Herpetological Conservation and Biology 10(3):959–968.
Submitted: 11 July 2015; Accepted: 19 October 2015; Published: 16 December 2015.

ANALYSIS OF POPULATION DENSITY AND DISTRIBUTION OF SPECTACLED CAIMAN (*CAIMAN CROCODILUS*) IN CAÑO PALMA, NORTHEAST COSTA RICA

LUIS M. FERNÁNDEZ*[1], *MANUEL ARIAS*, *AND EMILY S. KHAZAN

Caño Palma Biological Station, Canadian Organization for Tropical Education and Rainforest Conservation (COTERC), Tortuguero, Limón, Costa Rica
[1]Corresponding author, e-mail: lmfdezp@gmail.com

***Abstract.*—In nearly all ecosystems, top predators play a key role, influencing communities by driving top down effects. The Spectacled Caiman (*Caiman crocodilus*), one of two species of crocodilians in Costa Rica, plays this role in many Neotropical rivers. As a long-lived top predator, it can be used as environmental sentinel to help assess ecosystem conditions of inhabited areas. Here, we assess the population size of *C. crocodilus* in a canal in Northeast Costa Rica and the distribution and clustering of age classes throughout the canal. We conducted weekly surveys between May 2012 and April 2015. We estimated the relative age of the caimans as either juvenile, sub-adult, adult, or eyes only, and we recorded GPS coordinates for each individual. We estimated the total population size using the visible fraction (VF) method. The overall VF was 45.09% and the population was estimated at 32.39 caimans (6.48 caimans/km). The abundance of juveniles decreased over the study period while sub-adults and adults increased over time. Local Moran's I and Hot-Spot analyses demonstrated that caimans are clustered within the canal with juveniles showing the highest levels of clustering in discrete areas, followed by adults. This study provides a population estimation which can serve as a baseline for continued monitoring efforts and to detect long-term changes in density and age demographics of the Spectacled Caiman population of Caño Palma.**

Key Words.—neotropical rivers; population estimation; spatial clustering; Tortuguero; Costa Rica

***Resumen.*—En casi todos los ecosistemas, los grandes depredadores juegan un papel esencial, influyendo en las comunidades mediante diversos efectos en cascada. El caimán (*Caiman crocodilus*), una de las dos especies de cocodrilos de Costa Rica, juega este papel en muchos ríos neotropicales. Además, como depredador de vida larga, puede ser usado como centinela ambiental para ayudar a evaluar las condiciones de sus hábitats. Aquí, evaluamos el tamaño poblacional en un canal del noreste de Costa Rica y la distribución y el agrupamiento de las clases de edad a lo largo del canal. Se realizaron muestreos semanales entre mayo de 2012 y abril de 2015. Los caimanes observados se clasificaron en juveniles, sub-adultos, adultos o sólo ojos, y se registraron las coordenadas GPS. Se estimó la población total usando el método de la fracción visible (FV). La FV fue 45,094% y la población se estimó en 32,39 caimanes (6,476 caimanes/km). La abundancia de juveniles disminuyó a lo largo del periodo de estudio, mientras que los sub-adultos y adultos aumentaron. Los análisis espaciales (Local Moran's I y Hot-spot) mostraron una agrupación de los caimanes en el canal, especialmente de los juveniles seguidos por los adultos. Este estudio provee una estima poblacional que puede servir como base para esfuerzos de monitoreo continuado y para detectar cambios a largo plazo en la densidad y demografía de la población de caimanes de Caño Palma.**

INTRODUCTION

Top predators play a key role in nearly all ecosystems, influencing communities by many top down effects, including nutrient cycling (Fittkau 1970) and direct predation (Creel and Christianson 2008; Heithaus et al. 2008). In Neotropical riverine ecosystems, crocodilians represent a notable group of top predators whose presence has cascading ecological effects. For example, they are important in controlling prey populations (Medem 1981) and in the conservation of energetic balance (Escobedo-Galván and González-Maya 2008).

The Spectacled Caiman (*Caiman crocodilus*; Fig. 1) is one of two species of crocodilians in Costa Rica (Savage 2002). *Caiman crocodilus* inhabits a variety of freshwater habitats including streams, lagoons, and slow moving rivers (Savage 2002; Köhler 2008; Velasco and Ayarzagüena 2010). In most of Costa Rica, breeding takes place before the beginning of the rainy season (February/March), occurring later in the northwest of the country, between June and August (Savage 2002). *Caiman crocodilus* is the most abundant species of crocodilian in Costa Rica (Junier 2000; Leenders 2001; Cabrera et al. 2003) and in many regions across its range (King 1989; Ross 1998; Escobedo-Galván 2008). The abundance of *C. crocodilius* in Costa Rica is a result of higher current and former hunting pressure affecting the only other crocodilian inhabiting the country, the American Crocodile (*Crocodylus acutus*, Cuvier 1807; Thorbjarnarson et al. 2006), its higher resilience to

FIGURE 1. Adult Spectacled Caiman (*Caiman crocodilus*) from Caño Palma, Limón, Costa Rica. (Photographed by Emily S. Khazan).

hunting pressure, and to its reproduction at smaller sizes (King et al. 1990; Villamarín et al. 2011).

The assessment of *C. crocodilius* populations is important to help evaluate ecosystem conditions of their habitats. They can be used as environmental sentinels owing to their apex position in the food web, sensitivity to aquatic pollutants like pesticides, and life-history characteristics such as their long life span (Campbell 2003; Sergio et al. 2008; Grant et al. 2013). Long-term data collection and monitoring is necessary to detect trends in populations of long-lived species like crocodilians (King et al. 1990).

