0.222). Some segments had a higher probability of caiman occurrence than did others in the surveys performed during the monitoring period ($X^2=8.36$, $p \le 0.05$), especially the Jalova-Sierpe River, Caño Negro-Tortuguero, and Tortuguero-Samay Lake (Tortuguero subarea) segments. Ninety percent of the sightings occurred in the BACORE zone, and this was significantly

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different ($X^2=7.34$, $p\le0.026$) from the studied subareas. The number of crocodile sightings in the Colorado River segment was significantly different and higher than the other segments ($X^2=7.28$, $p\le0.05$). There was a significant statistical difference among the sizes in all areas of study ($X^2=5.529$, $p\le0.026$). The abundance of *C. acutus* and *C. crocodilus* in the north Caribbean part is lower than in the central Caribbean part of Costa Rica, where this species could use the resources available in more urbanized areas.

Key words: Barra del Colorado crocodiles; caimans; Caribbean; Costa Rica; Tortuguero National Park.

Introduction

Along the Caribbean shoreline in Costa Rica, one could find the only member of the family Crocodylidae in the country, *Crocodylus acutus* (Cuvier, 1807), also known as the American crocodile, which reaches a reported maximum size of 6 m in total length (Medem 1981). Likewise, sharing this shore environment sympatrically is the only representative of the family Alligatoridae, the spectacled caiman, *Caiman crocodilus* (Linnaeus, 1758), which grows up to 2.8 m in total length (Bolaños et al. 1995). Both species inhabit areas of the Caribbean shore wetlands.

In the Caribbean watershed, a physical limit that divides this region into two large subregions can be distinguished: the North Caribbean, from Limón city to the San Juan River, and the South Caribbean, from Limón city to the Sixaola River. Between the North and South Caribbean subregions, a third subregion can be delimited, corresponding to what Bolaños et al. (2019) described as the Central Caribbean. The authors defined this subregion as the area in-between the city of Limon and the mouth of the Parismina River, at the Jalova Station of Tortuguero National Park. Those authors considered the Central Caribbean subregion as the most human populated zone in the entire Caribbean coast of Costa Rica.

The North Caribbean occurs within the alluvial plains lying north from the Parismina River's mouth, up to the Barra del Colorado River, bordering the northern shore. This subregion is irrigated by La Suerte, Tortuguero, Colorado, and San Juan rivers, and crossed by long, wide and deep aquatic canals that facilitate human transit among the distant communities of the Caribbean shoreline region but also enable the movement of the wildlife species inhabiting it (Venegas 2013).

In northeastern Costa Rica, along the Northern and Southern Caribbean, in the Sarapiquí district, Bolaños et al. (1997) found in the zone of La Rambla and Río Frío towns crocodile and caiman populations with densities of 2.33 ind./km and 2.55 ind./km, respectively. Additionally, in the Costa Rican Northern Zone, Cabrera et al. (2003), and later Aranda-Coello et al. (2015), found evidence showing that within the Caño Negro Wildlife Refuge there is an important *C. crocodilus* population; however, this population has been exposed to exploitation, usage, and depletion by the human population.

As part of a limited group of researchers who have studied the crocodilian populations in the Caribbean region, Bolaños et al. (2019) found that *C. crocodilus* and *C. acutus* are commonly encountered, though they recommended increasing the level and effort of investigation. Bolaños et al. (2019) reported a *C. crocodilus* density of 8.64 ind./km, while for *C. acutus*, the density was lower, 2.80 ind./km; these authors found a male-to-female sex ratio of 1.25 and 0.83 for caimans and crocodiles, respectively, in the Central Caribbean. Given the fact that there is generally little information about the crocodilian populations in the Caribbean watershed, and practically nothing known about them for the North

Caribbean subregion, we proposed to study the status of the American crocodile (*Crocodylus acutus*) and the spectacled caiman (*Caiman crocodilus*) populations in this Costa Rican subregion.

