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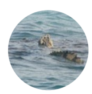

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Population Ecology of American Crocodile (*Crocodylus acutus*) in Coiba National Park, Panama

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Abstract.—We conducted nocturnal surveys in the insular and coastal areas of Coiba National Park (CNP) and its mainland buffer zone in Panama (Chiriquí conservation site) from 2009–2012 to determine the conservation status of *Crocodylus acutus*. In 99 nights, we surveyed 147.2 km and captured 185 animals during nocturnal transects inspection with headlamps. Overall, sex ratio was 1.00:1.01 female/male with significant differences by size/age class and year. Females were slightly larger in total length than males (115.1 ± 56.9 cm-females, 105.4 ± 71.8 cm-males). The encounter rate was calculated based on number of animals captured per km of surveyed transect. The *C. acutus* encounter rate per year was 1.8 ind/km (60 ind/33.5 km/12 places visited) in 2009, 1.0 ind/km (90 ind/87.4 km/18 places visited) in 2010, and 1.3 ind/km (35 ind/26.3 km/8 places visited) in 2012. Based on our spatial analysis, the animals showed a dispersed pattern in most sites on CNP. Captured *C. acutus* were found in 581.1 km^2 total area within 78% natural habitat, including mangroves and beaches, and 22% disturbed habitat on both the mainland and the islands. In addition, the spatial analysis showed reduction in natural land cover; crocodile habitat showed limited conversion to agricultural land use; and we found correlation between crocodile population size and protected areas. The differences between mainland and island populations regarding ecology suggest that a long-term monitoring program for American Crocodiles is necessary to distinguish between natural fluctuations and anthropogenic changes on population dynamics and conservation status.

Resumen.—Entre 2009 al 2012 hicimos varias expediciones en la parte insular y en las áreas costeras del Parque Nacional Coiba y su zona de influencia en Panamá (Sitio de conservación para la diversidad), para determinar el estado de conservación de *Crocodylus acutus* y sus hábitats asociados. En 99 noches recorrimos 147.2 km y capturamos 185 animales usando linternas de cabeza. La proporción de sexos fue 1.00:1.01 hembra/macho, la cual fue significativamente diferente cuando los animales fueron clasificados por grupo etario y año. Las hembras fueron un poco más grandes que los machos (115.1 ± 56.9 cm-hembras, 105.4 ± 71.8 cm-machos). La tasa de encuentro fue calculada con base en el número de animales capturados por kilómetro. La tasa de encuentro para *C. acutus* por año fue de 1.8 ind/km (*n* = 60; 33.5 km; lugares visitados: 12) en 2009, 1.0 ind/km (*n* = 90; 87.4 km; lugares visitados: 18) in 2010 y 1.3 ind/km (*n* = 35; 26.3 km; 26.3; lugares visitados: 8) en 2012. El análisis espacial mostró a *C. acutus* distribuido en la isla de Coiba en un patrón disperso, excepto en El María y el Playa Blanca donde el patrón de dispersión fue de agrupamiento. Los animales capturados se encontraban en un área total de 581.12 km^2 cubierta por un 78% de manglares y playas y un 22% por hábitats modificados. Comparando la cobertura vegetal de 1992 y 2000, nuestros resultados mostraron baja densidad poblacional asociada a la reducción de hábitat. Las diferencias en la ecología poblacional entre los sitios continentales y los insulares sugieren que un programa de monitoreo a largo plazo del Cocodrilo Americano permite distinguir entre las fluctuaciones naturales y los cambios antropogénicos sobre la dinámica poblacional y el estado de conservación.

The American Crocodile (*Crocodylus acutus*) is one of two crocodilian species found in Panama (Auth, 1994). Heavy hunting of crocodiles for skins used in the tanning industry severely diminished wild populations in the 20th century (Medem, 1981; Thorbjarnarson, 2010). Currently, *C. acutus* is listed as Vulnerable by the International Union for Conservation of Nature (Ponce-Campos et al., 2012) and Endangered on the Panamanian National Red List (Ibáñez, 2006). Also, it is listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora throughout its natural distribution, except in Cuba, where it is listed as Appendix II (CITES, 2012).

Our study sites, the Coiba National Park (CNP) and its buffer zone, cover 60% of the continental shelf and 90% of the insular part of the Gulf of Chiriqui (Fig. 1). The extraordinary diversity of ecosystems and organisms found in the Gulf of Chiriqui was sufficient for The Nature Conservancy (TNC) to declare it a regional priority area for conservation in 2000 (Ibáñez, 2006). The CNP is comprised of Coiba, the largest island in the Central Pacific, and 38 smaller islands and rocky islets (ANAM, 2009). In 2005, Coiba was added to the World Heritage List under natural criteria II and IV attributable to its biological and ecological relevance (ANAM, 2009). These islands are mainly volcanic and were last connected to the continent during the Quaternary glaciation period (10,000–12,000 years ago); this length of isolation has generated high levels of endemism at different taxonomic ranks (one subfamily, four genera, one subgenus, 66 species, and 24 sub-species) (ANAM, 2009).

The CNP buffer zone includes the continental area of the Gulf of Chiriqui from Remedios Port in Chiriqui Province to Punta Mariato in Veragua Province (ANAM, 2009) (Fig. 1). This area shares many ecosystems and species with the insular part of CNP (Ibañez, 2006). This area has been a scene of human activity since before the Spanish conquest and continues to be exploited to the extent that only small remnants of mature tropical rain forest and a highly modified area of mangroves, fresh water, and coastal marine ecosystems occur where American Crocodile exist.