We assessed the size and distribution of the Spectacled Caiman population inhabiting Caño Palma, a narrow canal located near the southern border of the Barra del Colorado National Wildlife Refuge in northeast Costa Rica. Spectacled Caimans are common within the small canals throughout the refuge and act as top predators therein (Grant et al. 2013). Knowing the current size of this population will allow for more effective monitoring in the future and long-term population declines may reflect threats to the ecosystem at large. In addition to assessing population size, using demographic data collected at Caño Palma Biological Station (CPBS), we examined the differential distribution and clustering of age classes (juvenile, sub-adult, and adult) throughout the canal. This spatial analysis allows us to begin to understand the differential habitat use of size classes and provides a starting point from which nest searches and studies on breeding ecology may begin.

MATERIALS AND METHODS

***Study area.*—**The Barra del Colorado National Wildlife Refuge (812 km^2) is located in northeastern Costa Rica, bordering Tortuguero National Park to the north and the Indio Maíz Biological Reserve (Nicaragua) to the south. The refuge lies within the Tortuguero Conservation Area (ACTo), which encompasses both the refuge and the national park. The palm-dominated forests of the region experience periodic flooding (Myers 1981; Lewis et al. 2010) and settlements and farms are connected by a network of canals and waterways. This study was conducted in Caño Palma, a 5 km long canal (Fig. 2). This area is defined as Atlantic Lowland Tropical Wet Forest (Holdridge 1967), with annual rainfall exceeding 500 cm and an average daily temperature throughout the year of 26º C (Lewis et al. 2010). There are no distinct wet and dry seasons as in much of the Neotropics; however, there are rainfall peaks in July and again in December, which often results in flooding (Myers 1981).

***Surveys.*—**We conducted weekly surveys between May 2012 and April 2015 along 5 km of the canal (Start: 10º35´4.4808´´N -83º31´54.5874´´W; End: 10º37´44. 2878´´N -83º32´57.624´´W) beginning at 2000 ($\bar{X}$ = 1.98 h per survey). They took place under all moon phases and weather conditions except for when rain was so heavy that eyeshine was no longer visible. Survey teams consisted of five people: Manuel Arias drove the boat (a 4.9 m length motor boat, with a 50 horsepower outboard) for each survey and served as the most experienced team member with respect to spotting and determining the size class of caimans; the other four members were trained volunteers and Caño Palma Biological Station staff. All participants scanned the water with flashlights looking for eyeshine of caimans. The count methodology followed that described by Chabreck (1966) and Magnusson (1983). Individuals were located using eyeshine; we did not capture or otherwise handle caimans. We visually estimated the relative size of caimans as either juvenile (Total Length [TL] < 75 cm), sub-adult (TL = 75–120 cm), or adult (TL > 120 cm; Staton and Dixon 1975), and recorded GPS coordinates for each spotted individual (GPSmap 62s, Garmin Ltd.,

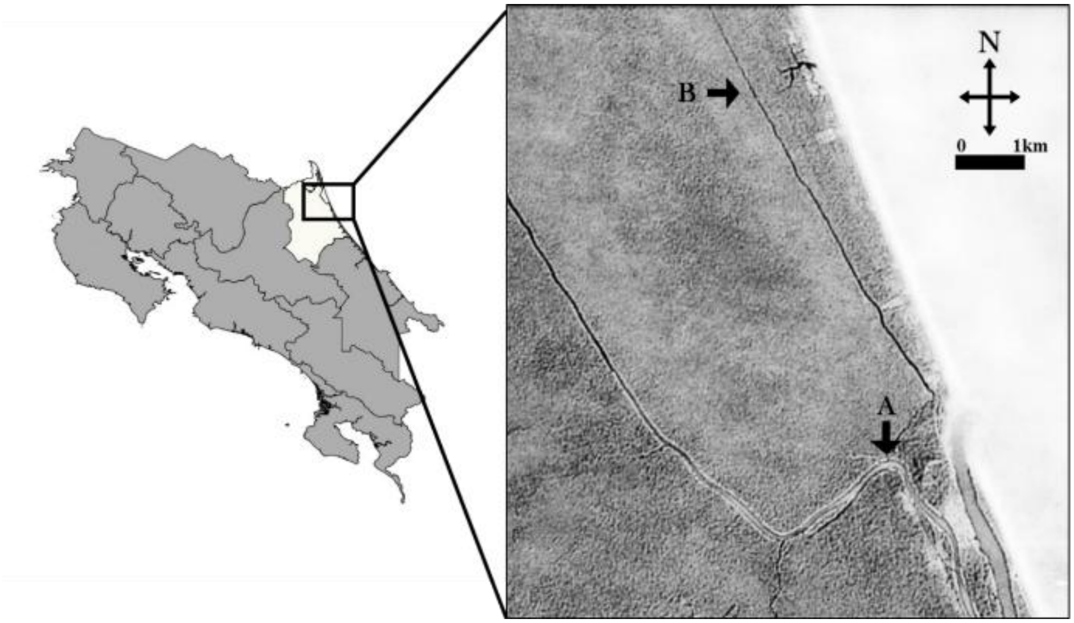

FIGURE 2. Study area within Caño Palma, Costa Rica. A) Start point of the transect. B) End point of the transect. (Taken from Google Earth 2015).

Schaffhausen, Switzerland). If an individual submerged itself before its size could be estimated, we classified it as Eyes Only (EO), and recorded the coordinates.

We included all caimans observed, regardless of size. This method differs from some other comparable studies that do not include hatchling caimans (SVL < 20 cm) in censuses due to their high mortality (e.g., Da Silveira and Thorbjarnarson 1999). We observed very few hatchlings throughout the course of the study, perhaps because of their lower detection probability, and grouped them with juveniles. This omission is particularly important for the management of hunted populations. However, as this study was not carried out to provide information for harvest quotas, and the caiman population of Caño Palma has little hunting pressure (pers. obs.), we recorded all juveniles, including hatchlings.

