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How to estimate population size in crocodylians? Population ecology of American crocodiles in Coiba Island as study case

Sergio A. Balaguera-Reina,[1,2,†] Miryam D. Venegas-Anaya,[3] Betzaida Rivera-Rivera,[1] Diego A. Morales Ramírez,[4] and Llewellyn D. Densmore III[1]

[1]Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409 USA
[2]Programa de Biología Ambiental, Facultad de Ciencias Naturales y Matemáticas, Universidad de Ibagué, Carrera 22 Calle 67, Ibagué 730001 Colombia
[3]Smithsonian Tropical Research Institute, Apartado Postal, 0843-03092 Balboa, Ancón, Panama
[4]Programa de Biología, Universidad El Bosque, Cra. 9 No 131 A 02, Bogotá, Colombia

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Abstract. Reliable estimates of crocodylian population size are desirable for both understanding the ecology and natural history of species and developing sound conservation and management plans. However, choosing appropriate methods to estimate population numbers can be difficult due to the paucity of comprehensive analyses regarding their effectiveness, robustness, and applicability. We estimated the American crocodile population size in the southern tip of Coiba Island, Panama, using both spotlight surveys (Messel's and King's visible fraction estimations) and mark–recapture (POPAN formulation–superpopulation) methods. We assessed and compared the outcomes of these methods with the overall capture record for the study area from 2009 to 2013, evaluating their applicability, accuracy, strengths, and limitations. Using historical and current capture data, we defined a minimum population size of ~112 non-hatchling animals in our study area, which was larger than both Messel's (19.00 ± 7.50 individuals) and King's (25.71 ± 7.25 individuals) population size estimates, revealing that these latter approaches clearly underestimate population numbers. We estimated a total population size that range between 147 and 257 individuals based on POPAN formulation grouping the data by sex and age groups as the most plausible population size of the American crocodile population in this area at the time. We analyzed and discussed sources of bias in population size estimations for all methods used in the present study, providing recommendations to minimize errors and improve estimations. Finally, we analyzed and compared population ecology attributes obtained in our study with what have been reported in other insular and coastal areas across the American crocodile range, increasing knowledge about the ecology of the species.

Key words: crocodiles; mark–recapture; population density; population ecology; population size estimate; relative abundance; spotlight surveys.

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† **E-mail:** segio.balaguera@unibague.edu.co

Introduction

A key attribute population ecologists try to elucidate or at least estimate is the population size of a species in a defined area, mainly because this provides the information needed to measure ecological change (Thompson 2002) and offers relevant insights about the conservation status of the species (Lettink and Armstrong 2003). To accomplish this, direct methods such as censusing and mark–recapture have been developed and improved through time, obtaining accurate and useful outcomes for several species (Southwood and Henderson 2003). There also have been ways developed to estimate this attribute indirectly from non-conspicuous species where direct methods are inefficient and/or ineffective (Southwood and Henderson 2003).

Historically, crocodylian population sizes have been estimated indirectly via spotlight surveys based on sighting fractions (Messel et al. 1981, King et al. 1990) and directly via mark–recapture (Murphy 1980, Bayliss et al. 1986). The former method was designed specifically for crocodylians based on two primary equations, whereas the latter is the common mark–recapture method applied broadly in population ecology since Petersen (1896) and Lincoln (1930). Messel et al. (1981) defined sighting fraction (p) as:

$$p = \frac{\bar{X}}{\sum_{i=1}^{SC} \max}$$

where $\bar{X}$ is the average number of crocodiles spotted, and max is the maximum number of crocodiles seen within each size class (SC), assuming field data fit a theoretical binomial distribution. In contrast, King et al. (1990) defined p as:

$$p = \frac{\bar{X}}{(2\mathrm{SD} + \bar{X})1.05}$$

where SD is the standard deviation of the data, assuming normal distribution. Both equations attempt to estimate the unknown relationship between the sample population and the true population. Based on solving these two equations, Messel et al. (1981) and King et al. (1990) defined the crocodile population size (N) as:

$$\mathrm{N} = \frac{\bar{X}}{p} \pm \frac{[1.96(\mathrm{SD})]^{1/2}}{p}$$

with a 95% confidence interval (CI). However, even though these efforts have brought important insights regarding the ecology of some crocodylian species, because the data distribution must fit a theoretical distribution to estimate sighting fractions, meeting the inherent statistical assumptions is not easy to achieve in natural populations. Furthermore, some of these methods can drastically underestimate true population sizes (Webb et al. 1989), making it necessary to define correction factors derived from empirical experience (Messel et al. 1981) or direct–indirect method adjustments (Bayliss et al. 1986, Hutton and Woolhouse 1989).

Regarding direct methods, mark–recapture has been the preferred technique to estimate crocodylian population sizes mainly using the Petersen-Lincoln (Murphy 1980, Bayliss et al. 1986, Hutton and Woolhouse 1989) and Jolly-Seber (Garcia-Grajales et al. 2007, Espinosa et al. 2012) models. All are based on the same four basic assumptions: (1) Marking does not affect individuals, (2) marked and unmarked individuals are completely mixed in the population, (3) capture probabilities for both marked and unmarked individuals are the same for each sex or age group, and (4) sampling must be at discrete time intervals (Southwood and Henderson 2003). However, because crocodylians are not conspicuous in the field and have cryptic habits, hierarchal demographic structure (both temporally and spatially), a wide range of body sizes (i.e., from 0.25 to 6 m in some species), and considerable habitat diversity (Medem 1981, Thorbjarnarson 1989, Balaguera-Reina et al. 2015), these general assumptions are difficult to meet, often yielding high levels of uncertainty in estimated numbers of crocodylians.

American crocodile (*Crocodylus acutus*) populations are no exception to this rule due to the lack of thorough research in many localities, ecological constraints (as stated above), and scarcity of integrative analyses assessing strengths and flaws of estimation methods and their applicability. This species has the largest range of all crocodylians in the New World, inhabiting both coasts (Pacific and Atlantic–Caribbean) from 0 to 500 m above sea level (Thorbjarnarson 2010). However, even with this widespread range, *C. acutus* is considered as Vulnerable (Ponce-Campos et al. 2012) and is threatened in most of the countries where it occurs (Thorbjarnarson 2010) Thus, a standardized method for estimating the population size in American crocodiles with a clearly defined level of certainty must be a priority to measure ecological change as well as to robustly define the current conservation status of the species.

Herein, we estimate the population size of American crocodiles on the southern tip of Coiba Island, Panama, using both spotlight surveys (Messel's and King's visible fraction estimations) and mark–recapture (POPAN formulation–superpopulation) methods. We assess and compare the outcomes of these methods with the overall capture record for the area from 2009 to 2013, discussing the applicability, accuracy, strengths, and limitations of the methods. Finally, we estimate several other population attributes (relative abundances, demographic structure, and sex ratio), increasing our understanding of *C. acutus* population ecology in insular areas.

Methods

Study area

The coastal zone of the study area encompasses tide-modified reflective beaches with high tide range (~3 m) and low waves based on Short's (2006) classification. Tidal mud flats, sand flats, and low tide terraces are the most common types of beaches occurring in the area with medium and low sand banks across them. Shoreline vegetation is characterized by mangrove areas primarily comprised of *Rhizophora mangle* (red mangrove) and *Avicennia germinans* (black mangrove), and secondary tropical rain forest and riparian forest (Ibañez 2006). Seasonal freshwater/brackish streams and flooded areas are present in Playa Blanca and El Maria beaches (Balaguera-Reina et al. 2015). However, Coiba conditions are dry from December to April (precipitation < 200 mm per month) with maximum precipitation in October (around 600 mm per month; ETESA 2015).