Pioneer efforts by John Thorbjarnarson favored the development of conservation strategy for the American Crocodile based on information of an expert group of IUCN Crocodile Specialist Group. They identified critical habitats for population status to know the potential risks for local and regional populations across of the range of the American Crocodile (Thorbjarnarson et al., 2006). Some factors such as reduced population size, habitat fragmentation, and land use change; and human conflicts were identified as the primary threats to conservation

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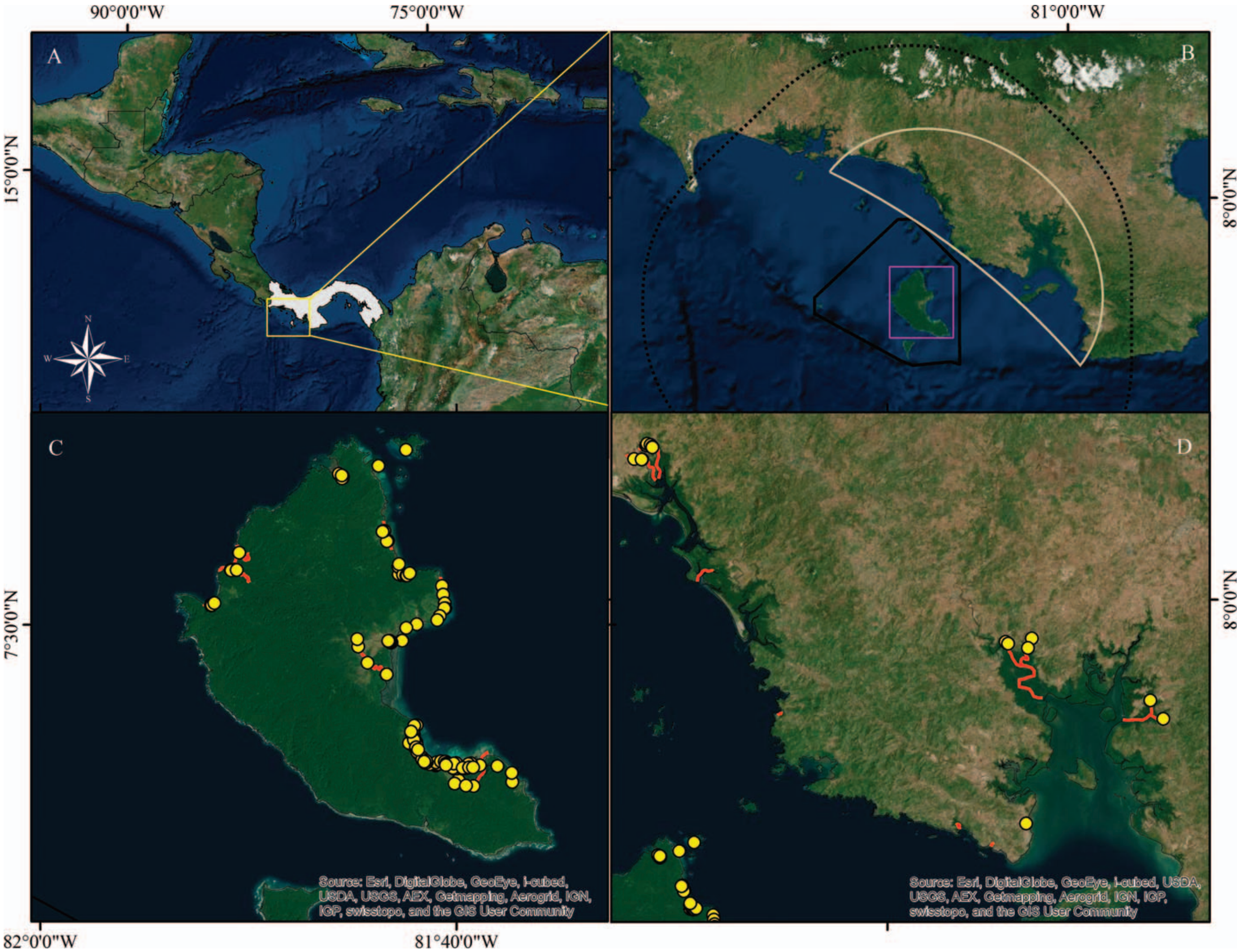

FIG. 1. A, B, C, and D are showing location and samples sites. A = Yellow lines are encompassing Coiba National Park and its marine and continental areas of influence. B = Coiba National Park and its marine and continental areas of influence = black dashed line Coiba National Park and its marine buffer zone = yellow line Coiba Island = Study area = purple square; Continental area of study = white half-circle. Localization of Coiba Island (purple) and Montijo Gulf (red) in the Chiriqui province in Panama (scale 1 : 2500000). C = Yellow dots are collection sites on Coiba Island. D = Transects assessed through of study in Coiba Island and Montijo Gulf and showing the individuals captured (scale 1 : 400000). Source: ESRI, DigitalGlobe, GeoEye, I-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS used community.

(Thorbjarnarson et al., 2006; Thorbjarnarson, 2010).Unfortunately, demographic, ecology and/or life-history information from Panama is limited and anecdotal. which could lead to erroneous conclusions on conservation status of the American Crocodile.