Analysis.—We estimated the total population using the visible fraction (VF) method according to the formula

$$\mathrm{VF} = \bar{X}/(2\ \mathrm{SD} + \bar{X})1.05,$$

where $\bar{X}$ is the mean census value. This equation has been used previously to calculate populations of caiman and other crocodilians (Cabrera et al. 2003; King et al. 1990). The population estimation was then back calculated as $\bar{X}$/VF. We used negative binomial regression to test for differences in total number of caimans observed across years and differences in abundance of the different age classes across years. If that test produced significant results, we followed up by conducting Kruskal-Wallis tests (α = 0.05) with post-hoc pair-wise tests using the Dunn method in SPSS version 20 (SPSS Inc., Chicago, Illinois, USA).

We performed a linear regression to examine the relationship between the canal depth and the number of caimans observed using canal depth data recorded daily by Caño Palma Biological Station. As water level impacts caiman detection (Messel et al. 1981), we split the dataset by depth using 1.53 m (the median depth value) as the splitting point and calculated the visible fraction and density estimation for high and low canal levels separately. To gain a better understanding of the use of the canal by the different size classes, we conducted spatial clustering analyses including Global Moran's I (Moran 1950) and Getis-Ord General G (Getis and Ord 1992) tests in ArcGIS 10.1 (Esri, Redlands, California, USA). We performed other cluster mapping analyses including Anselin Local Moran´s I (Anselin 1995) and Hot Spot Analysis (Ord and Getis 1995) using the same software. All maps were created with QGIS 2.6 Brighton (QGIS Development Team 2014, Boston, Massachusetts, USA).

RESULTS

We conducted 147 surveys over three years that produced 2,147 caiman observations (Table 1; Fig. 3). The number of caimans observed per survey ranged from 0 to 39 ($\bar{X}$ ± SD = 14.61 ± 9.70). We found no significant differences in the total number of caimans

TABLE 1. Total number seen, mean number seen per survey, visual fraction (VF) of the population seen, and the estimated population size (EstPop.) by size classes of Spectacled Caimans (*Caiman crocodilus*) at Caño Palma, Costa Rica during the three year study period (May 2012 to April 2015). Total number seen is larger than the sum of size classes because some caimans seen could not be classified to a group. The abbreviation OM is the overall mean.

Group	Year	Total	Mean ± SD	VF (%)	EstPop.
Juveniles	1	369	8.02 ± 6.22	41.15	19.5
	2	299	5.86 ± 4.00	44.37	13.2
	3	171	3.42 ± 3.34	35.52	9.63
	Sum/OM	839	5.71 ± 4.97	38.31	14.9
Sub-Adults	1	99	2.15 ± 2.26	33.86	6.35
	2	180	3.53 ± 2.56	42.81	8.24
	3	227	4.54 ± 4.32	36.14	12.6
	Sum/OM	506	3.44 ± 3.23	35.83	9.61
Adults	1	155	3.37 ± 3.39	34.82	9.68
	2	285	5.59 ± 4.68	39.24	14.2
	3	337	6.74 ± 5.08	41.86	16.1
	Sum/OM	777	5.29 ± 4.65	38.04	13.9
Total	1	627	13.6 ± 9.17	44.76	30.5
	2	770	15.1 ± 8.82	48.41	31.2
	3	750	15.0 ± 11.1	42.42	35.4
	Sum/OM	2,147	14.6 ± 9.71	45.09	32.4

observed between years ($H = 0.555$, $P = 0.758$). The VF for the three-year period was 45.09% and the population was estimated at 32.38 caimans. The density was calculated at 6.48 caimans/km.

As established, there are no distinct wet and dry seasons in the area; however, the depth of the canal changed dramatically throughout the year ($\bar{X}$ ± SD = 1.53 ± 0.286 m; range 1.14–2.51 m). Based on the results of a linear regression, we found a significant relationship between canal depth and the number of caimans detected per survey (Number of caimans = -22.06 canal depth + 48.16; $r^2 = 0.433$; $P < 0.001$). In light of these results, we divided surveys depending on the canal depth (based on CPBS data) as opposed to seasons as other studies have done (e.g., Allsteadt and Vaughan 1992a, b; Cabrera et al. 2003). For the surveys when the canal was shallower or equal to 1.53 m (n = 79), the VF was 49.78% and we estimated the population at 36.99 caimans. However, for surveys completed when the canal was deeper than 1.53 m (n = 54), the VF was 34.34% and the estimated population size was 24.47. For the regression, we omitted data from 14

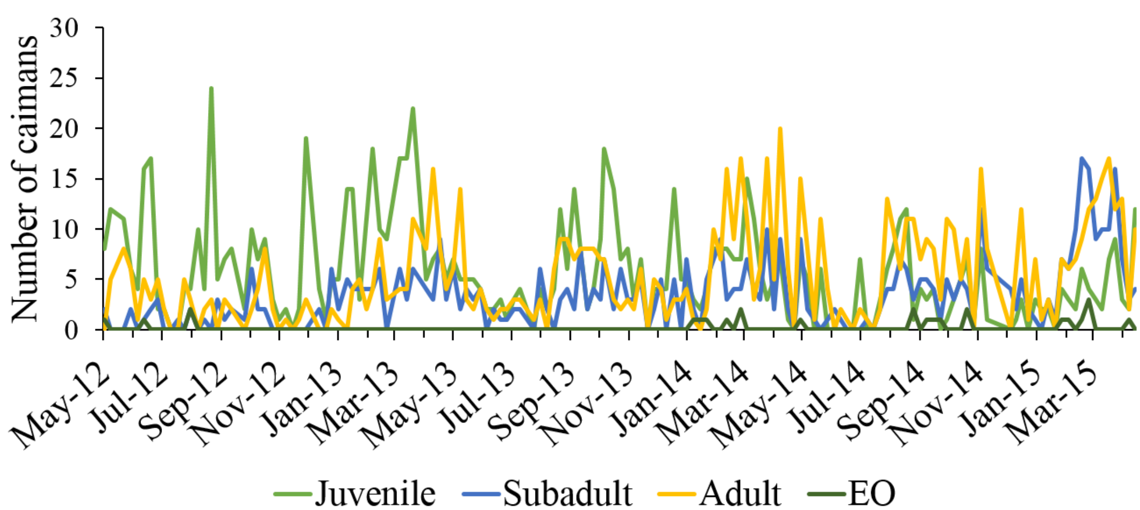

FIGURE 3. Total number of Spectacled Caiman (*Caiman crocodilus*) observed per survey divided by relative age classes over the three year study period.