Data collection

We assessed the population size of American crocodiles as well as their relative abundance, demographic structure, and sex ratios from Playa Blanca to El Maria beaches on Coiba Island, Panama, using two methods, spotlight surveys and mark–recapture. To do so, we defined two teams [spotlight team (one researcher) and capture team (three researchers)] who assessed four transects (T1: 3.3 km, T2: 2.4 km, T3: 2.2 km, and T4: 2 km) each separated by 300 m, from February to December 2013. These transects were monitored by foot at night across open areas and walkable zones along the coast throughout four habitats (beach, mangrove, riparian forest, and rocky coastline; Fig. 1). Transects 1 and 4 were characterized by large areas of mangrove and secondary tropical rain forest with seasonal sources of freshwater and fine-grain beaches with medium sand banks. Transect 2 included an exposed wind area with shingle beaches and a mangrove muddy area with low wave incidence. Transect 3 consisted of shingle beaches with small mangrove stands across it as well as drastic changes in slope dominated by tropical rain forest (Fig. 1).

Even though the method as described in the present study is not the standard survey technique reported elsewhere (Chabreck 1963, Messel et al. 1981, King et al. 1994, Platt and Thorbjarnarson 2000), it could be defined as appropriate to survey tidal coastal areas in an efficient manner because (1) foot surveys can potentially create less disturbance (i.e., less noise and water movement) compared to vessel surveys, increasing the likelihood of an efficient approach to the animal, (2) the speed of progress through the transect will not be directly affected by the tide, and (3) it is logistically feasible given the study site conditions while boat surveys are not. However, the major limitation of foot surveys is the distance covered by night (e.g., around 3 km) comparing with boat surveys (e.g., around 20 km).

Pre-sampling

Tide has a strong effect on the number of crocodiles spotted in any survey since it increases or decreases habitat availability, affecting also the effective sampled area (Messel et al. 1981). In our case, it also defines the time when coastal areas are walkable after the highest tide. We pre-sampled the study area in January 2013 to determine the holding time required after the highest tide to survey transects, allowing us walk through them and spotlight the maximum number of American crocodiles. We also defined the time needed between spotlight and capture teams per transect to minimize effects on the number of animals spotted by the two teams. In the former case, we walked throughout four transects for three weeks doing spotlight surveys. We found that the first transect was perfectly walkable 2 h after highest tide and transects 2, 3, and 4 were walkable 3 h after highest tide mainly due to distance from basecamp. In the latter cases, we monitored these transects for two weeks, increasing the time between spotlight and capture teams by 10 min each day up to 50 min, determining that 30 min was the time

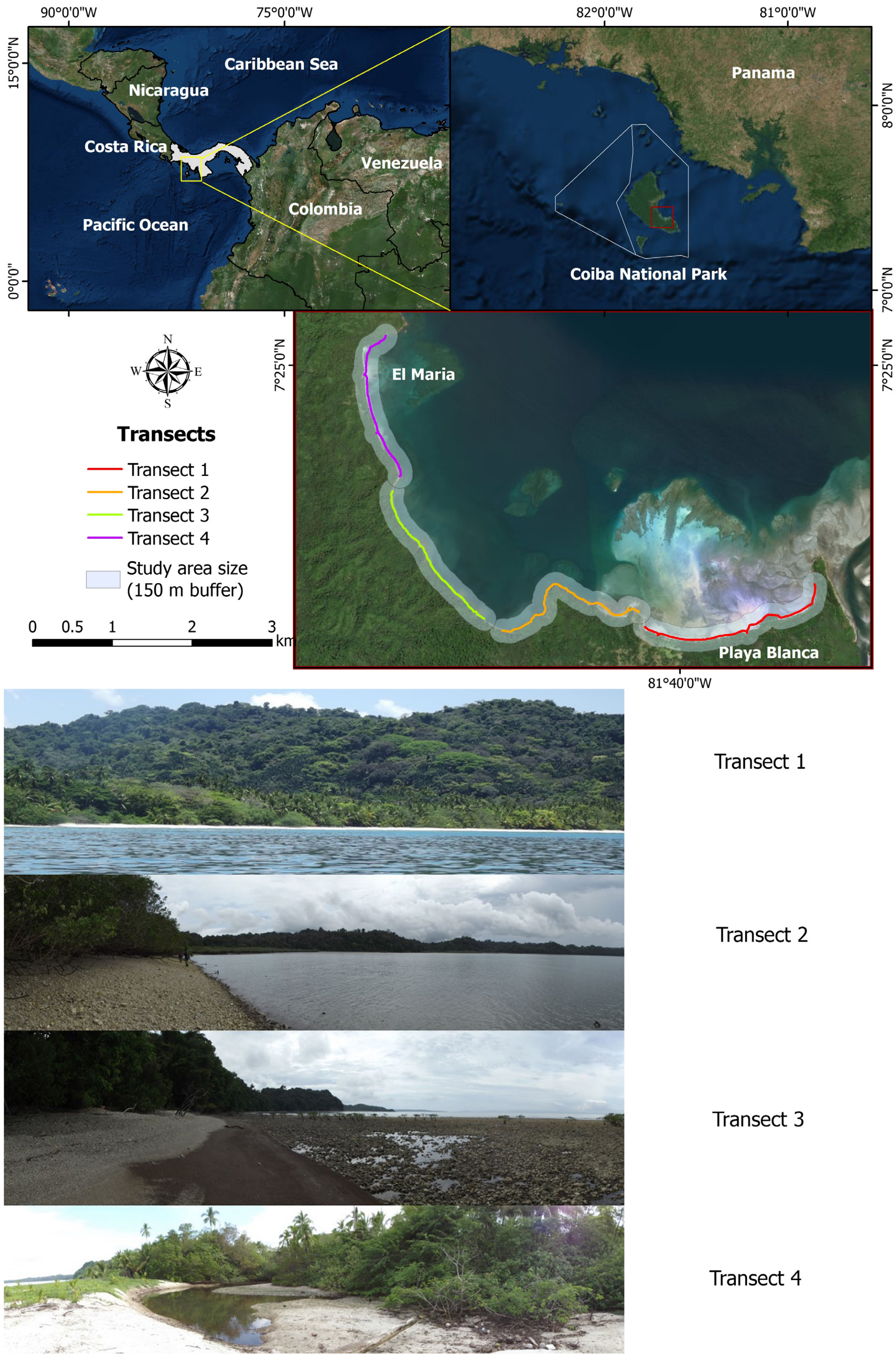

Fig. 1. Study area on Coiba Island, Panama, highlighting the transects we followed across 2013 (T1: 3.3 km, T2: 2.4 km, T3: 2.2 km, and T4: 2 km) as well as the area estimated based on a 150-m buffer around each transect.

between groups with less effect on the number of animals spotted.

Sampling

Spotlight and mark–recapture surveys were carried out one transect per night at monthly intervals sequentially using industrial Rayovac headlamps (405 lm), always during the new moon phase (Medem 1981). Transects always followed open areas through the beach and rocky coastlines spotlighting the area 180° at the front, getting close to the shore to spot animals in the sea (limited only by the distance reached by the beam), and doing incursions under the vegetation (mainly mangrove and riparian forests) to make sure we were not leaving animals unspotted. Crocodiles were detected by the reflection of light from their eyes (Chabreck 1963), getting as close as possible to the animal to geo-locate it and to estimate its total length (spotlight team) or capture it (mark–recapture team). Special attention was paid on the time spent collecting information from an animal by the spotlight team due to the effect it could have on the sampling. Thus, a single uninterrupted, fast-as-possible traverse of each transect was performed in every survey. For mark–recapture, animals were captured by noosing (Chabreck 1963) with handcrafted PVC catch poles within a 3-min capture window. After this time, if the capture was not accomplished, information about the animal was recorded as non-captured and we resumed looking for other individuals along the transect. If captured, animal was marked by scute notching using the single and double crest on the tail following a numerical sequence, sexed (via cloacal probing), and measured (total length—TL—and weight). We used a 20-min time limit for the process, trying to reduce the effect it could have on the encounter rate of individuals across the transect.