For conserving biodiversity, long-term monitoring of the natural environment is irreplaceable for forming baselines on which we can establish current and future impacts and distinguish between natural fluctuations and anthropogenic changes. Long-term monitoring programs require estimates of population size, sex ratio, size/age class (Thorbjarnarson, 1989; Platt and Thorbjarnarson, 2000) and measurements of general health, ecological integrity, restorative capabilities, and ecosystem trends (Doren et al., 2009; Mazzotti et al., 2009) to form the best decisions about designing, applying, and evaluating management plans for conservation. Top predator species like crocodiles have been used as indicators of the conservation status of several ecological systems before and after restoration programs have been established (Sergio et al., 2008; Doren et al., 2009; Mazzotti et al., 2009). As a result, *C. acutus* has been chosen as one of the focal species to conduct baseline monitoring of marine, coastal, freshwater, and mangrove ecosystems of CNP and its buffer zone. Our main objectives were to assess the population ecology of *C. acutus* (relative encounter rate, spatial distribution, and habitat status) in both insular and mainland areas of CNP and to establish the baseline conservation status of American Crocodile populations and their associated habitats.

Materials and Methods

In 2009, 2010, and 2012, we conducted 25 expeditions to the insular and coastal areas to assess, for the first time, the population ecology of American Crocodile in the Gulf of Chiriqui. We collected data on the insular populations from July and August of 2009, June to November of 2010, and March 2012. These populations were on two of the 39 CNP islands, Coiba and Rancheria. Research sites in Coiba and Rancheria were sampled once, twice, or three times based on logistical limitations. Mainland populations and their habitats from Remedios to Gulf of Montijo were evaluated from July and

TABLE 1. Transects and places assessed in Coiba National Park and its buffer zone, reflected transect and survey types. We carried out one transect by locality.

Name	Transects length (km)	Kind of transect	Spotlight surveys	Category of protection
North island				
Playa Hermosa	1.9	Beach and river	Walking	Heritage site
Playa Brava	4.6	Beach and river	Walking	Heritage site
Los Pozos	5.2	Beach and river	Walking	Heritage site
Santa Cruz	2.2	River	By boat	Heritage site
ANAM	0.3	Beach	Walking	Heritage site
Rancheria	0.3	Beach	Walking	Heritage site
Juncal 1	1.8	Beach	Walking	Heritage site
Juncal 2	1.4	Beach	Walking	Heritage site
La Producción	1.4	Beach and river	Walking and by boat	Heritage site
Punta Damas 1	4.2	Beach	Walking	Heritage site
Punta Damas 2	1.4	Beach	Walking	Heritage site
Catival	1.9	River	By boat	Heritage site
San Juan	7.3	River	By boat	Heritage site
South island				
El Maria	5.6	Beach	Walking	Heritage site
Playa Blanca	3.6	Beach	Walking	Heritage site
Boca Grande	6.6	River	Walking and by boat	Heritage site
Rio Amarillo	0.7	River	By boat	Heritage site
Mainland				
Remedios Norte	9.5	River	By boat	No protection
Remedios	8.5	River	By boat	No protection
Tabazara	3.9	River	By boat	No protection
Pixvae	0.9	River	By boat	No protection
El Banco	1.5	River	By boat	No protection
Santa Catalina	0.7	River	By boat	No protection
Rio San Pablo 1	18.5	River	By boat	Ramsar
Rio San Pablo 2	8.0	River	By boat	Ramsar
Rimadero	8.4	River	By boat	Ramsar
Lagartero	0.6	River	By boat	Ramsar
Los Guabitos	2.7	River	By boat	Ramsar

August of 2010. Survey localities were selected on the basis of accessibility, previous reports of crocodiles, and habitat suitability for crocodiles (Thorbjarnarson, 1989).

We inspected nocturnal transects throughout coastal and river areas capturing the largest possible number of animals. We measured (total length, TL), sexed, marked, and released animals at the site of capture. Encounter rate (number of animals captured per kilometer of surveyed transect) was calculated and used as an index of the relative density of *C. acutus* (Cassey and Ussher, 1999; Platt and Thorbjarnarson, 2000; Villegas and Reynoso, 2013). We surveyed transects by walking (in beaches and along shallow streams in the insular areas) and navigating by boat (in El Banco, Lagartero, Los Guambitos, Pixvae, Remedios, Remedios Norte, Rimadero, Santa Catalina, San Pablo, and Tabasar Rivers in mainland) along definite transects of variable lengths (Table 1). For each transect, we used 3.6W/6V RAYOVAC® headlamp to detect crocodile eye shine and captured the animal with 2.5-m long handmade snare poles made of PVC pipe of 1 inch in diameter and steel wire coated with plastic. Beaches and shallow stream transects were defined by length and the distance we could walk between low and high tide. Transect width was 20–100 m depending on the habitat (river, beach, coastline, etc.). The speed of the boat was 5 km per hour or less, and we inspected both sides of the river at the same time when the tide was going down. At the insular area, most of the capture efforts took 20 min, whereas at mainland areas most of the captures took 30 min.