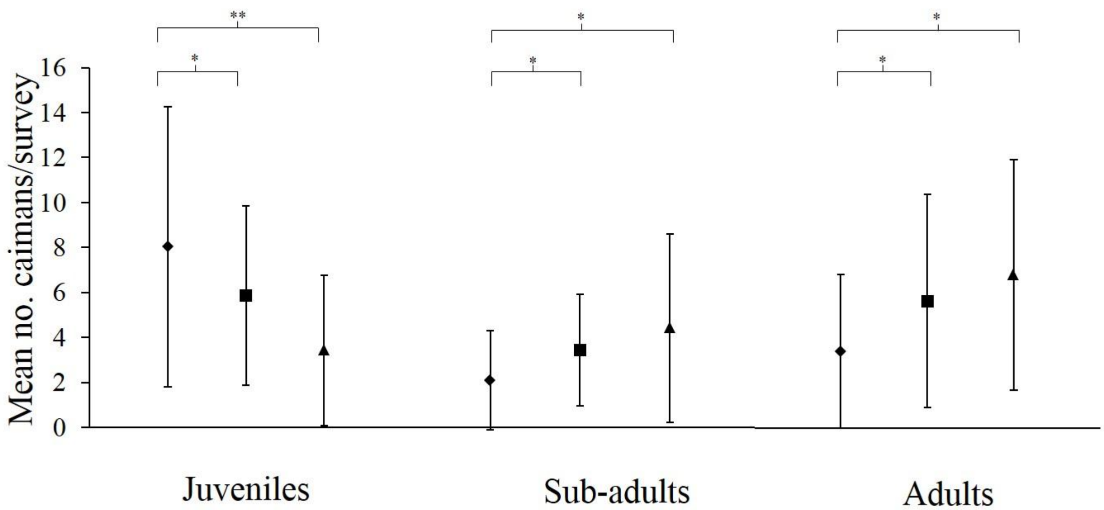

FIGURE 4. Average number (± SD) of Spectacled Caimans (*Caiman crocodilus*) observed per survey divided by age class and year. Year 1 are diamonds, year 2 squares , and year 3 triangles. Pair-wise Dunn's test (following Kruskal-Wallis test): ***:** $P < 0.05$; ****:** $P < 0.001$.

surveys conducted on days when we did not measure the canal depth. The estimations under conditions of low and high canal levels resulted in densities of 7.39 and 4.89 caimans/km, respectively. These contrasting estimates are due to the difference in detection probability based on canal depth.

The number of adults found per survey ranged from 0 to 20 individuals ($\bar{X} \pm SD = 5.29 \pm 4.65$); sub-adults from 0 to 17 ($\bar{X} = 3.44 \pm 3.32$), and juveniles from 0 to 24 ($\bar{X} = 5.71 \pm 4.97$). Across the three years, we found significant differences in abundance of individuals per age class ($H = 43.9$, $P < 0.001$; Fig. 4). Post-hoc pairwise comparisons demonstrated that the number of juveniles was significantly higher in the first year than the second and third year ($z = -26.86$, $P = 0.004$; $z = -37.07$, $P < 0.001$, respectively). In concert, the number of sub-adults increased from year one to year two ($z = -22.95$, $P = 0.022$). We documented significantly more sub-adults in year one compared with year three as well ($z = -26.86$, $P=0.005$). There were only marginally more adults in year two than year one, and significantly more in year three than year one ($z = -21.20$, $P = 0.042$; $z = -29.00$, $P = 0.002$, respectively).

The results of the spatial cluster analysis demonstrate that the distribution of individuals is not random, and is clustered (Global Moran´s $I = 0.264$; $P < 0.001$; $Z = 52.67$). Further analysis showed that juveniles were significantly clustered (Getis-Ord General $G = 0.0027$; $P < 0.01$; $Z = -2.64$). While it is possible that the same individual was counted in the same place during sequential surveys, the number of surveys and length of time of the study make these analyses robust to pseudoreplication. Anselin Local Moran´s I and Hot Spot Analysis showed that both juveniles and adults were significantly clustered in specific zones (Fig. 5).

DISCUSSION

Based on regular weekly surveys carried out for three years, the estimated caiman population in Caño Palma is between 24.47 and 36.99 individuals. Due to the discrepancy between estimations based on canal depth and because combining all surveys covers all environmental conditions (Coutinho and Campos 1996), we have accepted the population estimation of 32.39 caimans (6.48 caimans/km) based on the population estimation from all surveys, further supported by the estimates produced from surveys conducted under deep and shallow canal conditions. The most influential factor in caiman detectability is water level, as demonstrated in other studies (e.g., Messel et al. 1981); however, other factors such as air and water temperature, rainfall, wind speed, and/or moon phase can influence detectability (Pacheco 1990; Campos et al. 1994; Escobedo-Galván 2003; Escobedo-Galván and González-Maya 2006). Lower water levels diminish available habitat for caimans and restrict them to wet areas closer to the center of a given waterway. Higher water levels provide increased available habitat (Allsteadt and Vaughan 1992b) for resting, feeding (Ouboter and Nanhoe 1988), or hiding from predators and disturbances, and additional microhabitats for facilitating thermoregulation (Allsteadt and Vaughan 1992a; Grant et al. 2008).