We classified animals counted in spotlight surveys by size classes (SC) (I: <60 cm, II: 61–120 cm, III: 121–180 cm, IV: 181–240 cm, V: >240 cm; Seijas 1988) or eyes only (EO) if the animal submerged before size could be estimated (Messel et al. 1981), and individuals captured and measured by age group (juvenile TL 30–90 cm, sub-adult TL 91–180 cm, and adult TL > 180 cm; Platt and Thorbjarnarson 2000). The difference in classes was because size classes were assigned with the purpose of reducing the estimation error (Messel et al. 1981) while age groups represent life stages based on reproductive and ecological features measured directly from the animal. Even though these two concepts are sometimes used interchangeably, they have serious implications on the ways one can interpret and analyze the data collected.

Paired *t*-tests (P-*t*) were performed in R (R Development Core Team 2012) to determine any differences in the number of American crocodiles spotted between methods (spotlight and mark–recapture) per transect and for the whole study. Average nearest neighbor analyses were done using ArcGIS 10.4.4 (ESRI 2016) to define spatial distribution patterns of American crocodiles in the whole study area, assessing differences between them.

Spotlight survey data analyses

We estimated the relative abundance (individuals per km; ind/km) and the population structure observed in the area per month and per transect as well as throughout the whole year. Shapiro-Wilk and Bartlett analyses were performed to test for normality and homoscedasticity of the data, respectively. Kruskal-Wallis analyses were run to test for differences in the number of crocodiles spotted among transects and months.

Population size was estimated by transects and for the whole study based on the sighting fraction approximations postulated by Messel et al. (1981) and King et al. (1990). Sightings from class I with a TL estimated <35 cm were not included in these analyses because they likely hatched in the area in April or May, which mean fewer than 5% of these animals will survive until July due to the low recruitment rate present in the area (Balaguera-Reina et al. 2015).

Mark–recapture data analyses

We analyzed mark–recapture data using MARK 8.1 software (White and Burnham 1999) based on the POPAN formulation, where φ represents the apparent survival parameter, p the recapture parameter, β the entry probability, and N the initial population size (Schwarz and Arnason 1996). Recapture data were grouped by sex (females, f; males, m; and not determined, nd) and age group (hatchlings, h; juveniles, j; and sub-adults, s), assessing four models for each set:

(1) full time dependence {$\varphi_{(t)}$, $p_{(t)}$, $\beta_{(t)}$}; (2) no time dependence {$\varphi_{(.)}$, $p_{(.)}$, $\beta_{(.)}$}; (3) either *nd* and *h* allowed to vary as (a) {$\varphi_{[.(f^*m)]}$, $p_{[.(f^*m)]}$, $\beta_{[.(f^*m)]}$ $\varphi_{[t(nd)]}$, $p_{[t(nd)]}$, $\beta_{[t(nd)]}$} or (b){$\varphi_{[.(j^*s)]}$, $p_{[.(j^*s)]}$, $\beta_{[.(j^*s)]}$ $\varphi_{[t(h)]}$, $p_{[t(h)]}$, $\beta_{[t(h)]}$}; and (4) and either *m* and *nd* and *j* and *h* allowed to vary as (a){$\varphi_{[.(f)]}$, $p_{[.(f)]}$, $\beta_{[.(f)]}$ $\varphi_{[t(m^*nd)]}$, $p_{[t(m^*nd)]}$, $\beta_{[t(m^*nd)]}$} or (b) {$\varphi_{[.(s)]}$, $p_{[.(s)]}$, $\beta_{[.(s)]}$ $\varphi_{[t(j^*h)]}$, $p_{[t(j^*h)]}$, $\beta_{[t(j^*h)]}$}. We did not include adults due to the lack of occurrence in the capture data, and we assumed non-time dependence in sub-adults and females for all models. This assumption was made because a study has shown that older American crocodiles are more stable (i.e., have smaller home ranges) in the population compared to younger animals and that males have larger utilization distribution areas than females (Balaguera-Reina et al. 2016). The not-determined sex group encompassed individuals ≤45 cm TL due to the impossibility of differentiating a clitoris from a penis at these small sizes.

We used a sin link function to estimate survival and recapture parameters, a mlogit(1) function to estimate entry parameters, and a log link function to estimate superpopulation size as recommended by Cooch and White (2007) for this formulation. We used an information-theoretical approach to model selection (Akaike information criterion, AIC), considering that models with ΔAICc values <2 were well supported by the data, whereas those models with ΔAICc values greater than 10 were not supported (Burnham and Anderson 2002). We estimated goodness-of-fit chi-square values from the model with the lowest AIC using RELEASE software (Burnham et al. 1987), which is available within MARK, to assess how well these models fit the data. The chi-square values were added for the entire sampling period and divided by the degrees of freedom to estimate the c-hat ($\hat{c}$). Values of 1 indicated good model fit, between 1 and 3 indicated moderately good fit, and >3 indicated probable violation of model assumptions (Williams et al. 2011). In the case when $\hat{c}$ values were <1 (under-dispersed), we raised them to 1 following recommendations from Cooch and White (2007).

Capture efficiency was estimated based on the number of individuals captured over the total number of individuals seen for all transects and for the whole study. The size of the study area was estimated based on transect distances from Playa Blanca to the El Maria beaches plus a 150-m buffer estimated via ArcGIS 10.4 (ESRI 2016) based on the estimated distance reached by the light beam from the shoreline out to the sea. We report the accuracy of sample means using a standard deviation (SD) for data distribution and standard error (SE) for sampling distribution with 0.05 as the critical value, claiming significance when probabilities were below this threshold.

Results

We spotted a total of 206 American crocodiles in the spotlight surveys and 189 in the mark–recapture assessments (Table 1) across 2.93 km^2 ($\bar{X}$ = 0.73 ± 0.06 km^2; Fig. 1). We found no statistically significant differences in the number of animals observed by these two methods on any of the four transects (P-*t* df = 10, *P*-value = 0.78, 0.23, 0.05, 0.89, respectively) or between months (P-*t* df = 43, *P*-value = 0.45). Spatial distribution patterns were, for the most part (e.g., February–May and September), clustered by both methods (*z*-score = <−1.96, *P*-value = <0.001). However, we found some discrepancies in patterns between methods in June (from clustered to random), August (from random to clustered), October (from clustered to random), and November (from dispersed to clustered; Appendix S1: Fig. S1).

Spotlight survey

From the 206 American crocodiles observed, 24.8% were classified as EO (51 observations), 39.8% as class I (82 observations), 13.6% as class II (28 observations), 16.5% as class III (34 observations), 3.9% as class IV (eight observations), and 1.5% as class V (three observations; Fig. 2). Crocodiles registered as EO were likely large animals (classes IV and V) as they are warier than the small ones (Webb and Messel 1979). We did not find significant differences among the number of individuals observed among transects (K-W χ^2 = 6.99, df = 3, *P*-value = 0.07) and among months (K-W χ^2 = 18.49, df = 10, *P*-value = 0.05), even though values approached significance. The average relative abundance per month ranged from 9.0 ± 8.3 ind/km in May to 0.6 ± 0.5 ind/km in November (Fig. 3). However, when we eliminated May due to sightings that were mainly hatchlings, the maximum relative abundance value reported was reduced to 3.6 ± 2.2 ind/km in April.

Table 1. American crocodiles observed by the spotlight (ST) and capture (CT) teams by transects and during the entire study (Total) on Coiba Island, Panama, highlighting the total number of animals observed as well as the mean and standard deviation (SD).