Sex was determined by inspecting the cloaca with the inspector's little finger or by opening with forceps (Allsteadt and Lang, 1995; Ziegler and Olbort, 2007). TL always was measure from the anterior tip of the snout to the posterior tip of the tail measured along the ventral surface using measure tape. Animals with truncated tails were not included in the study. We worked with each animal at the point of capture, and we marked it with a consecutive unique number by notching the simple and double scales of the tail before release (Webb, 1977). Crocodiles were categorized into one of the following age classes based on size: juveniles (TL 30–90 cm), subadults (TL 90–180 cm), and adults (TL $>$ 180 cm) (Thorbjarnarson 1989, Platt and Thorbjarnarson, 2000). We used our database of captured animals to establish sex ratios and the demographic structure of the populations on the islands and the mainland.

Data were tested using the goodness-of-fit test ($\chi 2$) against the null hypothesis of a discrete uniform distribution of sex and size/age class at each locality in the insular and continental areas. Means are reported with standard deviation (SD). After testing for normality (Shapiro-Wilk test), we used a nonparametric statistics (Wilcoxon test) to compare the distribution of encounter rate and the SD values against the null hypothesis.

Crocodile habitat was assessed on the basis of land cover cartography developed by the Smithsonian Tropical Research Institute (STRI), National Environmental Authority, and the Tommy Guardia National Geographic Institute (ANAM, 2009) and the geographic coordinates of the capture sites. Land covers were defined as lowlands, flooding areas, mangrove areas, beaches, rivers, and fresh water bodies of marine coastal habitats in CNP. Marine coastal habitats in CNP are influenced by dramatic tide changes from 2.5 m up to 7.5 m every 6 h. In addition, we compared the status of *C. acutus* habitats (variation in the landscape-areas) from 1992 and 2000 using land cover layers developed by STRI-ANAM-Tomas Guardia to establish a preliminary trend of habitat change. Using the point locality of each capture, we calculated a 1-km buffer zone as the area where crocodiles dwell (Balaguera-Reina et al., in press).

Population distributions and dispersal patterns were assessed on the basis of geo-statistical analysis by locality (Average Nearest Neighbor function) and landscape units in ArcGIS 9.3. Landscape units used in this study are described based on Ibañez's land-covers (Ibañez, 2006). Analysis of spatial trends has been used to research wildlife management because the distribution of individuals into a specific landscape is determined by geographic or ecological processes (Guisan and Zimmermann, 2005; Cortina et al., 2006). If pattern of spatial distribution changes, it could be associated with natural or anthropogenic landscape changes or resources modifications (Linchstein et al., 2002). Also, we used an Average Nearest Neighbor algorithm in ArcMap software (Ebdon, 1991; Mitchell, 2005). This method calculates a nearest-neighbor index based on the average distance from each feature to its nearest neighboring feature and compares the average distance against null distribution (Random distribution). If the average distance is less than the average for a hypothetical random distribution, the distribution of the features being analyzed is considered clustered. If the average distance is greater than a hypothetical random distribution, the features are considered dispersed (Ebdon, 1991; Mitchell, 2005). In this study, the spatial analysis took into account only localities with sample size $\geq$5 individuals.

Results

Of 33 localities visited in the Gulf of Chiriqui conservation site, 28 were included in the analyses (mainland, 11; islands, 17). We captured crocodiles at 24 of the 28 localities (mainland, 7; insular area, 17). The assessment was replicated three times in Catival and Playa Blanca (2009, 2010, and 2012) and twice in La Producción, Playa Brava, Los Pozos, Playa Hermosa, Santa Cruz, and El María (2009 and 2012). The Environmental Station of the National Environmental Authority (ANAM), Boca Grande, Juncal 1 and 2, Punta Damas 1 and 2, Rancheria, Playa Brava, Amarillo, Remedios, Remedios Norte, Tabazara, Pixvae, El Banco, Santa Catalina, San Pablo, Lagartero, San Juan, Los Guabitos, and Rimadero Rivers were surveyed only once (Table 1). We surveyed on 99 nights over three years.

We captured 164 animals on islands and 21 animals on the mainland. Of these, 37.8% (70) were females (islands = 32%, mainland = 5%); 38.3% (71) were males (islands = 33%, mainland = 5%); and 23.7% (44) were too young to confidently determine sex (islands = 23%, mainland = 0.5%). We caught 60 individuals in 2009 (32% females, 22% males, 42% sex not determined), 90 individuals in 2010 (30% females, 55% males, and 14% sex not determined), and 35 individuals in 2012 (68% females, 23% males, and 8% sex not determined). Overall, there was a 1.00 : 1.01 sex ratio (F : M). The sex ratio at islands and mainland was 1.00 : 1.02 and 1 : 1, respectively. The sex ratio per year was 1.50 : 1.00 in 2009, 1.00 : 1.90 in 2010, and 3.00 : 1.00 in 2012. The statistical analysis showed significant differences in sex ratio by year ($\chi 2$ $P = 0.017$).

Of the 185 individuals caught, 55% (101) were juveniles, 32% (60) were subadults, and 13% (24) were adults with F : M sex ratios of 1.00 : 1.18, 1.63 : 1.00, and 1.00 : 1.18, respectively. We found statistically significant differences in the sex ratio by size/age class and year ($\chi 2$ $P = 0.025$). Seventeen juveniles and 4 subadults were caught on the mainland, whereas the insular size/age class distribution was 84 juveniles, 56 subadults, and 24 adults. In 2009, we captured 32 juvenile, 19 subadults, and 9 adults; in 2010, we got 56 juvenile, 24 subadults, and 10 adults; and in 2012 we got 13 juvenile, 17 subadults, and five adults (Fig. 2). Demographic structure reflects the proportion of 1 adult per 2.50 subadults and 1 adult per 4.21 juveniles throughout all three years of sampling.