This density estimation per linear kilometer of the caiman population at Caño Palma is smaller than other Costa Rican caiman populations, but comparable to

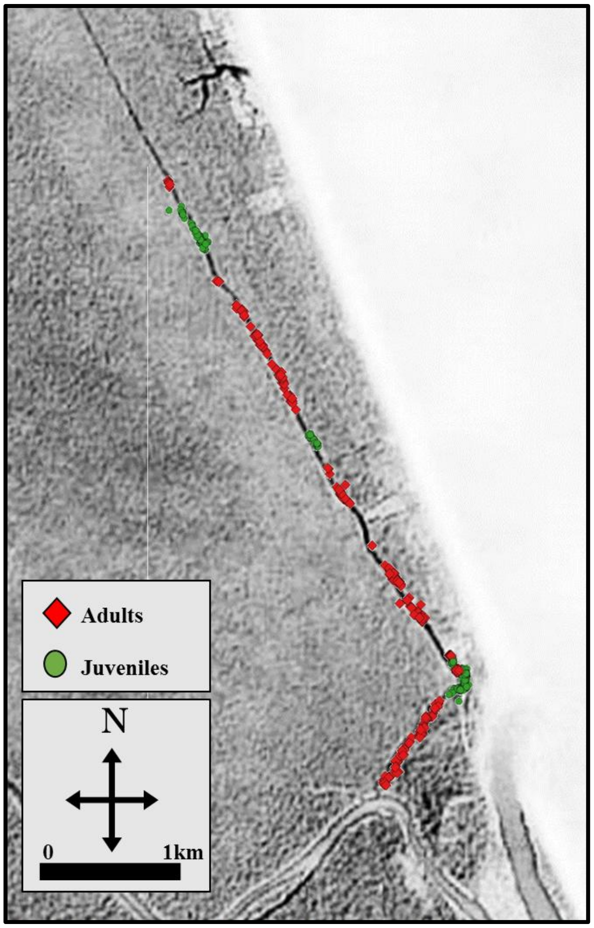

FIGURE 5. Significant clustering (Anselin Local Moran´s I, $P<0.01$) of adult (red diamonds) and juvenile (green dots) Spectacled Caiman (*Caiman crocodilus*) along the canal at the study site in Caño Palma, Costa Rica.

TABLE 2. Population density estimates (individuals/km) of Spectacled Caiman (*Caiman crocodilus*) in the range of the species.

Site	Density	Study
Río Frío, Caño Negro, Costa Rica	74.4	Cabrera et al. 2003
Río Frío, Caño Negro, Costa Rica	53.0	Allsteadt and Vaughan 1992a
Río Frío, Caño Negro, Costa Rica	66.1	Junier 2000
Río Sierpe, Costa Rica	10.5	Bolaños et al. 1996-1997
La Rambla, Sarapiquí, Costa Rica	2.33	Bolaños et al. 1996-1997
Río Maria, Perú	6.60	Morley and Sanchez 1982
Atlantic zone, Honduras	6.17	King et al. 1990

other studies throughout the range of the species (Table 2). The estimated population density of 6.48 caimans/km, while conservative, seems realistic for Caño Palma in the context of the aforementioned studies. As hunting pressure is not a threat for this population, it is likely that nest predation and flooding (an important cause of mortality of caiman eggs; Campos 2003) are limiting factors for the growth of the population.

The abundance of juveniles decreased over the study period while abundance of sub-adults and adults increased over time. While growth rates differ between male and female *C. crocodilus* (Da Silveira et al. 2013), making it difficult to estimate age (in years) of the caimans seen throughout this study, it is likely that some of the increase of the larger two age classes reflects recruitment of individuals seen from one year to the next. Because growth in crocodilians has been associated with prey availability (Webb et al. 1983; Ouboter and Nanhoe 1984; Rootes et al. 1991; Wilkinson and Rhodes 1997), this indirect measure of growth indicates the productivity (i.e., prey availability) of the ecosystem of Caño Palma. The lack of recruitment to the juvenile age class over the study period may be attributable to higher mortality of hatchlings and variation in nest success over the years as a result of nest flooding, invasion by ants, or temperatures incompatible with viable eggs (Staton and Dixon 1977; Webb and Smith 1984; Campos 2003). The likelihood of nest failure leading to the lack of juvenile recruitment is further supported by the higher proportions of adults over time, and thus the increase of sexually mature individuals. Another hypothesis to explain the decline in juvenile abundance is that larger caimans prey on hatchlings and other small juveniles, which is supported by the simultaneous increase in adults and decrease in juveniles, especially as larger caimans have been found to commonly eat larger prey including vertebrates such as mammals and large fish (Thorbjarnarson 1993).

Caiman crocodilus in Costa Rica breeds before the rainy season starts (February to March) in the majority of the country, but this period is delayed in the northwest (June to August; Savage 2002). However, over the three years of study, we encountered juveniles throughout the year experiencing stochastic peaks in abundance. This is likely a reflection of the lack of distinct seasons in the region, and the risk of heavy rains and flooding year-round (Myers 1981).

Despite the extreme dynamism of the canal depth, there were clear spatial patterns of occurrence of the age classes. Within Caño Palma, juveniles congregated in distinct areas, which may represent the most elevated riparian regions and thus the best (or maybe the only) nesting sites (Savage 2002). Spatial clustering of juveniles has been documented in other studies (Stanton and Dixon 1977; Savage 2002; Velasco and Ayarzagüena 2010) in which clustering was associated with various habitat characteristics including water level, temperature, and substrate type. The lack of adequate cartographical data and the large number of water bodies (e.g., permanent and ephemeral pools, canals, and small rivers) in the surrounding forest make finding nests difficult; however, the areas of juvenile clustering represent a good starting point for nest searching. We did not search for nests as a part of this research, and nest locations have not been documented in this canal in the past. We were also unable to measure canal depth in the areas where juveniles clustered; however, those data should be recorded in the future as they would be complementary to nest searching and may provide more explanation for the spatial clustering of juveniles.