	Transect 1		Transect 2		Transect 3		Transect 4		Total		
Month	ST	CT	ST	CT	ST	CT	ST	CT	ST	CT	TAC
	3	3	13	5	6	4	3	2	25	14	
March	4	0	9	5	4	3	3	2	20	10	4
April	11	27	9	4	2	1	5	3	27	35	27
May	35	30	6	5	2	3	22	21	65	59	27
June	1	1	4	3	2	2	12	10	19	16	6
July	1	0	2	1	3	1	1	5	7	7	4
August	1	2	4	4	2	2	4	4	11	12	5
September	3	3	3	5	1	0	2	6	9	14	5
October	2	1	3	2	1	1	4	5	10	9	6
November	1	0	1	5	0	0	3	2	5	7	3
December	0	0	2	3	2	1	4	2	8	6	2
Total	62	67	56	42	25	18	63	62	206	189	92
Mean	5.64	6.09	5.09	3.82	2.27	1.64	5.73	5.64	18.73	17.18	8.36
SD	9.72	10.64	3.58	1.34	1.54	1.23	5.82	5.38	16.30	15.27	8.87

Note: We also included the total number of American crocodiles captured (TAC) by the capture team.

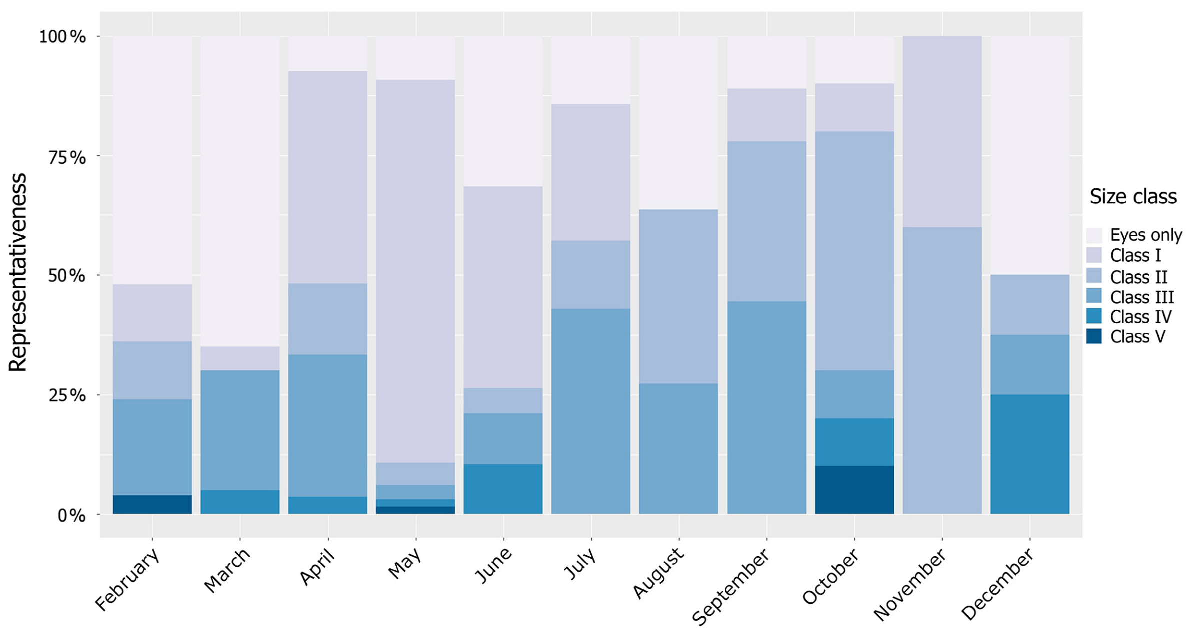

Fig. 2. American crocodile demographic structure by size classes found throughout all 2013 in Coiba Island, Panama.

Sighting fractions ranged between 0.32 (transect 3) and 0.48 (transect 4) for Messel's equation and 0.37 (transect 2) and 0.57 (transect 4) for King's equation (Table 2). Population size (N) estimates based on Messel's visible fraction equation ranged between 5 ± 6.18 (transect 1) and 11 ± 8.61 (transect 2) crocodiles, with a total of 19 ± 7.5 crocodiles for the whole study area. N varied between 4.32 ± 3.81 (transect 1) and 13.19 ± 7.37 (transect 2) crocodiles, with a total of 25 ± 7.25 crocodiles based on King's visible fraction equation. Overall population densities were estimated

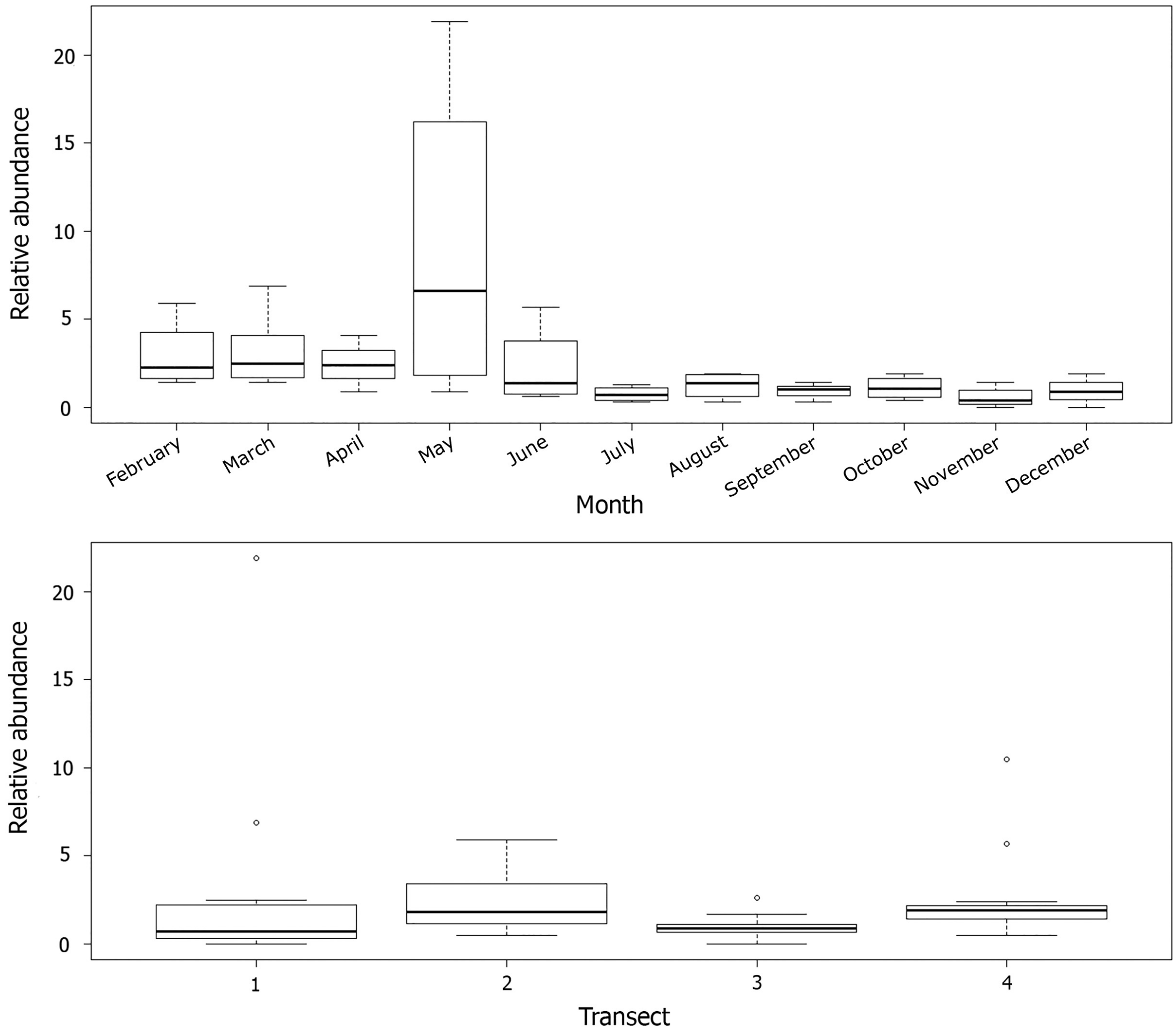

Fig. 3. American crocodile relative abundance by months (top) and by transects (bottom) found throughout all 2013 in Coiba Island, Panama, expressed as median and quartiles with whiskers at minimum and maximum values. Outliers are represented as open circles.

at 6.48 and 8.77 American crocodiles/km^2 based on Messel's and King's approaches, respectively.

