
DEMOGRAPHY AND HABITAT USE OF *CAIMAN CROCODILUS* IN TWO CONTRASTING CHANNELS IN THE MIDDLE MAGDALENA RIVER DRAINAGE, COLOMBIA

VIVIANA M. CARTAGENA-OTÁLVARO, VIVIAN P. PÁEZ¹, DIEGO ALZATE-ESTRADA,
AND BRIAN C. BOCK

*Grupo Herpetológico de Antioquia, Instituto de Biología, Universidad de Antioquia, Calle 67 # 53–108,
A.A. 1226, Medellín, Colombia*

¹Corresponding author, e-mail: vivianpaez1@gmail.com

Abstract.—A rigorous monitoring project provides a means for guaranteeing the conservation or sustainable use of a population, allowing the quantification of changes in its demographic parameters and associating them with spatial and temporal variation in environmental factors. We present the results of a monitoring project of a population of Spectacled Caiman (*Caiman crocodilus*) conducted from 2013 to 2018 in two contrasting channels in the middle Magdalena River drainage in Colombia. We employed three monitoring methods: nocturnal counts, capture-mark-recapture study, and N-mixture models. Although nocturnal counts and N-mixture models are comparable methods, the estimates of population size and of detection probabilities that they provided were different. Both methods, however, agreed in general by indicating that detection probabilities were low and population sizes were large, in comparison to similar estimates from other populations. In the deeper channel with more riparian vegetation and less fishing activity, relative densities were 3.3 orders of magnitude greater than in the other channel, and had a population comprised of a larger proportion of subadult and adult individuals. Low recapture rates precluded estimation of population sizes, survivorship rates, or detection probabilities with the capture-mark-recapture data; however, this method provided a more reliable summary of the size distribution of individuals, population sex ratios, and patterns of habitat use. Water depth was the only covariable that significantly influenced detection probabilities. This study is the first application of N-mixture models to estimate population size and detection probabilities in a *Caiman* population.

Key Words.—crocodilians; detection probabilities; monitoring methods; population size; population structure; sex ratios; Spectacled Caiman

INTRODUCTION

A rigorous monitoring program is an essential tool for guaranteeing the successful conservation, management, and sustainable use of biodiversity in its distinct levels (Chediack 2009; Mancina and Cruz-Flores 2017). Thus, it is an indispensable component in the design of public policies that are biologically sustainable and socially viable (Chediack 2009). At the population level, monitoring allows for quantification of changes in demographic parameters (survivorships, size/age distributions, and population sizes and growth rates) and permits inspection of associations of these parameters with spatial and temporal variation in environmental factors (Given 1994; Tucker et al. 2005). In the specific case of crocodilian populations, rigorous monitoring has been emphasized not only because of the functional role crocodilians play in their ecosystems (Medem 1981; Mazzotti and Brandt 1994), but also because of the traditional commercial demand for their hides that makes them economically important resources (Sánchez-Herrera et al. 2011). In some countries where

crocodilians are commercially harvested, monitoring projects have been conducted to help ensure their use is sustainable (Sánchez-Herrera et al. 2011; Barrios-Quiroz and Cremieux 2018).

In monitoring projects of crocodilian populations, the most commonly employed methods for estimating population parameters are nocturnal counts based on detection of eye-shine and capture-mark-recapture analyses (García-Grajales et al. 2007). Both methods, however, suffer from biases related to imperfect detection and spatial variation in environmental variables, which limits their abilities to discern temporal changes in population dynamics or associate them with stochastic or anthropogenic factors (Llobet and Seijas 2003; Sarkis-Gonçalves et al. 2004; García-Grajales et al. 2007). Recently, Hierarchical Models (HM) have become popular alternative methods for monitoring natural populations (Kery and Royle 2015), with N-mixture models (also known as Binomial-Poisson models) being one of the most used HMs for estimating densities (Royle 2004). They are statistically formalized to model detection probability (imperfect detection),

linking it to density estimates and associating it to spatial and temporal environmental variability (Royle and Dorazio 2008; Kery and Royle 2015). While these models have been employed recently in studies of other crocodylians (Fujisaki et al. 2011; Mazzoti et al. 2019), to date these models have not been applied towards monitoring populations of *Caiman*.