The mean TL of individuals sampled (island and mainland combined) was 97.7 $\pm$ 62.7 cm (115.1 $\pm$ 56.9 cm, females; 105.4 $\pm$ 71.8 cm, males; and 57.4 $\pm$ 31.9 cm, sex not determined). The mean TL in the islands was 102.0 $\pm$ 64.0 cm (122.7 $\pm$ 55.2 cm, females; 113.8 $\pm$ 73.5 cm, males; and 56.5 $\pm$ 31.5 cm, sex not determined). On the mainland, mean TL was 63.6 $\pm$ 37.4 cm (69.5 $\pm$ 46.4 cm, females; 54 $\pm$ 25.8 cm, males; and 100.1 cm, sex not determined) (Table 2). Overall female averaged was 11.4 $\pm$ 3.6 cm longer than males.

The encounter rate (total captured animals/total distance covered) per year was 1.8 ind/km (60; 33.5 km; places visited: 12) in 2009, 1.0 ind/km (87.4 km; places visited: 18) in 2010, and 1.3 ind/km (26.3 km; places visited: 8) in 2012. The average of encounter rate in Coiba island and the buffer zone based on these 3 yr of surveys was 1.3 ind/km (147.2 km; places visited: 28), of which the encounter rate in the insular and the mainland areas were 1.95 ind/km (84.0 km; places visited: 17) and 0.33 ind/km (63.2 km; places visited: 11), respectively (Table 3). We found a statistical relationship between the number of replicates and the variations (SD) of the average relative density (Wilcoxon test, $P = 0.29$), which means a reduction in the variation of encounter rate values in the places with more replicates, showing the necessity of increase the sampling effort to get accurate estimates.

We recaptured 5 individuals (2.7% of the total captures) in El María, Playa Blanca, and Playa Brava (Table 4). Three of these recaptures were at the same locality of capture. For these individuals, the mean time to recapture was 730 $\pm$ 205 days, and the mean straight distance from the site of first capture was 1.7 $\pm$ 2.3 km. The average growth rate was 0.04 $\pm$ 0.03 cm/days (Table 4).

The spatial analysis used 12 localities with $\geq$5 animals captured. The dispersion models for crocodiles at Boca Grande, Catival, Juncal 2, Punta Damas, Playa Hermosa, Santa Cruz, and San Juan was dispersed ($P < 0.05$; alpha: 0.01); in contrast, the disperse model at El María and Playa Blanca were clustered ($P < 0.05$). The dispersion model for crocodiles in Lagartero was random (neither dispersed nor clustered $P > 0.05$). The dispersion model for crocodiles in La Producción was clustered, but it was not statistical significant ($P < 0.05$; alpha: 0.10). We did not find a statistical relationship between the amount of animals captured and the dispersal pattern (ANOVA, $P = 0.01$).

Based on size/age class, we found juveniles can occur in a variety of landscape units (primary forest, mangrove, pioneer forest, croplands); subadults are more restrictive comparing with juveniles (primary forest, mangrove, pioneer forest); and adults occur in landscapes with unique characteristics (mangrove and primary forest). The area where we encountered *C. acutus* was 581.1 km^2, of which 39% was primary forest, 25% was mangrove areas, 12% was secondary forest, 20% was agricultural areas, and 2% was disturbed forest. In the islands, primary (61%) and secondary (18%) forests were the main *C. acutus* habitats, followed by mangroves (13%), agricultural areas (6%), and disturbed forest (0.6%). Conversely, the mainland crocodiles occurred mainly in the mangrove forests (48%) and