Mark–recapture

From the 189 American crocodiles observed by the capture team, 51.3% (97 individuals) were not captured, 37.0% (70 individuals) were captured once, and 11.6% (22 individuals) were recaptured twice or more, with an overall mean capture of 8.36 ± 8.87 per month (Table 1). From these, 17 were sub-adults, 39 were juveniles, and 25 were hatchlings, 11 of which reached the subsequent age group (from hatchlings to juveniles) between the capture and recapture time (April and May, respectively). Two individuals (ID536: juvenile; TL last recapture = 49.3 cm; male and ID523: juvenile; TL last recapture = 50.5 cm; male) had the highest numbers of recaptures throughout the study, with five and four times, respectively.

We found significant differences in the number of individuals observed among transects (K-W χ^2 = 11.86, df = 3, *P*-value = 0.01) but not among months (K-W χ^2 = 11.61, df = 10, *P*-value = 0.31). Capture efficiency ranged between 21% in February and 77% in April, with a mean of 45 ± 15%.

Table 2. Coiba Island American crocodile population size estimates (N) derived from the Messel's and King's sighting fraction equations, highlighting the standard distribution (SD), the sum of maximum number of observations recorded by size class (Max), the sighting fraction estimated (p), and the confidence intervals (CIs).

Variables	Transect 1	Transect 2	Transect 3	Transect 4	Total
Mean	1.73	4.90	2.27	3.36	12.27
SD	1.19	3.83	1.61	1.12	6.11
Shapiro-Wilk test	0.90	0.87	0.88	0.89	0.92
P-value	0.17	0.07	0.11	0.14	0.29
Length (km)	3.3	2.4	2.2	2	9.9
Area	0.83	0.74	0.69	0.67	2.93
Messel et al. (1981)					
Max	5.00	11.00	7.00	7.00	19.00
p	0.35	0.45	0.32	0.48	0.65
N	5.00	11.00	7.00	7.00	19.00
CI	6.18	8.61	7.67	4.32	7.50
Density (ind/km^2)	6.02	14.86	10.14	10.45	6.48
King et al. (1990)					
p	0.40	0.37	0.39	0.57	0.48
N	4.32	13.19	5.76	5.88	25.71
CI	3.81	7.37	4.51	2.59	7.25
Density (ind/km^2)	5.20	17.82	8.35	8.78	8.77

Table 3. No time dependence by sex model (female, male, and not determined) and hatchlings-allowed-to-vary by age group model (juveniles and sub-adults) parameters estimated via POPAN formulation, highlighting the standard error (SE) and the lower and upper confidence intervals (CIs) by each parameter (φ, p, and β).

Parameters	Female	Male	Not determined	Juvenile	Sub-adult
Survival (φ)	0.88	0.97	0.28	0.43	0.87
SE	0.09	0.05	0.07	0.06	0.07
Lower CI	0.59	0.59	0.16	0.32	0.67
Upper CI	0.98	1.00	0.44	0.55	0.96
Recapture (p)	0.03	0.10	0.77	0.77	0.02
SE	0.03	0.03	0.20	0.04	0.02
Lower CI	0.00	0.05	0.27	0.69	0.00
Upper CI	0.17	0.17	0.97	0.83	0.11
Entry (β)	0.00	0.00	1.00	1.00	0.00
SE	0.00	0.00	0.00	0.00	0.00
Lower CI	0.00	0.00	0.00	0.00	0.00
Upper CI	0.00	1.00	1.00	1.00	1.00
Initial population (N)	62.67	29.82	54.60	50.87	181.80
SE	60.84	8.14	15.45	4.78	178.49
Lower CI	18.67	21.49	43.93	44.55	46.31
Upper CI	330.11	58.08	124.36	64.37	943.52

Note: Since hatchlings results were time-dependent, their results (described by months) are not included in this table.

Juveniles (40.3%) and hatchlings (37.3%) were the age groups captured the most, followed by sub-adults (22.4%). No adults were captured during the entire study. Animal capture sizes and weights ranged from 25 to 168.7 cm TL and 0.035 to 15.5 kg, with a sex ratio of 1:1.6 (9 females:14 males).

The time dependence by sex model and the hatchlings-allowed-to-vary by age group model had the lowest AIC (121.95 and 119.55, respectively). Survival, recapture, and entry probabilities were highly variable among both sex and age groups (Table 3). Initial population size (N) by sex was 62.67 (CIs 18.67–330.11) females, 29.82 (CI

21.49–58.08) males, and 54.60 (CI 43.93–124.36) sex-not-determined animals, with an overall population density of 21.39, 10.18, and 18.63 ind/km^2, respectively. In contrast, N by age groups was 25 (CI 25–25) hatchlings, 50.87 (CI 44.55–64.37) juveniles, and 181.80 (CI 46.31–943.52) sub-adults, with an overall population density of 8.53 hatchlings/km^2, 17.36 juveniles/km^2, and 62.05 sub-adults/km^2. It is important to highlight that the absence of variation in hatchling's N is due to the short period of time being considered; hatchlings become early juveniles (from ~25 to 30 cm TL; Platt and Thorbjarnarson 2000) in about one month (Balaguera-Reina et al. 2015); biasing the analysis.

Gross population estimates (i.e., superpopulation; Schwarz and Arnason 1996) were similar to the initial population size with some increasing numbers in the case of sex-not-determined individuals (476.83) and juveniles (293.71; Table 4). There were some possible violations of model assumptions related to homogeneity in survival and capture probability by sex (χ^2 = 3.75, df = 8, P-value = 0.87) and age group (χ^2 = 3.28, df = 10, P-value = 0.97), which might implicate biases in the survival, recapture, and entry probabilities as the numbers of crocodiles estimated. Values of $\hat{c}$ were in both cases <1, implying that data were under-dispersed likely due to the low numbers of individuals captured and recaptured throughout the study.

Discussion

This study is one of the few investigations with crocodylians that provides population size estimates based on both direct (mark–recapture) and indirect (spotlight) methods which permits comparison and discussion regarding the methods' effectiveness, robustness, and applicability. Comparisons of data collected from both spotlight and mark–recapture methods showed no significant differences with respect to the number of American crocodiles spotted throughout the study, confirming the assumption of no effect derived from the pre-sampling.

Table 4. American crocodile gross population on Coiba Island, Panama (N*-hat; superpopulation) estimated via POPAN formulation by sex and age groups, highlighting the standard error (SE), and the lower confidence interval and upper confidence interval (LCI and UCI).

Sex/age group	N*-hat	SE	LCI	UCI	Density (ind/km^2)
Female	62.67	60.84	12.69	309.51	15.59
Male	29.82	8.14	17.63	50.43	7.42
Not determined	476.83	123.19	289.73	784.76	118.62
Sub-adult	181.80	178.49	36.33	909.71	45.22
Juvenile	293.71	59.62	198.10	435.47	73.06
Hatchling	25.00	0.00	25.00	25.00	6.22

Previous studies on Coiba Island captured a total of 190 American crocodiles between 2009 and 2012, of which 69 individuals (33 juveniles, 22 sub-adults, and 14 adults) were captured in our study area (from Playa Blanca to El Maria beaches; Bashyal 2012, Venegas-Anaya et al. 2015). Studies done in 2013 in the same area (Balaguera-Reina et al. 2015, 2016), including the present investigation, captured a total of 43 new (never marked) animals, giving a total of 112 non-hatchling crocodiles captured and marked. Nesting ecology analysis has revealed that only 5% of the hatchlings survived after two months and only 0.5% survived until the end of the year (Balaguera-Reina et al. 2015), indicating a low recruitment rate. Therefore, we can safely say based on these data that the minimum population size of non-hatchling American crocodiles between Playa Blanca and El Maria was ~112 animals (until 2013), with a recruitment rate that likely oscillates between one and two individuals per year.