While this three-year dataset shows a consistent and stable caiman population in Caño Palma, previous studies and current climatic trends highlight important conservation concerns. For example, Grant et al. (2013) showed that this population of caimans is affected by pesticides used in banana plantations upstream, which reduce their body condition. Rainwater et al. (2007, 2011) also found traces of pesticides and subsequent negative health impacts on additional populations of crocodilians in Costa Rica and other parts of Central America. Other studies have demonstrated that chemical compounds found in locally used pesticides can lead to an increase in disease not only in the wildlife (Gilbertson et al. 1991; Guillette 2006), but also in humans (Wesseling et al. 1993, 1996). Other anthropogenic influences including boat traffic have also been demonstrated to have negative effects on caimans of Caño Palma (Grant and Lewis 2010).

Rising global temperatures pose additional conservation concerns for caimans and other ectothermic vertebrates. This phenomenon will likely negatively affect many herpetofauna with specific and limited distributions, and specialized trophic niches (Laurence et al. 2011; Escobedo-Galván et al. 2012), thus further justifying long-term monitoring like that carried out by Caño Palma Biological Station. Species with temperature-dependent sex determination may be particularly affected by rising temperatures, especially those species for which higher temperatures result in male-biased sex ratios, like caimans (Lang et al. 1989). Increased incubation temperature can also affect egg viability (Webb and Smith 1984; Campos 2003) and has already been documented in caiman populations (Campos 2003; Escobedo-Galván 2006).

The caiman population at Caño Palma is likely important for local food webs. The spatial clustering of age groups demonstrates interesting differential use of the canal and should inspire future research on distinct microhabitats in the canal. Future research on ecological distinctions between age classes should also shed light on recruitment and maturity rates of the species. This study provides a population estimation that can serve as a guide for future studies and provide a baseline for continued monitoring efforts and to detect long-term changes in density and age demographics.

Acknowledgments.—We thank Don Shepard and Jessica Beyer for statistical help; Charlotte Foale, former Caño Palma Biological Station staff including Paul Grant, Todd Lewis, Aidan Hulatt, Elias Bader, and many interns and volunteers for continuous data collection and logistical support; COTERC; and MINAE for facilitating research permits (ACTo-GASP-PIN-06–2013; 010–2014-SINAC-ACTo-GASP-PIN; SINAC-ACTO-D-RES -038–2014).

LITERATURE CITED

Allsteadt, J., and C. Vaughan. 1992a. Population status of *Caiman crocodilus* (Crocodylia: Alligatoridae) in Caño Negro, Costa Rica. Brenesia 38:57–64.

Allsteadt, J., and C. Vaughan. 1992b. Dry season habitat selection of *Caiman crocodilus* (Crocodylia: Alligatoridae) in Caño Negro, Costa Rica. Brenesia 38:65–69.

Anselin, L. 1995. Local indicators of spatial association – LISA. Geographical Analysis 27:93–115.

Bolaños, J.R., J. Sánchez, and L. Piedra. 1996–1997. Inventario y estructura poblacional de crocodílidos en tres zonas de Costa Rica. Revista de Biología Tropical 44/45:283–287.

Cabrera, J., M. Protti, M. Urriola, and R. Cubero. 2003. Distribución y abundancia de *Caiman crocodilus* en el Refugio Nacional de Vida Silvestre Caño Negro, Costa Rica. Revista de Biología Tropical 51:571–578.

Campbell, K.R. 2003. Ecotoxicology of crocodilians. Applied Herpetology 1:45–163.

Campos, Z. 2003. Effect of habitat on survival of eggs and sex ratio of hatchlings of *Caiman crocodilus yacare* in the Pantanal, Brazil. Journal of Herpetology 27:127–132.

Campos, Z., M. Mourao, M. Coutinho, and C. Abercrombie. 1994. Night-light, size structures, and sex ratios in wild populations of Yacaré (*Caiman crocodilus yacare*) in the Brazilian Pantanal. Vida Silvestre Neotropical 4:46–50.

Chabreck, R.H. 1966. Methods of determining the size and composition of Alligator population in Louisiana. Proceedings Annual Conference Southeast Association Game Fishing Community 20:105–112.

Coutinho, M., and Z. Campos. 1996. Effect of habitat and seasonality on the densities of caiman in southern Pantanal, Brazil. Journal of Tropical Ecology 12:741–747.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194–201.

Da Silveira, R., and J.B. Thorbjarnarson. 1999. Conservation implications of commercial hunting of

Black and Spectacled Caiman in the Mamirauá Sustainable Development Reserve, Brazil. Biological Conservation 88:103–109.

Da Silveira, R., Z. Campos, J.B. Thorbjarnarson, and W.E. Magnusson. 2013. Growth rates of Black Caiman (*Melanosuchus niger*) and Spectacled Caiman (*Caiman crocodilus*) from two different Amazonian flooded habitats. Amphibia-Reptilia 34:437–449.

Escobedo-Galván, A.H. 2003. Períodos de actividad y efecto de las variables ambientales en cocodrilos (*Crocodylus acutus* Cuvier 1807): evaluando los métodos de determinación de la fracción visible. Ecología Aplicada 2:136–140.

Escobedo-Galván, A.H. 2006. Temperature variation in nests of *Caiman crocodilus* (Crocodylia: Alligatoridae). Acta Herpetológica 1:131–134.

Escobedo-Galván, A.H. 2008. Estructura poblacional y proporción de sexos en *Caiman croodilus* en Caño Negro, Costa Rica. Iheringia, Série Zoologia 98:489–492.