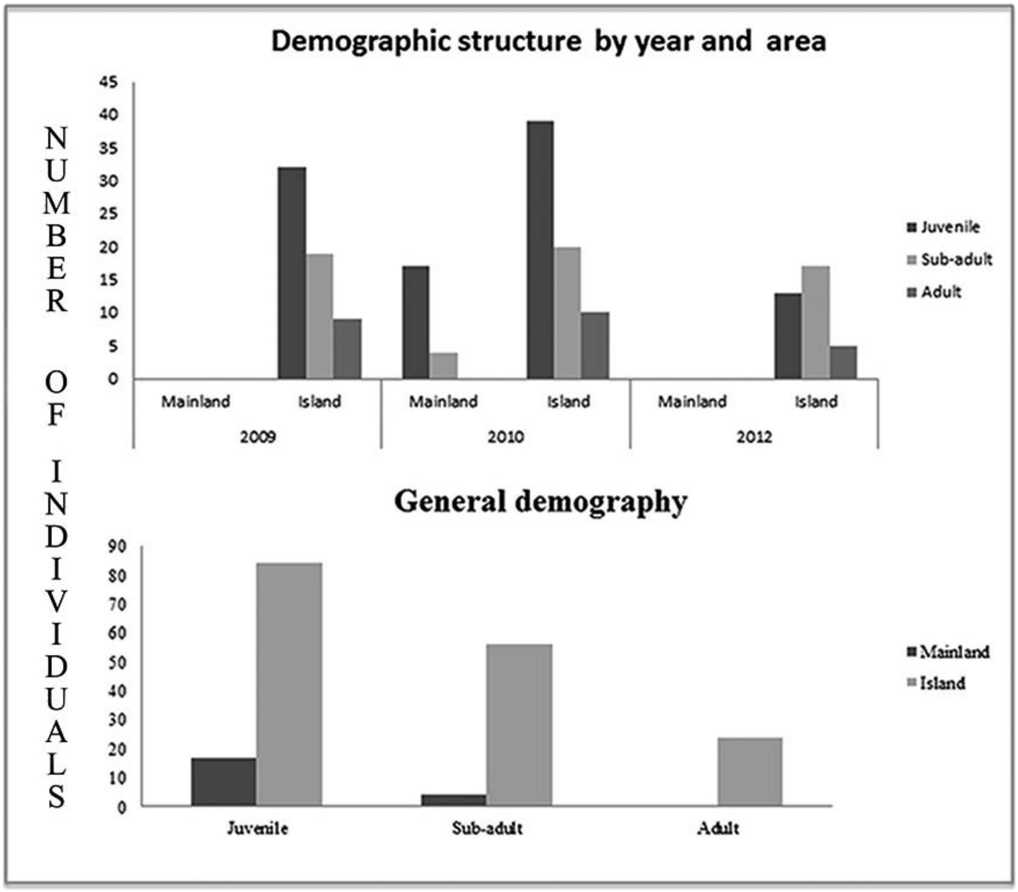

FIG. 2 .Size/age class structure by year and area of American Crocodiles (*Crocodylus acutus*) capture in Coiba National Park and its buffer zone, Panama 2009, 2010, and 2012.

agricultural areas (40%). Disturbed (3%) and secondary forests (3%) were used in smaller proportions. Land covers included in this study belong to marine coastal habitats, permanent or partial flooding areas influenced by cycles of 12 h of low and high tides. Rivers or small fresh water bodies surrounded by mangrove forest or crops were considered as mangrove and agricultural land covers, respectively. The analysis did not include rivers of other fresh water bodies as separated habitats because they were included into the GIS information as lines and not as polygons.

Comparing the 1992 and 2000 landscapes, we estimated a general reduction of 0.23 km^2 of the primary forest, 0.34 km^2 of the mangroves, and 3.62 km^2 of the secondary forest. Also, we estimated an increase of 3.05 km^2 in agricultural areas and 1.14 km^2 in disturbed forest. Within the mainland, we estimated a reduction of 0.76 km^2 and 10.56 km^2 in mangroves and secondary forest, respectively, and an increase of 3.06 km^2 and 8.26 km^2 in disturbed forest and agricultural areas, respectively. We estimated a reduction of 0.33 km^2 and 0.12 km^2 in primary forest and mangroves on the island, respectively. Secondary

TABLE 2. Mean (±) Standard deviation (SD), total length (TL), sex not determined (SND) of American Crocodiles (*Crocodylus acutus*), by sex and size/age class, capture in Coiba National Park and its buffer zone, Panama in 2009, 2010, and 2012.

	Juvenile (30–90 cm)						Subadult (90–180 cm)						Adult (>180 cm)			
	Fem	±SD	Male	±SD	SND	±SD	Fem	±SD	Male	±SD	SND	±SD	Fem	±SD	Male	±SD
2009	69.1	20.6	59.3	6.0	39.2	6.5	125.1	24.7	126.9	39.2	90.0	0.0	215.6	22.7	230.9	77.7
North Island	66.2	24.1	57.1	5.3	38.3	5.8	119.7	29.9	90.0	N/A	90.0	0.0	205.4	12.2	276.6	127.3
South Island	78.0	N/A	65.6	N/A	43.0	8.5	134.6	8.5	139.2	37.4	N/A	N/A	246.3	N/A	200.4	21.9
2010	57.1	19.5	53.1	19.0	51.3	15.2	140.0	21.0	122.1	19.2	112.5	25.3	191.9	17.5	227.6	35.7
Mainland	49.6	21.8	48.7	21.0	N/A	N/A	149.1	14.1	101.2	N/A	100.1	N/A	N/A	N/A	N/A	N/A
North Island	38.2	0.6	34.5	N/A	51.3	15.2	150.4	N/A	119.1	0.8	115.7	28.1	N/A	N/A	N/A	N/A
South Island	69.3	10.6	55.9	18.2	N/A	N/A	130.4	27.0	124.8	20.7	N/A	N/A	191.9	17.5	227.6	35.7
2012	66.1	15.4	59.8	13.4	46.4	5.2	129.9	26.5	140.3	16.9	160.0	N/A	220.9	11.3	231.0	N/A
North Island	63.3	15.5	54.7	8.4	46.4	5.2	124.8	23.8	N/A	N/A	N/A	N/A	220.0	N/A	N/A	N/A
South Island	80.0	N/A	80.0	N/A	N/A	N/A	142.6	32.2	140.3	16.9	160.0	N/A	221.2	13.8	231.0	N/A
Mean values	60.7	18.9	54.6	17.5	42.5	10.3	130.2	24.7	125.0	23.4	108.3	27.2	211.1	20.3	229.1	51.5

TABLE 3. Encounter rate used as relative densities index (number of caught crocodiles per km of surveyed transect) for *Crocodylus acutus* surveyed in Coiba National Park and its buffer zone, Panama in 2009, 2010, and 2012. N/V: Not visited.