Materials and methods

Study area

We conducted the field research between October 6, 2018 and August 31, 2019 in the Costa Rican North Caribbean (Limón province, Pococí canton, Colorado district). This area corresponds to that between the Jalova Station of Tortuguero National Park (10°20'37.43"N 83°23'55.65"W) and the mouth of the Agua Dulce Lake (10°52'18.08"N 83°37'13.70"W), in the northern extreme of the Machuca Island, about 8 km North of the mouth of the Colorado River, and that along the shore at the mouth of the Colorado River (10°47'53.20"N, 83°35'20.26"W); we also included other connected wetlands (i.e., Sierpe River, Samay Lake) (Figure 1 and 2). Overall, the study area had an approximate extension of 408 km², characterized by wide and deep canals forming a vast wetland with small meanders and adjacent lakes that shape the main hydric structure of this important network of watercourses.

In the North Caribbean, the average annual precipitation is above 4000 mm, with temperatures averaging 24°C and a relative humidity ranging from 70% to 100% (Solano and Villalobos 2020). The predominant vegetation here consists of the yolillal flooded forests, mixtures of yolillo (*Raphia taedigera*) and kativo (*Prioria copaifera*) that are distributed

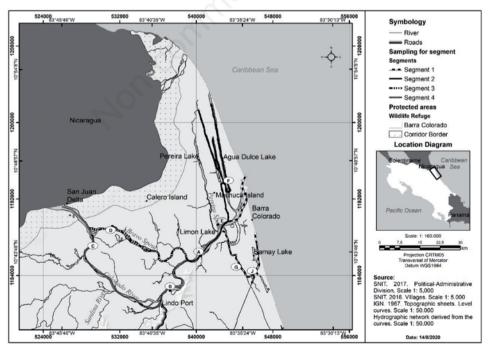


Figure 1. Work segment identification in the Barra del Colorado Wildlife Refuge (BACORE), Costa Rica, 2019.

along the pluvial canals, usually parallel to the shoreline (Hurtado-Hernández and González-Ramírez 2013; Zúñiga Calderón and Moya Calderón 2016; SINAC 2020).

The Colorado River originates at the Delta Costa Rica outpost; it starts as a branch of the San Juan River on the border with Nicaragua and it ends in Barra del Colorado, 40 km downstream. To perform the nocturnal monitoring survey, the study area was divided in 10 sampling segments (identified alphabetically; segments A to J), with the intention that each one could be easily repeated and compared with previous or subsequent monitoring efforts. Segments A, B, C, D, E, F, and G were positioned within the Barra del Colorado Wildlife National Refuge (BACORE), while segments H, I, and J were located within the Tortuguero National Park (TNP). These sampling segments are shown in Figures 1 and 2, with their details given in Table 1.

Relative abundance and demographic structure estimate

We collected the data during nocturnal surveys between October 6, 2018 and August 31, 2019. Each visit consisted of four days and three nights of work, always working during the new moon phase. To determine the presence of crocodilians, LED dazzling headlamps (Macway/OEM) with 6 V and up to 1000 lumens were utilized (Levy 1991).

During the nocturnal surveys, size estimates were made using the following parameters: (a) distance from the eyes to the tip of the snout; (b) the distance between the eyes; (c) the total length of the animal; (d) any animals that hid before their size could be assessed were noted as "undetermined" and were included in the general count of crocodilians present at a given location, without verification of size or species (Bolaños et al. 2019).