In evaluations of crocodylian populations, changes in estimates of demographic parameters have been shown to be related to different physical and environmental variables in the study areas (Campos et al. 1995; Coutinho and Campos 1996). In general, the basic components of evaluations of habitat quality and the demographic characteristics of these populations are the type of water body, the principle types of vegetation, and the presence of human impacts (García-Grajales et al. 2007). While it is not easy to define which aspects of the landscape, vegetation, and local human activities most influence crocodylian populations, an evaluation of the general status of populations with demographic indicators provides useful reference points for long-term monitoring (Sánchez-Herrera et al. 2011).

In addition, for most species of crocodylians that have been evaluated, habitat use has been shown to vary with body size (Medem 1981; Fujisaki et al. 2011; Morales-Betancourt et al. 2013). For example, in species in the family Alligatoridae, neonates and juveniles congregate in shallow water with aquatic and emergent vegetation that provides a refuge from predators, as well as offering ample insect densities as prey (Ayazargüena 1983; Morales-Betancourt et al. 2013). Adults more typically are found in wetlands and the main channels of rivers (Medem 1981). Also, individuals in this family have been shown to prefer microhabitat with floating vegetation and snags formed by downed trees (Balaguera-Reina and González-Maya 2009; Balaguera-Reina et al. 2010).

In this study, we investigated two populations of Spectacled Caiman (*Caiman crocodilus*), the most widely distributed crocodylian of the New World, which ranges from southern Mexico to Peru and Brazil (Velasco and Ayarzagüena 2010). This species is considered a habitat generalist because it occurs in river channels, streams, lagoons, lakes, marshes, and borrow pits (Velasco and Ayarzagüena 2010); however, habitat characteristics have been shown to influence *C. crocodilus* population structure and dynamics (Coutinho and Campos 1996; De la Ossa and De la Ossa-Lacayo 2013). Here we present the results of a monitoring project conducted from 2013 to 2018 in two tributary channels to the Magdalena River with contrasting environmental characteristics in terms of physical conditions (mean channel width and depth), environmental condition (vegetative cover), and human impacts (levels of active fishing and human densities along the shores of the channels). We implemented

three sampling methods (nocturnal counts, capture-mark-recapture effort, and N-mixture density models) to evaluate the effectiveness and appropriateness of these methods for estimating demographic parameters. For each population, we estimated population size (N), relative density (d), detection probability (*p*), and the proportion of individuals in each size class and sex. We also associated these demographic parameters to different characteristics of the two study sites, such as water temperature, air temperature, water depth, and the extent of riparian vegetative cover. Finally, we evaluated the proportion of individuals seen in each type of micro-habitat, with the goal of documenting habitat use patterns for each size class of individuals.

MATERIALS AND METHODS

Study area.—We conducted our study in two channels located along a section of the Magdalena River bordered by the municipality of Puerto Berrío (Department of Antioquia) to the west and the municipality of Cimitarra (Department of Santander) to the east in Colombia (Fig. 1). This region originally contained Tropical Moist Forest (TMF; Holdridge 1947), although most has been cleared for agriculture and cattle ranching. Median daily high temperatures exceed 25° C, with from 2,000–4,000 mm of precipitation annually (López 1991). A bimodal precipitation regime affects the hydrology of the river and associated wetlands, with dry/low water periods occurring from December to March (*verano*) and again from July to September (*veranillo*), and rainy/high water periods occurring from April to June and again in October and November (Brian Bock et al., unpubl. data).