	2009 (ind/km)	2010 (ind/km)	2012 (ind/km)	Mean (ind/km)	SD (ind/km)
Santa Cruz	1.8	N/V	1.4	**1.6**	**0.2**
Playa Hermosa	2.1	N/V	1.6	**1.8**	**0.3**
Playa Brava	1.8	N/V	0.4	**1.1**	**0.7**
La Producción	4.3	N/V	5.8	**5.1**	**0.7**
Catival	4.3	2.1	2.7	**3.0**	**0.9**
Playa Blanca	2.5	6.5	2.3	**3.7**	**1.9**
El Maria	N/V	5	0.9	**2.9**	**2.1**
Los Pozos	N/V	N/V	0.2	**0.2**	**0.0**
ANAM	3.6	N/V	N/V	**3.6**	**0.0**
Boca Grande	1.1	N/V	N/V	**1.1**	**0.0**
Juncal 1	1.1	N/V	N/V	**1.1**	**0.0**
Juncal 2	3.6	N/V	N/V	**3.6**	**0.0**
Río Amarillo	3.0	N/V	N/V	**3.0**	**0.0**
San Juan	0.6	0.1	N/V	**0.3**	**0.2**
Punta Damas 1	N/V	1.7	N/V	**1.7**	**0.0**
Punta Damas 2	N/V	1.5	N/V	**1.5**	**0.0**
Rancheria	N/V	12.1	N/V	**12.1**	**0.0**
Remedios	N/V	0.4	N/V	**0.4**	**0.0**
Remedios Norte	N/V	0.5	N/V	**0.5**	**0.0**
Pixvae	N/V	0.0	N/V	0.0	0.0
Tabazara	N/V	0.0	N/V	0.0	0.0
El Banco	N/V	0.0	N/V	0.0	0.0
Santa Catalina	N/V	0.0	N/V	0.0	0.0
Lagartero	N/V	9.6	N/V	**9.6**	**0.0**
Los Guabitos	N/V	0.4	N/V	**0.4**	**0.0**
Rimadero	N/V	0.1	N/V	**0.1**	**0.0**
Río San Pablo 1	N/V	0.2	N/V	**0.2**	**0.0**
Río San Pablo 2	N/V	0.3	N/V	**0.3**	**0.0**
Total mean per year	**1.8**	**1.0**	**1.3**	**1.3**	

forest, agricultural areas, and disturbed forest showed increases of 0.28 km^2, 0.10 km^2, and 0.06 km^2, respectively. Overall, the habitat types were predominantly forest and mangroves (66.8%) with low presence of agricultural areas (18.2%) and disturbed forest (1.7%). Although the spatial analysis showed reduction in natural land cover, crocodile habitat showed limited conversion to agricultural land use, and we found many crocodiles within protected areas. Of the 28 areas sampled, only 6 are not under any kind of protection.

DISCUSSION

Although replicates were not obtained for all sites, we documented baseline population demographics, unevenness of spatial distributions, and coarse habitat status for *C. acutus* in CNP and its buffer zone between Remedios Port in the Chiriqui Province and Punta Mariato in the Veragua Province. This first approximation of population demography allowed us to estimate population sizes based of captured animals for all the islands and mainland localities included in the study as minimums of 164 and 21 individuals, respectively. Although previous reports of male sex bias in *C. acutus* in other areas such as Haiti (Thorbjarnarson, 1989) and the Banco Chinchorro Atoll, Mexico (Charrau, 2012), the female : male ratio in this study in Panama was relatively equal in both the insular and mainland areas. Our results agreed with information reported for *C. acutus* by Platt and Thorbjarnarson (2000) in Belize and by Cedeño-Vazquez et al. (2006) in Quintana Roo, Mexico. Unlike the balanced sex ratio in our study, some previous studies of American Crocodile among islands and atolls has found a skewed sex ratio towards males (Platt and Thorbjarnarson, 2000; Charruau et al., 2005; González-Cortés, 2007). However, the population sex ratio across the range of the American Crocodile should relate with local environmental conditions rather than a geographic or latitude pattern (Escobedo-Galván et al., 2011).

In the present study, the possibility that the determined sex ratios may be biased because of the ecological differences such as size- and gender-specific habitat use. It is possible we

TABLE 4. Growth rates and distances traveled by American Crocodiles (*Crocodylus acutus*) captured and recaptured in Coiba National Park and its buffer zone, Panama 2009, 2010, and 2012.Id = individual leveled number, DBC = days elapsed between capture and recapture, TLi (cm) = total length at initial capture (cm), TLr(cm) = total length at recapture (cm), SD = size = difference between initial capture and recapture, GR = growth rate(cm/day), DT = distance traveled between initial capture and recapture from the original place capture to the place recaptured.

Id	Capture	Recapture	DBC	TLi (cm)	Size/age class first capture	TLi (cm)	Size/age class recapture	SD (cm)	GR (cm/day)	DT (km)
016	18/07/2009	15/03/2012	971	39.9	Juvenile	127.7	Subadult	87.8	0.09	0.11
062	15/08/2009	07/03/2012	935	96.3	Subadult	128.3	Subadult	32.0	0.03	0.81
088	19/07/2010	06/03/2012	596	69.4	Juvenile	80.0	Juvenile	10.6	0.02	0.38
091	20/07/2010	06/03/2012	595	67.3	Juvenile	80.0	Juvenile	12.7	0.02	5.65
0121	02/09/2010	08/03/2012	553	89.6	Juvenile	109.1	Subadult	19.5	0.04	1.72
Mean			730					32.5	0.04	1.73
SD			204.7					32.0	0.03	2.27

sampled one size/age class or sex disproportionately because these individuals were found in a more accessible habitat or individuals were congregated together because of temporal or physiological factors (Seijas, 1990). Fukuda et al. (2011) showed a relationship between seasons and *Crocodylus porosus* habitat use, dispersion patters and relative densities. Other reasons for sex ratio bias could be the difficulty to determine sex in small animals and inability to capture larger animals. Ongoing sampling and surveys will allow us to assess the effect of those factors on sex ratio at the locations.