For the trips in the northern areas of sampling within BACORE, we used a 9-m-long

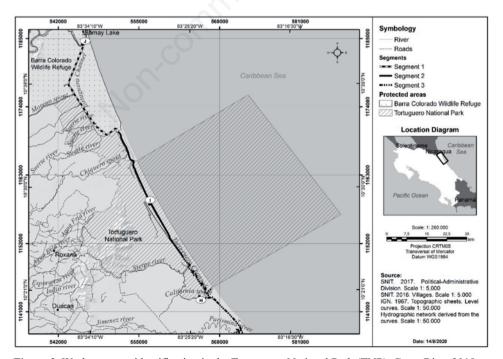


Figure 2. Work segment identification in the Tortuguero National Park (TNP), Costa Rica, 2019.

and 2.5-m-beam panga boat powered by a 45 horsepower (Hp) motor. Within TNP, the surveys were conducted in an inflatable APEX boat (6 m in length, with a beam of 1.5 m), equipped with an 18 Hp outboard Nissan engine.

Capture, measuring, marking, and identification

Animals were captured by hand, or using a 2-m-long noose, consisting of a rope inside a PVC pipe (0.75-inch diameter). Captured animals were marked, measured, sexed, and released. Several variables were registered: (a) total body length, (b) snout cloaca length, (c) cloaca-distal end of the tail length, (d) head length, between the cranial slab and the tip of the snout. All measurements were taken using a measuring tape (+/- 0.5 mm) (Bolaños et al. 1997). Every captured animal got an ID Trovan microchip implanted in its left groin. Captured specimens of *C. acutus* were also marked by amputating their caudal scales (Bolton 1989). Caimans could only be implanted with the microchip for marking, given the characteristics of their caudal scales.

Crocodylus acutus individuals were classified using eight size classes (Bolaños et al. 2019), based on 50 cm intervals (Table 2). This classification allows for size estimates with minimum error and the comparison of data with those obtained in different censuses performed in Costa Rica, especially those reported for the Central Caribbean by Bolaños et

Segment	Segment identification	Length (km)
A	Barra Colorado-Lindo Port cross (occidental margin)	10.88
В	Caño Bravo Cross-Lindo Port	7.5
С	Colorado river	17.69
D	Caño Bravo	13.27
Е	Barra Colorado-Lindo Port cross (oriental margin)	10.25
F	Agua Dulce Lake	13.09
G	Samay Lake	14.13
Н	Jalova	13.38
I	Caño Negro-Tortuguero	19.03
J	Tortuguero-Samay Lake	29.49

Table 1. Work segment identification, in the North Carribbean, Costa Rica, 2019.

Table 2. Crocodile (*Crocodylus acutus*) and caiman (*Caiman crocodilus*) classification by body size, in the North Caribbean, Costa Rica, 2019.

	C. acutus			C. crocodilus	
Class	Name	Size (m)	Class	Name	Size (m)
I	Recruit	0 - 0.5	I	Recruit	0 - 0.5
II	Recruit	0.5 - 1.0	II	Juvenile	0.5 - 1.0
III	Juvenile	1.0 - 1.5	III	Adult	1.0 – 1.5
IV	Juvenile	1.5 - 2.0	IV	Adult	1.5 - 2.0
V	Adult	2.0 - 2.5	V	Adult	2.0 - 2.5
VI	Adult	2.5 - 3.0	VI	Adult	2.5 - 3.0
VII	Adult	3.0 - 3.5			
VIII	Adult	3.5 - 4.0			

al. (2019). Due to their smaller size, *C. crocodilus* were classified into six size classes, likewise using 50 cm intervals (Table 2).

A grouping control was applied to the sightings performed, by placing a number "1" beside each observation for those individuals considered as "grouped", in that they were observed within 50 m of other individuals. Conversely, a number "2" was assigned to those individuals observed at greater distances apart, these considered as "dispersed" (Bolaños et al. 2019).

Statistical analysis

The collected data were organized in an MS Excel 2019 spreadsheet and analyzed by the Statistical Package for the Social Sciences (IBM, SPSS-Statistics 22). Analyses were first run corresponding to each variable, as well as the compound behavior of two or more variables. Whenever needed, contrasting non-parametric analyses were performed on one, two and more samples (Chi square, Wilcoxon, Kolmogorov-Smirnov, and Kruskall-Wallis).