The San Juan (SJ) channel (6°43'N, 74°07'W) begins in the Carare River near its confluence with the Magdalena River and connects to the La Duda wetland. It is approximately 30 m wide, with an average depth of 3.5 m and a total length of 17.3 km. It is a relatively well-conserved channel with a low level of human impacts, including low levels of fishing activity, and a high proportion of its shorelines contains mature riparian vegetation (Páez et al. 2015). In contrast, the second study channel, Caño Negro (CN; 6°29'N, 74°22'W) is located across the Magdalena River from the town of Puerto Berrío, and connects the Magdalena River to the La Chiquita and El Encanto wetlands. It is approximately 11 m wide, with an average depth of 1 m and a total length of 3 km. Most of its shoreline is deforested, and local fishermen frequent the channel often. The distance between San Juan and Caño Negro is approximately 60 km. For logistic reasons, it was not possible to conduct surveys using each of the three sampling methods simultaneously. We conducted nocturnal counts in both channels from 2014 to 2018,

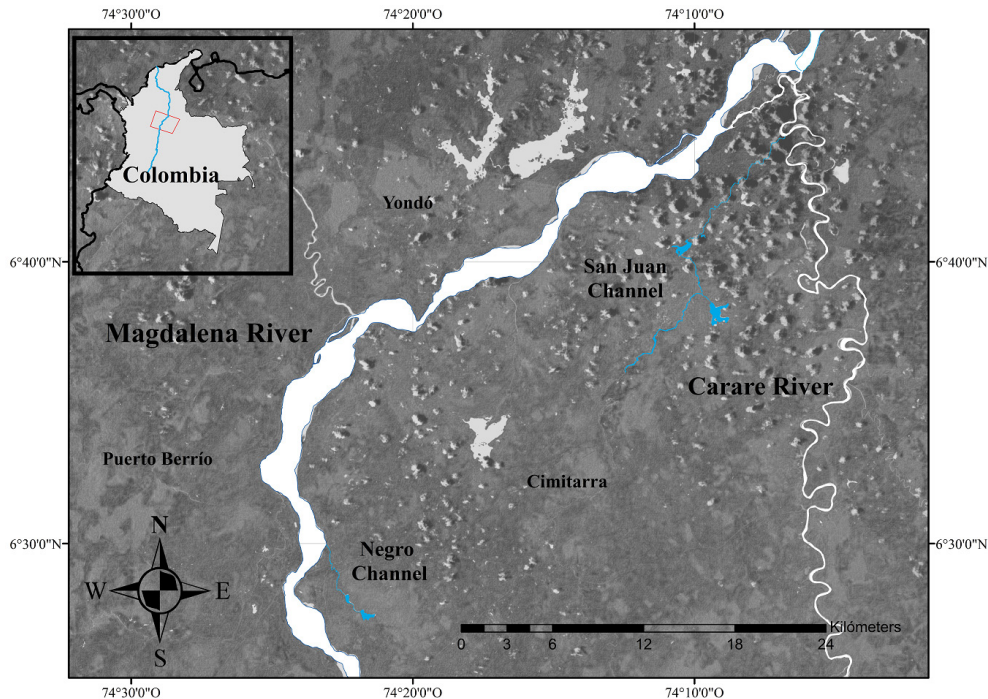


FIGURE 1. Map of the study area in the middle Magdalena River drainage, Colombia. The Caño Negro and San Juan channels are indicated in blue. Reference coordinates WGS 84.

while our capture-mark-recapture efforts occurred from 2013 to 2016, and the N-mixture model censuses from 2016 to 2018.

Nocturnal counts.—We conducted 23 nocturnal counts of individuals by detection of their eye-shine (Chabreck 1966) to permit the estimation of relative density in each channel. We calculated relative density as the number of individuals registered per kilometer searched during each census event. The total census distances were 9 km of the 17.3 km available in SJ and 3 km in CN. We conducted censuses between 1900 and 2100 by slowly trolling (10 km/h) in a boat while searching for individuals using a 350-lumen spotlight. To minimize the effect of our capture activities (see below) on the wariness of the individuals, on each field trip we always conducted the shoreline censuses on nights before we attempted to capture individuals. In the censuses, for each individual detected, we registered the type of micro-habitat used: (1) on land, for individuals observed out of the water along the shoreline; (2) macrophytes, for individuals observed partially submerged under floating vegetation, usually along the shoreline; (3) woody snags, for individuals observed partially submerged under fallen tree trunks and branches or accumulations of driftwood, usually along the shoreline; and (4) open water, for individuals observed at the surface in the center of the channel. In addition to these 23 nocturnal counts conducted from 2014 to 2018, we also estimated the absolute size of