Demographic structure in the islands was similar in 2009 and 2010, with chiefly juveniles, followed by subadults and adults. In 2012, the structure changed to favor the subadults, followed by juveniles and adults. In contrast, the mainland showed a lack of adults, which could be a result of habitat modification or the constant presence of fishers and boats in the deeper parts of the rivers where adult crocodiles are commonly found. The variability among the number of juveniles per year also has been reported in Haiti (Thorbjarnarson, 1989), Florida (Mazzotti et al., 2007), and Venezuela (Seijas, 1990), mainly attributable to change in temporal abiotic habitat conditions (e.g., temporal aggregation in dry season), temporal habitat segregation influenced by human presence (animals move from natural habitats and concentrate in artificial lakes on shrimp farms), and stochastic changes in demography and recruitment.

We captured individuals between 31.3 and 277 cm in TL. Females were larger than males on the islands and the mainland. We attributed this variation in size to differences in sampling season by year: our field trips in 2009 and 2010 were during the rainy season (May to December), whereas trips in 2012 were at the end of the dry season (January to April). In different seasons and reproductive stages, females and males are found in dissimilar mean relative densities, which could contribute to a sampling bias (Gaby et al., 1985; Kushlan and Mazzotti, 1989). When water bodies are reduced during the dry season, crocodile habitat availability also is reduced, and animals tend to congregate in the freshwater that remains.

The mean of encounter rate recorded within the islands were similar to those reported in coastal areas such as Venezuela (Seijas, 1986), Colombia (De La Hoz-Villarreal et al., 2008) and Mexico (Martinez-Ibarra et al., 1997). Mainland values also were comparable to values reported for populations with a similar degree of disturbance in Belize (Platt and Thorbjarnarson, 2000), Honduras (Thorbjarnarson, 1989; King et al., 1990), and Colombia (Balaguera-Reina, 2012).

Despite the low recapture rate (mainly attributable to lack of replicates in all places), the mark–recapture enabled us to obtain initial information on the individual growth rates and dispersion of American Crocodile in the islands. The mean growth rate in length estimated in our study was within reported values in previous studies for American Crocodile in natural conditions (0.044 ± 0.033 cm/day, Charruau et al., 2010; 0.056 ± 0.049 cm/day, García-Grajales et al., 2012).

Currently, there are few studies on dispersal patterns of the American Crocodile. Thorbjarnarson (1989) proposed that animals are distributed depending on size/age class, season, and habitat conditions. Our results show evidence that patters of animal geographic distribution depend on other underlying variables like season, physiological state, and habitat stability. In the future, it would be valuable to track the changes in distribution and relative densities of crocodiles throughout the landscape based on our preliminary data.

In general, the habitats in CNP are highly conserved because the land has been established as a Heritage Site. The habitat types at CNP were predominantly forests and mangroves (67%) with low presence of agricultural areas (18%) and disturbed forest (2%). CNP agricultural and disturbed forest areas are remnant changes from historical times when Coiba was a prison island. Although the mainland habitats included a large proportion of developed areas, there was still a significant proportion of undisturbed protected area available for crocodiles. Occupancy patters of current habitats reflect the importance of the CNP and Gulf of Montijo as areas for the conservation of *C. acutus* populations in relatively undisturbed conditions. Although areas between Remedios and Santa Catalina have habitat available for crocodiles, we did not find crocodiles in the Tabasara, Pixvae, or El Banco Rivers. Also, we saw a few sizeable crocodiles in the mouth of the Rio San Pedro, but we were not able to capture those animals possibly because the constant presence of fishermen in the area that makes crocodiles wary. Conversely, the unwary behavior of crocodiles in Lagartero River may be the result of protection imposed by landowners.

The suitable habitats in CNP and some areas of its buffer zone are attributable to conservation management practices: all insular locations are classified in the CNP's II National Park IUCN management category (ANAM, 2009). On the mainland, Los Guabitos, Lagartero, Rimadero, and San Pablo Rivers are part of Gulf of Montijo, which is classified as an important international wetland site (RAMSAR site). Comparing the available information about landscapes in Panama for 1992 and 2000, we found minimal transformation of land use on the mainland and an increase in the percentage of forest cover on the islands.

Our study were the first step toward establishing a long-term monitoring program for the coastal marine habitats in one of the most important areas for conservation in Panama using *C. acutus* as a focal species. Multiple studies have suggested that top predators such as crocodiles promote species richness because they are spatiotemporally associated with other species for at least six causative or non-causative reasons: resource facilitation, trophic cascades, dependence on ecosystem productivity, sensitivity to dysfunctions, selection of heterogeneous sites, and links to multiple ecosystem components (Sergio et al., 2008; Doren et al., 2009; Rosenblatt and Heithaus, 2011). As a result, Coiba Island crocodile populations should be considered as priority conservation units of the Tropical Eastern Pacific Marine Corridor.

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