Escobedo-Galván, A.H., and J.F. González-Maya. 2006. Estructura poblacional y proporción de sexos del caimán (*Caiman crocodilus*) en el río Sierpe, Costa Rica. Acta Zoológica Mexicana 22:151–153.

Escobedo-Galván, A.H., and J.F. González-Maya. 2008. Estado poblacional del caimán, *Caiman crocodilus*, en el Refugio Nacional de Vida Silvestre Caño Negro, Costa Rica. Yu´am: Revista Mesoamericana de la Conservación 1:15–22.

Escobedo-Galván, A.H., J.A. Retana, C. Méndez, and J.F. González-Maya. 2012. Efecto potencial del cambio climático en la proporción de sexos del caimán en Costa Rica. Ambientales 44:49–60.

Fittkau, E.J. 1970. Role of caimans on the nutrient metabolism of mouth-lakes of Amazon effluents (an hypothesis). Biotropica 2:132–142.

Getis, A., and J.K. Ord. 1992. The analysis of spatial association by use of distance statistics. Geographical Analysis 24:189–206.

Gilbertson, M., T. Kubiak, J. Ludwig, and G. Fox. 1991. Great Lakes embryo mortality, edema and deformities syndrome (GLEMEDS) in colonial fish-eating birds: similarity to chick edema disease. Journal of Toxicology and Environmental Health 33:455–520.

Grant, P., and T. Lewis. 2010. High speed boat traffic: a risk to crocodilian populations. Herpetological Conservation and Biology 5:456–460.

Grant, P., M.B. Woudneh, and P.S. Ross. 2013. Pesticides in blood from Spectacled Caiman (*Caiman crocodilus*) downstream of banana plantations in Costa Rica. Environmental Toxicology and Chemistry 32:2576–2583.

Grant, P., T. Lewis, T.C. Laduke, and C. Ryall. 2008. *Caiman crocodilus*: opportunistic foraging. Herpetological Review 39:345–346.

Guillette, L.J. 2006. Endocrine disrupting contaminants: beyond the dogma. Environmental Health Perspectives 114:9–12.

Heithaus, M.R., A. Frid, A.J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution 23:202–210.

Holdridge, L.R. 1967. Ecología Basada en Zonas de Vida. 3rd Edition. Editorial del Instituto Interamericano de Cooperación para la Agricultura (IICA), San José, Costa Rica.

Junier, E. 2000. Análisis de la población de *Caiman crocodilus* en el Refugio Nacional de Vida Silvestre Caño Negro, Costa Rica. Lic. Thesis. Universidad Nacional, Heredia, Costa Rica. 46 p.

King, F.W. 1989. Conservation and management. Pp. 216–229 *In* Crocodiles and Alligators. Ross, C.A. (Ed.). Golden Press Pty. Ltd, Silverwater, Australia.

King, F.W., M. Espinal, and C. Cerrato 1990. Distribution and status of the crocodilians of Honduras. Pp. 313–354 *In* Crocodiles: Proceedings of the Working Meeting of the Crocodile Specialist Group. International Union for Conservation of Nature, Gland, Switzerland.

Köhler, G. 2008. Reptiles of Central America. 2nd Edition. Herpeton Verlag, Offenbach, Germany.

Lang, J.W., H. Andrews, and R. Whitaker. 1989. Sex determination and sex ratios in *Crocodylus palustris*. American Zoologist 29:935–952.

Laurence, W.F., D.C. Useche, L.P. Shoo, S.K. Herzog, M. Kessler, F. Escobar, G. Brehm, J.C. Axmacher, I.-C. Cheng, L. Arellano, et al. 2011. Global warming, elevational ranges and the vulnerability of tropical biota. Biological Conservation 144:548–557.

Leenders, T.A. 2001. A Guide to the Amphibians and Reptiles of Costa Rica. Distribuidores Zona Tropical. Miami, Florida, USA.

Lewis, T., P. Grant, M. García, C. Ryall, and T. LaDuke. 2010. A botanical survey of Caño Palma Biological Station (Estación Biológica Caño Palma), Tortuguero, Costa Rica. Brenesia 73–74:73–84.

Magnusson, W.E. 1983. Size estimates of crocodilians. Journal of Herpetology 17:86–88.

Medem, F. 1981. Los Crocodylia de Sur América. Editorial Carrera, Bogotá, Colombia.

Messel, H., G.C. Vorlicek, A.G. Wells, and W.J. Green. 1981. Surveys of Tidal River Systems in Northern Territory of Australia and Their Crocodile Populations. Monograph 1. Pergamon Press. Sydney, Australia.

Moran, P.A.P. 1950. Notes on continuous stochastic phenomena. Biometrika 37:17–23.

Morley, S., and S. Sánchez. 1982. Censo Preliminar de la Fauna Ribereña en el Bajo Urubamba. Universidad Nacional Agraria, Lima, Perú.

Myers, R.L. 1981. The ecology of low diversity palm swamps near Tortuguero, Costa Rica. Ph.D. Dissertation. University of Florida, Gainesville, Florida. University Microfilms International. 300 pp.

Ouboter, P.E., and L.M.R. Nanhoe. 1984. An ecological study of *Caiman crocodilus crocodilus* in northern Suriname. M.Sc. Thesis, Report no. 233, Zoölogisch Laboratorium Afdeling Dieroecologie, Kath. University of Nijmegen, Nijmegen, Netherlands. 65 pp.

Ouboter, P.E., and L.M.R. Nanhoe. 1988. Habitat selection and migration of *Caiman crocodilus crocodilus* in swamp and swamp-forest habitat in northern Suriname. Journal of Herpetology 22:283–294.

Ord, J.K., and A. Getis. 1995. Local spatial autocorrelation statistics: distributional issues and an application. Geographical Analysis 27:286–306.