Based on our data, we estimated a population size of 19.00 ± 7.50 individuals via Messel's approach and of 25.71 ± 7.25 individuals using King's approach, both of which are well below the minimum population size recorded for the area. In contrast, we estimated a total population size ranging between 147 and 257 individuals by sex and age groups, based on the POPAN formulation, which is above the minimum population size defined for the area.

Chabreck (1966) stated that it was possible to estimate population numbers (N) based on the relationship of the number of nests (nn) present in a defined area and the proportion of adults in the population (A), females in the adult population (F), and nesting females in the female population (E) (N = nn/$A \times F \times E$). Thus, based on the data collected for several authors through almost 10 yr of studies in our study area (Bashyal 2012, Balaguera-Reina et al. 2015, 2016, Venegas-Anaya et al. 2015), the population size using Chabreck's approach (nn = 10 nest, $A = 20/112$, $F = 11/20$, and $E = 10/11$) is 119.04 individuals, which is very close to the value we estimated from the overall capture data for the study area (~112 individuals). Even so, this is also an underestimation of the American crocodile population size because it was impossible for us to have captured anything close to all individuals in the area, since newly non-hatchling animals have been captured and marked (~30 crocodiles) since 2013 (M. D. Venegas-Anaya, *unpublished*).

It is important to understand that populations change over time and the population size estimate (does not matter the method used) reflects only a photograph in an instant and is highly influenced by the ecosystem in which the estimation was done. Therefore, temporality (i.e., make this exercise more than once) and use of different methods (as done in the present study) are important factors that help to define the most certain value that logically represents the actual population number.

Source of bias in population size estimations

It is known that the mean number of animals seen in a survey series will always be below the actual number of individuals present if there is no way to identify each individual (Southwood and Henderson 2003). However, if we find a way to relate these data to the number of individuals present in a survey series and can estimate the variation of the number based on repeated sampling, it can give us a fair estimation of the fraction we spotted with respect to the true population present at the time of surveys (Messel et al. 1981). Even though Messel's and King's sighting fraction equation attempted to do this, King et al. (1990) underestimated population sizes due to the inclusion of the mean number of crocodiles seen as main descriptor of the true population, which is clearly below the actual number of crocodiles present in the area. Although Messel et al. (1981) included a more sophisticated way to estimate the minimum number of crocodiles present in a survey series based on the maximum number of crocodiles seen by age groups (max), they failed to estimate and relate the actual variation present in the data as a descriptor of the distribution of the mean number of crocodiles spotted; thus, they clearly underestimated the true population size. These two equations are also likely biased by the necessity for the data to fit theoretical distributions, which is difficult to achieve in ecology because data are generally skewed (Southwood and Henderson 2003). This represents a new challenge for crocodylian biologist to develop a more consistent way to estimate visible fractions (p) avoiding all the issues described above and allowing researchers to use a well-spread method (spotlight surveys) to infer population numbers.

Crocodylian population distributions could approach normality only if they are randomly distributed and the population is very dense, or if the size of sampling unit is large enough that large numbers of animals are present in each sample. However, none of these assumptions is routinely applied to crocodylian surveys due to the animals' tendency to cluster together (as found in this study), the scarcity of some age groups in the field (mainly large animals; Messel et al. 1981, Medem 1981), and the way surveys are done (mainly following transects in boats or on foot instead of setting traps randomly distributed; Chabreck 1963). Therefore, striving for theoretical distributions in crocodile populations should be not of interest to ecologists as a means of describing dispersion (Southwood and Henderson 2003).

The POPAN formulation is a variant of the Jolly-Seber open-population capture–recapture model, which includes inference about entry probabilities into the sampled population (Schwarz and Arnason 1996). It implies that all four general assumptions from mark–recapture must be met to obtain unbiased population size estimates. However, in our case, goodness-of-fit tests indicated possible violations of model assumptions related to homogeneity in survival and capture probability, which implies that both initial and gross population numbers could be biased in some unknown manner. It is likely that these violations derive from the unequal probability of found and captured age groups in crocodylians due to ecological (differences in habitat utilization, social hierarchization, seasonal range movements, individual wariness) and logistical (such as walkable/navigable areas and crocodylian size ranges) constraints (Messel et al. 1981, Kushlan and Mazzotti 1989, Webb et al. 1989). In addition, the low number of American crocodiles observed and captured per sample in the area due to the use of a standardized technique with a capture window (3 min) could also affect the estimation of population size due to a lack of data necessary to estimate variation in the model, which will be reflected by a lack of fit of the model given the data (Cooch and White 2007).

The American crocodile population in the study area has been described as highly dynamic both spatially (due to animal movements among transects; Balaguera-Reina et al. 2016) and demographically (due to immigration–emigration and births; Balaguera-Reina et al. 2015). In this area, the maximum distance movement reported has been ~5.5 km for adults, ~5.8 km for sub-adults, ~1.2 km for juveniles, and ~2.9 km for hatchlings, with juveniles moving around transects as far as ~8 km along coastlines (Balaguera-Reina et al. 2016). Thus, the ability to catch individuals varies greatly throughout the study area both spatially and temporally (particularly for juveniles and sub-adults), having implications at the time one wants to choose mark–recapture for crocodylian surveys, because of possible violations of model assumptions (Southwood and Henderson 2003).

American crocodile population size estimations

Despite American crocodiles' wide distribution, population sizes have only been estimated in few countries across its range using either spotlight surveys sighting fractions, mark–recapture, or some other type of modeling method (Table 5). However, it is important to recognize that estimates derived from Messel's and King's equations and to a lesser extent from Chabreck's equation underestimate population numbers, meaning that these populations are likely larger than reported at the time the study was done. Population size estimates based on mark–recapture techniques have been done in Mexico and Colombia (Table 5). However, it is not possible to make clear interpopulation comparisons (either among these studies or with the present study) due to the lack of standardized measures (e.g., density ind/km^2).

Relative abundance estimations from insular and coastal areas have been reported in Belize, Mexico, Ecuador, Venezuela, Honduras, and Colombia (Table 6). These values, except for the inland data from Banco Chinchorro (Charruau et al. 2005) and the landlocked lake in Haiti (Thorbjarnarson 1989), are similar to the data we collected, suggesting how this seasonal oscillation we reported in Coiba might also be found in other islands. These data also suggest that coastal habitats in both insular and mainland areas might not support relative abundances over 4 ind/km, which is low compared with inland relative abundances reported in places like Venezuela and Costa Rica (Table 6). We noted fluctuations in the proportion of SC observations across the year with the presence of class IV and V (adults) only at the hatching (April and May; likely females) and courtship-mating time (October-December; Balaguera-Reina et al. 2015) and classes II and III (juveniles and sub-adults) throughout the whole year (Fig. 2). This implies partial ecological assessments through the year may actually underrepresent the structure present in a defined area.

Conclusions

Exploring and understanding the natural history of the American crocodile as well as other crocodylian species requires trustworthy, repeatable,

Table 5. American crocodile population size (PS) estimations across its range collected from literature, including the standard deviation (±SD) or the variation range (min–max).