the population (King et al. 1990, Cerrato 1991) by conducting an extra census in each channel during 2018, which consisted of eight nocturnal counts on successive nights. We estimated the absolute size of the population by dividing the mean number of individuals seen each night by the maximum number of individuals registered during the counts (Morales-Betancourt et al. 2013). We also inspected for temporal trends in these data using Regression Analyses.

Capture-mark-recapture method.—We conducted 15 capture sessions, seven in CN and eight in SJ. We located individuals between 2100 and 2400 using a 350-lumen spotlight to detect their eye-shine and approached them in the boat to attempt to capture them using a cable noose attached to a 2.5 m long telescoping pole (Morales-Betancourt et al. 2013). We restrained captured individuals using an aluminum Animal Control Pole (The Ketch All Company, San Luis Obispo, California, USA) and we georeferenced their capture locations using a GPS Etrex 30 (Garmin Ltd, Olathe, Kansas, USA). We took individuals to the shore and measured their total length (TL). We classified individuals into four size classes (modified from Morales-Betancourt et al. 2013): class I (TL < 39.9 cm), class II (40 < TL < 79.9 cm), class III (80 < TL < 119.9 cm), and class IV (TL > 120 cm). We determined the sex of all individuals with TL > 80 cm by means of visual inspection of the cliteropenis (Leslie 1997).

For each capture session, we quantified three

TABLE 1. Population parameters estimated for two Spectacled Caiman (*Caiman crocodilus*) populations using the sampling methods of nocturnal counts, capture-mark-recapture effort, and N-mixture models. Mean relative density and estimated population size are number \pm standard error. For N-mixture Models, total count of individuals and mean relative density are the number of Sampling Units (SUs). The abbreviations SJ = San Juan channel and CN = Caño Negro channel.

Parameters	Nocturnal counts		Capture-mark-recapture		N-mixture models	
	SJ	CN	SJ	CN	SJ	CN
Total count of individuals	1,349	172	216	180	12	4
Mean relative density (individuals/km)	37 \pm 31	11 \pm 12			24 \pm 6	6 \pm 4
Estimated population size	383 \pm 72	45 \pm 7			2,493	500
Fraction visible or detection probability	0.76	0.69			0.17	0.17

hydrological/habitat variables at sites separated by 1 km distance in each channel (nine locations in SJ and four locations in CN). At each site, we measured channel depth and made three measures (one on each shoreline and one in the center of the channel) of the water temperature at 10 cm depth and the percentage riparian vegetative cover (using a convex spherical densitometer). To statistically examine possible associations between the values recorded for these variables and the body sizes of the individuals we captured, we used the Inverse Distance Weighting Interpolation Method (Burrough and McDonnell 1998) with the ArcMap10.4.1 software to generate a map for each variable in the two study sites with a cell size of 30 \times 30 m to interpolate values of water temperature, percentage vegetative cover, and channel depth for every caiman capture site. We then conducted a Multiple Step-wise Regression Analysis (Hutton and Woolhouse 1989) to examine the relation between TL of captured individuals and these three environmental variables. For all tests, $\alpha = 0.05$.

N-mixture model.—From 2016 to 2017, we made pilot visits to select sites for conducting surveys using this method. These sites, or Sampling Units (SUs), were separated by 1 km of lineal distance and we assumed them to be independent, given that mean daily distances moved by individuals in these populations is only 120 m (Cartagena-Otálvaro 2019). In SJ, the nine SUs were 100 m in length by 30 m wide, while in CN the four SUs were 100 m in length by 11 m wide.