Results

Regarding relative abundance estimate and demographic structure, for *C. acutus* we found that segments A and C yielded the highest recount of recruit animals, while segments E and I are those where larger-sized individuals occurred (Table 3). The majority of sightings were classified as sizes II, III, and IV (Table 3). For *C. crocodilus*, the distribution of its sightings was more uniform, with differences in body sizes that were not statistically significant, namely in the F, I, and J segments (Table 4). In addition, most of the sightings observed were of individuals in sizes II, III, and IV (Table 4).

The reconversion of the number of 108 undetermined individuals was added to the calculated average number of crocodilians, between crocodiles and caimans, and distributed proportionally by size class, according to the number of individuals sighted, as 31 *C. acutus* and 77 *C. crocodilus*. This resulted in estimated demographic totals of 85 *C. acutus* and 205 *C. crocodilus* in the study area.

Table 5 presents the distribution of both species of crocodilians in the different studied subregions. Evidently, the average values of caiman sightings were higher in the TNP than

Caribbean,	Costa Ki	za, 2019.							
Segment	II	Ш	IV		VI	VII	VIII	Total	
A	10							10	
В	5			2	2			9	
С	11	5	5					21	
D	6	3						9	
Е	3	2			2		2	9	
F	5	2	2					9	
G	6	3						9	
Н									
I		5				2		7	
J		2						2	
Total	46	22	7	2	4	2	2	85	

Table 3. Crocodile (*Crocodylus acutus*) distribution by segment according to body size, in the North Caribbean, Costa Rica, 2019.

in BACORE. There were significant differences in the sighting frequency of caimans and crocodiles, with the former arguably seen more often ($X^2=66.53$, $p\le0.0001$).

The occurrence of *C. acutus* or *C. crocodilus* differed significantly among the segments sampled (Kruskal-Wallis, p \leq 0.004). Likewise, the size distribution of either species was different among the segments studied (Kruskal-Wallis, p \leq 0.05), (Kruskal-Wallis, p \leq 0.05), respectively, with a slant in favor of BACORE for *C. acutus*, and TNP for *C. crocodilus*.

As seen in Table 5, many more large-sized individuals of *C. crocodilus* were sighted within the TNP than BACORE, and the corresponding data analysis revealed a statistically significant difference ($X^2=5.62$, $p\le0.05$) regarding its size distribution between these two areas. By contrast, the *C. crocodilus* total sightings were similar between BACORE and TNP (Z=-1.22, $p\ge0.222$). Some segments had a higher probability of harboring caimans than did others in the sightings performed during the monitoring period ($X^2=8.36$, $p\le0.05$), namely (respectively) segments H, I and J (Jalova-Sierpe River, Caño Negro-Tortuguero, and Tortuguero-Samay Lake), all which belonged to the TNP zone. The Kolmogorov-Smirnov test indicated that the size distribution of the studied caiman population is not Gaussian (i.e., not normally distributed) (Dn=0.284, $p\le0.00001$).

Regarding *C. acutus*, 90% of its sightings were made in the BACORE area, for which a statistically significant difference in the number of sightings per segment was found ($X^2=7.34$, $p\leq0.026$). Our analysis indicated that the Colorado River segment is significantly

Segment	I	II.C	III	IV	Total	
A			2		2	
В		2	3		5	
С		3	2		5	
D	G					
E						
F	5	19	6		30	
G		3	3		6	
Н	3	5	5	6	19	
I	3	35	11	2	51	
J	5	34	29	19	87	

Table 4. Caiman (*Caiman crocodilus*) distribution by segment according to body size, in the North Caribbean, Costa Rica, 2019.

Table 5. Caiman (*Caiman crocodilus*) and crocodile (*Crocodylus acutus*) headcount by body size according to sampling site, in Costa Rica, 2019.