Country	Study area	Method	PS ± SD or (min–max)	Author
Colombia	Tayrona National Natural Park	King's sighting fraction	3.7 ± 4.2	Farfan-Ardila et al. (in press)
Colombia	Portete Bay	Mark–recapture	134.3 ± 17.9	Espinosa et al. (2012)
Mexico	La Ventanilla estuary	Mark–recapture	749.2 ± 54.9	Garcia-Grajales et al. (2007)
Mexico	La Palmita Lake	King's sighting fraction	36 (26–45)	Brandon (2006)
Mexico	La Encrucijada Biosphere Reserve	King's sighting fraction	99.57 ± 14.32	Reserva de la Biosfera la Encrucijada (2010)
United States	Southern Florida	Chabreck's model	220 ± 78	Kushlan and Mazzotti (1989)
United States	Turkey Point	Chabreck's model	440	Wasilewski and Enloe (2006)

Table 6. American crocodile relative abundance estimations (RA) from insular and coastal areas across its range by country reported from literature.

Country	Study area	RA (ind/km)	Author
Belize	Turneffe Atoll	0.96	Platt and Thorbjarnarson (2000)
Belize	Turneffe Atoll	1.2	Platt et al. (2004)
Colombia	Portete Bay	1.2	Espinosa et al. (2012)
Colombia	Cispata Bay	1.1	Ulloa Delgado (2012)
Costa Rica	Tempisque River	18.3	Sánchez (2001)
Costa Rica	Las Baulas National Parks	1.2	Mauger et al. (2012)
Costa Rica	Palo Verde National Parks	4	Mauger et al. (2012)
Costa Rica	Santa Rosa National Parks	4.7	Mauger et al. (2012)
Costa Rica	Area of Conservation OSA	4.3	Mauger et al. (2012)
Costa Rica	Bebedero River	4.5	Sanchez et al. (1996)
Costa Rica	Tarcoles rivers	19.1	Sasa and Chaves (1992)
Ecuador	Bajen estuary	(0.90	Carvajal et al. (2005)
Ecuador	Plano Seco estuary	0.45	Carvajal et al. (2005)
Haiti	Etang Saumatre	6.3	Thorbjarnarson (1989)
Honduras		0.51	Klein, unpublished
Mexico	Banco Chinchorro Biosphere Reserve	13.90†; 1.3‡; 6.8§	Charruau et al. (2005)
Venezuela		1.57	Seijas (1986)
Venezuela	Yaracuy River	4.82	Arteaga and Sánchez (1996)
Venezuela	Tocuyo River	5.1	Arteaga (1997)

† Inland water bodies.
‡ Coastline systems.
§ Overall estimation.

and most importantly standardized methods that allow researchers to assess population dynamics in space and time. These approaches allow the estimation of unbiased population sizes with CIs and the definition of density (e.g., ind/km^2) or relative abundance (e.g., ind/km) values that are suitable for interpopulation comparisons (Thorbjarnarson 1989). Even though such efforts have been made in several countries where American crocodiles occur, the scarcity of density estimates makes it difficult to understand the big picture regarding the population ecology of the species (i.e., How many crocodiles can a system support? How does it vary with respect to habitats and seasonality and how do habitat reduction and climate change affect this dynamic?).

Determinations of relative abundances allow researchers to assess population trends (i.e., increasing, decreasing, stable) over extended time periods, providing important insights about population dynamics. However, estimates of population numbers also contribute additional information that allow evaluation of attributes such as carrying capacity (e.g., defining biomasses), energy fluxes, and crocodylian functionality in the community or ecosystem. Therefore, more studies covering different types of ecosystems should be done using different methodological approaches that allow researchers to define the effectiveness and robustness of these widely used methods (spotlight surveys and mark–recapture) as well as to strive to develop and improve them to obtain more accurate data, giving scientist and decision makers the opportunity to be better informed at the time to create conservation measurements and planning.

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Literature Cited

Arteaga, A. 1997. Actualización de la situación poblacional de *Crocodylus acutus* y *Caiman crocodilus ssp*. En las costas de Venezuela. Pages 6–16 in

Memorias de la 4ta Reunión Regional del Grupo de Especialistas en Cocodrilos de América Latina y el Caribe. Centro Regional de Innovación Agroindustrial, S.C, Villahermosa, Mexico.

Arteaga, A., and C. Sánchez. 1996. Conservation and management of *Crocodylus acutus* in the low Basin of the Yaracuy river, Venezuela. Pages 153–161 *in* Crocodiles. Proceedings of 13th Working Meeting of the Crocodile Specialist Group. IUCN-The World Conservation Union, Gland, Switzerland.

Balaguera-Reina, S. A., M. Venegas-Anaya, A. Sánchez, I. Arbelaez, H. A. Lessios, and L. D. Densmore III. 2016. Spatial ecology of the American crocodile in a tropical pacific island in central America. PLoS ONE 11:e0157152.

Balaguera-Reina, S. A., M. Venegas-Anaya, O. I. Sanjur, H. A. Lessios, and L. D. Densmore III. 2015. Reproductive ecology and hatchlings' growth rates of American crocodile (*Crocodylus acutus*) on Coiba island, Panama. South American Journal of Herpetology 10:10–22.

Bashyal, A. 2012. Population genetics of the American crocodile in Coiba National Park, Panama. Thesis. Texas Tech University, Lubbock, Texas, USA.

Bayliss, P., G. J. W. Webb, P. J. W. Whitehead, and A. M. A. Smith. 1986. Estimating the abundance of saltwater crocodiles, *Crocodylus porosus* Schneider in tidal wetlands of the Northern Territory: a mark-recapture experiment to correct spotlight counts to absolute numbers, and the calibration of helicopter and spotlight counts. Australian wildlife Research 13:309–320.

Brandon, J. 2006. Tamaño poblacional del *Crocodylus acutus* (Cuvier, 1807) (REPTILIA: CROCODYLIA) y su variación interanual en la laguna La Palmite, Jumiltepec, Oaxaca, durante el periodo 2004-2005. Thesis. Universidad del Mar. Mexico.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. P. Pollock. 1987. Design and analysis of methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5:1–437.

Carvajal, R. I., M. Saavedra, and J. J. Alava. 2005. Ecología poblacional, distribución y estudio de hábitat de *Crocodylus acutus* (Cuvier, 1807) en la ''Reserva de producción de fauna manglares El Salado'' del estuario del Golfo de Guayaquil, Ecuador. Revista de Biologia Marina y Oceanografía 40:141–150.

Chabreck, R. H. 1963. Methods of capturing, marking, and sexing alligators. Proceedings of the Annual Conference of the Southeast Game and Fish Commission 17:47–50.

Chabreck, R. H. 1966. Methods of determining the size and composition of alligator populations in Louisiana. Proceedings of the Annual Conference of the Southeast Game and Fish Commission 20:105–112.

Charruau, P., J. R. Cedeño-Vasquez, and S. Calme. 2005. Status and conservation of the American crocodile (*Crocodylus acutus*) in Banco Chinchorro Biosphere Reserve, Quintana Roo, Mexico. Herpetological Review 36:390–395.

Cooch, E., and G. C. White. 2007. Program MARK: a gentle introduction. Fifth edition. http://www.phidot.org/software/mark/docs/book/

Espinosa, M. I., A. Bertin, J. Gómez, F. Mejìa, M. Guerra, L. Baez, N. Gouin, and E. Patiño. 2012. A three-year mark-recapture study in a remnant population of *Crocodylus acutus* Cuvier in Portete Bay (Guajira, Colombia). Gayana 76:52–58.

ESRI (Environmental Systems Research Institute). (2016). Arc GIS Version 10.4.4. ESRI, Redlands, California, USA. https://www.esri.com/

ETESA. 2015. Hidrometeorología. Empresa de Transmisión de Energia S.A. Panamá. http://www.hidromet.com.pa/clima_historicos.php

Garcia-Grajales, J., G. Aguirre-León, and A. Contreras-Hernandez. 2007. Tamaño y estructura poblacional de *Crocodylus acutus* (Cuvier, 1807) (reptilia: Crocodylidae) en el estero de La Ventanilla, Oaxaca. Mexico. Acta Zoológica Mexicana 23:53–71.