Pacheco, L. 1990. Wariness of caiman populations and its effect on abundance estimates. Journal of Herpetology 30:123–126.

Rainwater, T.R., N.J. Millichamp, L.D.B. Barrantes, B.R. Barr, J.R.B. Montero, S.G. Platt, M.T. Abel, G.P. Cobb, and T.A. Anderson. 2011. Ocular disease in American Crocodiles (*Crocodylus acutus*) in Costa Rica. Journal of Wildlife Diseases 47:415–426.

Rainwater, T.R., T.H. Wu, A.G. Finger, J.E. Cañas, L. Yu, K.D. Reynolds, G. Coimbatore, B. Barr, S.G. Platt, G.P. Cobb, et al. 2007. Metals and organochlorine pesticides in caudal scutes of crocodiles from Belize and Costa Rica. Science of the Total Environment 373:146–156.

Rootes, W.L., V.L. Wright, B.W. Brown, and T.J. Hess. 1991. Growth rates of American Alligator in estuarine and palustrine wetlands in Louisiana. Estuaries 14:489–494.

Ross, J.P. 1998. Crocodiles. Status Survey and Conservation Action Plan. 2nd Edition. International Union for Conservation of Nature/Species Survival Commission. Gland, Switzerland.

Savage, J.M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas. University of Chicago Press, Chicago, Illinois, USA.

Sergio, F., T. Caro, D. Brown, B. Clucas, J. Hunter, J. Ketchum, K. McHugh, and F. Hiraldo. 2008. Top predators as conservation tools: ecological rationales, assumptions, and efficacy. Annual Review of Ecology, Evolution, and Systematics 39:1–19.

Staton, M.A., and J. Dixon. 1975. Studies on the dry season biology of *Caiman crocodilus crocodilus* from the Venezuelan Llanos. Memoria de la Sociedad de Ciencias Naturales La Salle 101:237–265.

Staton, M.A., and J. Dixon. 1977. Breeding biology of the Spectacled Caiman, *Caiman crocodilus crocodilus* in the Venezuelan llanos. U.S. Fish and Wildlife Service, Wildlife Research Report 5:1–21.

Thorbjarnarson, J. 1993. Diet of the Spectacled Caiman (*Caimal croodilus)* in the Central Venezuelan Llanos. Herpetologica 49:108–117.

Thorbjarnarson, J., F. Mazzotti, E. Sanderson, F. Buitrago, M. Lazcano, K. Minkowski, M. Muñiz, P. Ponce, L. Sigler, R. Soberon, et al. 2006. Regional habitat conservation priorities for the American Crocodile. Biological Conservation 128:25–36.

Velasco, A., and J. Ayarzagüena. 2010. Spectacled Caiman *Caiman crocodilus*. Pp. 10–15 *In* Crocodiles. Status Survey and Conservation Action Plan. Manolis, S.C., and C. Stevenson (Eds.). Crocodile Specialist Group - IUCN, Darwin, Australia.

Villamarín-Jurado, F., B. Marioni, J.B. Thorbjarnarson, B.C. Nelson, R. Botero-Arias, and W.E. Magnusson 2011. Conservation and management implications of nest-site selection of the sympatric crocodilians *Melanosuchus niger* and *Caiman crocodilus* in Central Amazonia, Brazil. Biological Conservation 144:913–919.

Webb, G.J.W., and M.A. Smith. 1984. Sex ratio and survivorship in the Australian freshwater crocodile *Crocodylus johnstoni*. Pp. 319–355 *In* The Structure, Development and Evolution of Reptiles. Ferguson, M.W.J. (Ed.). Academic Press, London, UK.

Webb, G.J.W., R. Buckworth, and S.C. Manolis. 1983. *Crocodylus johnstoni* in the McKinlay River area, N. T. III. Growth, movement and population age structure. Australian Wildlife Research 10:383–401.

Wesseling, C., A. Ahlbom, D. Antich, A.C. Rodriguez, and R. Castro. 1996. Cancer in banana plantation workers in Costa Rica. International Journal of Epidemiology 25:1125–1131.

Wesseling, C., L. Castillo, and C.G. Elinder. 1993. Pesticide poisonings in Costa Rica. Scandinavian Journal of Work, Environment and Health 19:227–235.

Wilkinson, P.M., and W.E. Rhodes. 1997. Growth rates of American alligators in coastal South Carolina. Journal of Wildlife Management 61:397–402.

LUIS M. FERNÁNDEZ graduated in Biology in the University of Salamanca (Spain) in 2010, then completed his Master's in Animal Biodiversity: Conservation and Evolution at the University of Valencia (2012). His Master's thesis focused on the maturation of a newly created habitat for the European Pond Turtle (*Emys orbicularis*), including the translocation and radio-tracking of this population. During the last two years, Luis has been working in Costa Rica, as a Research Assistant in the Sea Turtle Conservancy and as a Research Coordinator and Assistant Manager at Caño Palma Biological Station. His research interests include herpetology, animal biodiversity, and, especially, conservation as an indispensable tool to empowering people and to achieve long-term success. (Photographed by Cole Wang).

MANUEL ARIAS started his relationship with Caño Palma Biological Station in 2001 as a part-time Consultant due to his experience with local fauna and flora. Currently he is the Station´s Maintenance Manager and Long Term Project Consultant. He is also the main boat driver and one of the keystone staff members of the station. (Photographed by Emily S. Khazan).

EMILY S. KHAZAN began studying tropical biology and conservation as an undergraduate in 2009. In 2014 she graduated with her M.Sc. in Biology for which she conducted field work in Costa Rica and Mexico studying the ecology and conservation status of a family of giant damselflies. Since graduating she has been travelling and working in Costa Rica at Caño Palma Biological station as a Research Coordinator. Her research interests include conservation and ecological restoration. (Photographed by Rae Diaz-Diedrick).