61

27

205

101

16

Total

		BACOR	BACORE, Species		TNP, Species		
		Caiman	Crocodile	Caiman	Crocodile		
		Headcount	Headcount	Headcount	Headcount		
Size	Recruit	5	46	11	0		
	Juvenile	27	22	74	7		
	Adult	16	8	72	2		
	Total	48	76	157	9		

more populated by *C. acutus* than the other segments (X^2 =7.28, p≤0.05), the studied segments present a non-significant difference in the number of crocodiles observed. For this species, there was a statistically significant difference in counts among the size classes throughout the study area (X^2 =5.529, p≤0.026), having a non-normal distribution (Dn=0.354, p≤0.00001).

Relative abundance was estimated to be 0.55 *C. acutus* and 1.37 *C. crocodilus* individuals per linear km. From the capture of 39 *C. crocodilus* we obtained a sex ratio of 30 males to 9 females (3.3:1 M:H). Just 1 male and 1 female *C. acutus* were captured, however.

Finally, the results showed that individuals of *C. acutus* were grouped (Z=1.93, p \leq 0.028), whereas those of *C. crocodilus* featured a more homogenous distribution in the habitat (most of these found were youths and adults) (Z=2.35, p \leq 0.009).

Discussion

The results were unexpected, in that the size structure of the *C. crocodilus* in BACORE, as well as TNP, was negatively skewed. This differs from that usually found in other localities inside and outside the country, including the same area of study as reported by Bolaños et al. (2019). Studies done in Costa Rica's northern zone (close to the North Caribbean) indicated great variation among *C. crocodilus* populations (Allsteadt and Vaughan 1992; Cabrera et al. 2003; Escobedo-Galván and González-Maya 2008), but they did find a negative skew like the one here in the North Caribbean.

Compared to the above-mentioned studies, *C. crocodilus* was characterized by a more homogenous distribution, with a relative abundance of 8.63 ind./km, this being considerably larger than the 2.2 ind./km reported by King et al. (1990) in a similar environment in Honduras, yet less than the 12.5 ind./km reported by Bolaños et al. (1997) for La Rambla in Sarapiquí, in the north of Costa Rica. By contrast, Balaguera-Reina and González-Maya (2009) reported numbers as low as 0.063 ind./ha in terms of density but argued that those are normal for environments under exploitation.

We speculate that because the study area is a low-lying permanently flooded region, smaller-sized individuals (I and II) would find more suitable habitat in the inner areas of the wetlands, where they would be less vulnerable to the perturbations on open canals caused by boats and their transit. Further, these smaller individuals would be less exposed to attacks from their predators. This view agrees with the findings of Bolaños et al. (1997) in the higher watershed of the Sierpe River. Likewise, there are other studies that suppose these juvenile individuals remain on interior wetlands as a natural strategy of species conservation (Bolaños et al. 1997; Da Silveira et al. 1997).

For the observed C. crocodilus population, its estimated numbers are consistent with that expected for size of the study area and its zones. Nevertheless, the fact that no adults (classification by body size III) or specimens ≥ 1.5 m were found in our sampling survey does not mean that they are not present; rather, given the dense foliage and habitat heterogeneity these caimans could have remained hidden further within the wetlands and along the internal water courses, beyond the reach of our sampling efforts (Bolaños et al. 1997; Da Silveira et al. 1997).

Regarding the size distribution of *C. acutus* individuals, the right negative skew in both TNP and BACORE coincides with that reported for other zones by Sánchez et al. (1996), Bolaños et al. (1997, 2019), Bolaños (2011a, 2011b, 2012a, 2012b), Murray et al. (2015), Orozco (2015), and Bolaños et al. (2019), the last one for the Central Caribbean.

Unlike C. crocodilus, whose individuals tend to be more social and to remain within

the family unit of their distribution zones (Gorzula and Seijas 1989), it is known that *C. acutus* hatchlings are carried away by river currents soon after they hatch and continue to move along the river course until they establish their own living sites (Bolaños et al. 2019).