Hutton, J. M., and M. E. J. Woolhouse. 1989. Mark-recapture to assess factors affecting the proportion of a Nile crocodile population seen during spotlight counts at Ngezi, Zimbabwe, and the use of spotlight counts to monitor crocodile abundance. Journal of Applied Ecology 26:381–395.

Ibañez, A. 2006. Golfo de Chiriquí, Ecosistemas y Conservación de la Zona Insular y Costera. The Nature Conservancy, Panama City, Panama.

King, F. W., M. Espinal, and C. Cerrato. 1990. Distribution and status of the crocodilians of Honduras. Pages 313–354 *in* Crocodiles. Proceedings of 10th Working Meeting of the IUCN/SSC Crocodile Specialist Group. IUCN- The World Conservation Union, Gland, Switzerland.

King, F. W., J. P. Ross, and L. D. Gutierrez. 1994. Survey of the status of the crocodilians of Nicaragua. Pages 121–161 *in* Crocodiles. Proceedings of the 12th Working Meeting of Crocodile IUCN/SSC Crocodile Specialist Group. IUCN- The World Conservation Union, Gland, Switzerland.

Kushlan, J. A., and F. J. Mazzotti. 1989. Population biology of the American crocodile. Journal of Herpetology 23:7–21.

Lettink, M., and D. P. Armstrong. 2003. An introduction to using mark-recapture analysis for monitoring threatened species. Pages 5–32 *in* Department of Conservation (Eds.). Using mark-recapture analysis for monitoring threatened species: introduction and case study. Department of Conservation Technical Series 28, New Zeeland.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. USDA Circ. 118. USA.

Mauger, L. A., E. Velez, M. S. Cherkiss, M. L. Brien, M. Boston, F. J. Mazzotti, and J. R. Spotila. 2012. Population assessment of the American crocodile, *Crocodylus acutus* (Crocodilia: Crocodylidae) on the Pacific coast of Costa Rica. Revista de Biologia Tropical 60:1889–1901.

Medem, F. 1981. Los Crocodylia de Sur América. Los Crocodylia de Colombia. Carrera 7 Ltda., Santa Fe de Bogotá, Columbia.

Messel, H., G. C. Vorlicek, A. G. Wells, and W. J. Green. 1981. Surveys of tidal river systems in the Northern Territory of Australia and their crocodile populations. The Blyth-Cadell rivers system study and the status of *Crocodylus porosus* in tidal waterways of northern Australia. Sydney: Monograph No. 1. Pergamon Press, Australia.

Murphy, T. M. 1980. The population status of the American alligator at Savannah River National Environmental Research Park. SRP-NERP-4. University of Georgia. Savannah River Ecology Laboratory, Aiken, South Carolina, USA.

Petersen, C. G. J. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. Report of the Danish Biological Station 6:5–84.

Platt, S. G., T. R. Rainwater, and S. Nichols. 2004. A recent population assessment of the American crocodile (*Crocodylus acutus*) in Turneffe Atoll, Belize. Herpetological Bulletin 89:26–32.

Platt, S. G., and J. Thorbjarnarson. 2000. Status and conservation of the American crocodile, *Crocodylus acutus*, in Belize. Biological Conservation 96:13–20.

Ponce-Campos, P., J. Thorbjarnarson, and A. Velasco. (IUCN SSC Crocodile Specialist Group). 2012. *Crocodylus acutus* in IUCN 2012. IUCN red list of threatened species. Available from: Version 2012.2. http://www.iucnredlist.org

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reserva de la Biosfera la Encrucijada. 2010. Monitoreo Poblacional de Cocodrilianos (*Crocodylus acutus* y *Caiman crocodilus fuscus*) en la Reserva de la Biosfera La Encrucijada. Comisión Nacional de Áreas Naturales Protegidas, Mazatán, Chiapas, México.

Sánchez, J. 2001. Estado de la población de cocodrilos (*Crocodylus acutus*) en el río Tempisque, Guanacaste, Costa Rica. Technical Report. Área de Conservación Tempisque-Instituto Nacional de Biodiversidad (INBio), Heredia, Costa Rica.

Sanchez, R. J., J. Bolaños, and L. C. Piedra. 1996. Población de *Crocodylus acutus* (Crocodylia: Crocodylidae) en dos ríos de Costa Rica. Revista de Biología Tropical 44:835–840.

Sasa, M., and G. Chaves. 1992. Tamaño, estructura y distribución de una población de *Crocodylus acutus* (Crocodylia: Crocodilidae) en Costa Rica. Revista de Biologia Tropical 40:131–134.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of open-model capture recapture experiments. Biometrics 52:860–873.

Seijas, A. E. 1986. Situación actual del caimán de la costa *Crocodylus acutus* en Venezuela. Pages 96–108 *in* Crocodiles. Proceedings of 8th Working Meeting of the Crocodile Specialist Group. IUCN-The World Conservation Union, Gland, Switzerland.

Seijas, A. E. 1988. Habitat use by the American crocodile and the spectacled caiman coexisting along the Venezuelan coastal region. Thesis. University of Florida, Gainesville, Florida, USA.

Short, A. D. 2006. Australian beach systems - nature and distribution. Journal of Coastal Research 22:11–27.

Southwood, T. R. E., and P. A. Henderson. 2003. Ecological methods. Blackwell Science, Oxford, UK.

Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 119:18–25.

Thorbjarnarson, J. B. 1989. Ecology of the American crocodile (*Crocodylus acutus*). Pages 228–258 *in* P. M. Hall editor. Crocodiles: their ecology, management, and conservation. IUCN-The World Conservation Union, Gland, Switzerland.

Thorbjarnarson, J. B. 2010. American Crocodile *Crocodylus acutus*. Pages 46–53 *in* S. C. Manolis and C. Stevenson, editors. Crocodiles. Status survey and conservation action plan. Third edition. Crocodile Specialist Group, Darwin, Australia.

Ulloa Delgado, G. 2012. Proyecto de conservación del Crocodylus acutus de la bahía de Cispatá con la participación de las comunidades locales municipio de San Antero- departamento de Córdoba Caribe de Colombia. Documento de apoyo técnico para la solicitud de la enmienda del apéndice 1 al 2: 130 p.

Venegas-Anaya, M., A. Escobedo-Galván, S. A. Balaguera-Reina, F. Lowrance, O. I. Sanjur, and L. D. Densmore III. 2015. Population ecology of American crocodile (*Crocodylus acutus*) in Coiba National Park, Panama. Journal of Herpetology 49:349–357.

Wasilewski, J. A., and B. Enloe. 2006. The status of American crocodiles (*Crocodylus acutus*) at Turkey point nuclear power plant, Florida, USA. Pages 284–292 *in* Proceeding of the 18th working meeting of the crocodile specialist group. IUCN-The World Conservation Union, Gland, Switzerland.

Webb, G. J. W., P. G. Bayliss, and S. C. Manolis. 1989. Population research on crocodiles in the Northern Territory, 1984-86. Pages 22–59 *in* Crocodiles. Proceedings of the 8th Working Meeting of the IUCN-SSC Crocodile Specialist Group. IUCN-The World Conservation Union, Gland, Switzerland.

Webb, G. J. W., and H. Messel. 1979. Wariness in *Crocodylus porosus* (Reptilia: Crocodilia). Australian Wildlife Research 6:227–234.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement:120–138.

Williams, K. A., P. C. Frederick, and J. D. Nichols. 2011. Use of the superpopulation approach to estimate breeding population size: an example in asynchronously breeding birds. Ecology 92:821–828.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2474/full