The distribution and abundance of the two studied species are similar to those recorded in other studies (Allsteadt and Vaughan 1992; Cabrera et al. 2003; Escobedo-Galván and González-Maya 2008). These also showed how smaller-sized *C. acutus* arrive at the river mouths where they establish their territory (Thorbjarnarson 1989, 1992), a similar situation found in BACORE. We estimate that larger-sized *C. acutus* individuals could be revisiting the rivers in lower parts of the Caribbean coast recurrently, to not only maintain their territories but also procure sustenance as they do in the coastal area in the Central Caribbean of Costa Rica, as mentioned by Bolaños et al. (2019).

It is evident that the relative abundance of *C. acutus* is far less in the North Caribbean (0.55 ind./km) than the Central Caribbean where 1.77 ind./km was encountered (Bolaños et al. 2019). Nonetheless, it should be kept in mind that 89% of our sightings of this crocodilian species occurred within the BACORE study areas, in which about half (52%) of these individuals were sighted along segments A, B, and C. These correspond to the outermost part of the study, where the Colorado River and Caño Negro form two of these segments, and there is direct contact with San Juan River.

The abundance of *C. acutus* in the North Caribbean is considerably lower that what was recently reported for the Costa Rica's Central Caribbean (Bolaños et al. 2019). This disparity could be related to greater human activity in the Central Caribbean (which could provide more food supplies, mating and breeding areas, among others), a situation likewise evinced for other crocodilian distribution centers (Pooley et al. 1989; Pooley 2017) and those in Costa Rica (Sandoval-Hernández et al. 2017; Sandoval et al. 2019, 2020; Venegas-Anaya et al. 2015). The relative difference in abundance of *C. acutus* in the North Caribbean is high, if compared to that reported for rivers in the Pacific watershed of the Caribbean (Sánchez et al. 1996; Sánchez-Ramírez 2001; Valdelomar et al. 2012; Bolaños 2011a, 2012b; Orozco 2015; Sandoval et al. 2020).

Still, a key finding of this study is that the relative abundance of *C. crocodilus* (1.37 ind./km) is substantially less than in the neighboring Central Caribbean region (8.63 ind./km) (Bolaños et al. 2019). One reason for this latter value is due to animals occurring in zones where the human presence is more pronounced, so that *C. acutus* could take advantage of the resources generated in more urbanized areas (as food or biowaste resources, mating and breeding areas as mentioned). Similarly, this could also explain why the abundance of *C. crocodilus* in the TNP zone of the study area was considerably greater than that found in the BACORE zone. One hundred and fifty-six individuals (77%) were observed in the TNP. Of the remaining 33% in the BACORE, just 12 (24%) were encountered in the three segments in which sightings of *C. acutus* were highest, close to the San Juan River. This result is consistent with findings for other world areas by Amarasinghe et al. (2015), Saalfeld et al. (2016), Pooley (2017), and by Sandoval et al. (2019, 2020), on the Central Pacific side of Costa Rican.

We speculate that *C. acutus* aggregation could be driven by the found animals being in size class I and II, the recruits, since we know this social behavior is typically for that life stage according to observations by Sánchez et al. (1996), Sánchez-Ramírez (2001), Bolaños (2011a, 2012b), Espinal and Escobedo-Galván (2011), and Orozco (2015). Yet *C. crocodilus* could also benefit directly from the favorable conditions in a wide part of the study area for the persistence of this species, as reported on by Ouboter and Nanhoe (1988), Allsteadt (1994), Herron (1994), Da Silveira et al. (1997), Velazco and Ayarzagueña (2010), and Aranda-Coello (2017).

Conflict of interest

We declare that there is no conflict of interest.

Authors' contributions

JRBM conceived and designed the study, JJSR, ISH, JRBM collected the data, ISH, JRBM and JSMG interpreted the results and prepared the draft manuscript. All authors received the results and approved the final version of the manuscript.

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