In April 2018 during eight successive nights in each channel, we constructed a count history for each SU using the data obtained during the nocturnal censuses to test a static N-mixture model for closed populations, where variation in the counts was only attributed to individual detection probabilities. We used the Pcount function of the Unmarked packet, with the weights of each derived model based on corrected Akaike Information Criteria (AICc) to determine the relative support for each model. We only considered models with a $\Delta AICc \leq 3$. We used a Parsimony Fit Analysis from the observed data using the Nmixture.GOF.test, which calculates the goodness-of-fit of the models based upon a Pearson Chi Square

(MacKenzie et al. 2006; Linkie 2008).

In each SU, we recorded the water depth, air temperature, and percentage vegetative cover over the shorelines (see methodology below). We standardized these data as (original data - median)/standard deviation. We included percentage vegetative cover as a covariable that might influence mean density (λ) because other studies with crocodilians have shown that denser shoreline vegetation may increase abundances because of greater food availability and better conditions for nesting (Medem 1981; Ardila-Robayo 2009). We also included water depth and air temperature as covariables that might affect detection probabilities (p) because they have been shown to influence detection rates in other studies of crocodilians (Fujisaki et al. 2011; Mazzoti et al. 2019). We considered a covariable to have a significant effect on density or detectability when the P value of the test for the estimated parameters was ≤ 0.05 . After identifying the model with the best fit to the data and which environmental variables had significant effects on density and detection probability, we obtained the predictions of each model in each channel, based on the standardized values obtained from the inverse distance weighting interpolation method. Finally, we estimated population size as the sum of the predicted values for each 100 m SU in each channel. We used R software (version 3.5.0) for all statistical analyses.

RESULTS

With the nocturnal count method, we observed 1,521 individuals, with an annual mean of 173 \pm 83 (standard error) individuals. Our attempts to estimate sizes of the individuals detected with this method were too imprecise because of the large flight distances in each channel (SJ, 8 \pm 15 m; CN, 7 \pm 12 m), so we did not calculate size distributions with these data. Both the total number of individuals seen, as well as the estimate of relative density, were greater in SJ (1,349 individuals counted, mean relative density = 37 individuals/km) than in CN (172 individuals counted, mean relative density = 11 individuals/km), while the indices of the fraction visible were comparable in the two study sites (Table 1). The

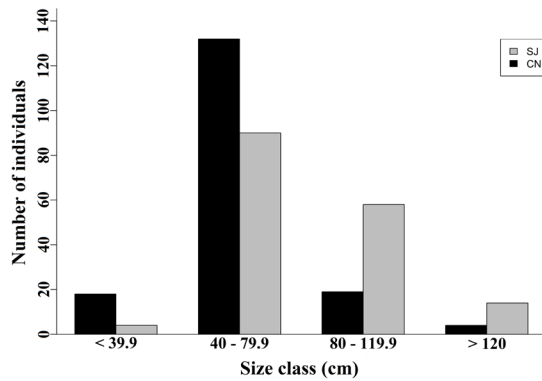


FIGURE 2. Size distributions of individuals of Spectacled Caiman (*Caiman crocodilus*) captured in Caño Negro (black) and San Juan (grey), two channels in the middle Magdalena River drainage, Colombia.

estimated population size for SJ based upon the eight successive night censuses (383 individuals) also was greater than that estimated for CN (45 individuals), but in both cases, there was a decreasing trend in the number of individuals seen on successive nights (SJ, $r^2 = 0.614$, $F_{1,6} = 9.55$, $P < 0.001$; CN, $r^2 = 0.759$, $F_{1,6} = 18.93$, $P < 0.001$).

With the N-mixture model data, we observed a maximum of 12 individuals per SU, with a mean of 2 ± 2.2 individuals. We examined 16 N-mixture abundance models, but only retained three models, λ (channel + cover), p (depth), λ (channel), p (depth), and λ (channel + cover), p (temp + depth) for interpretation based upon their low $\Delta AICc$ values because all evaluated models lacked goodness-of-fit (GOF, $P < 0.001$) and exhibited over-dispersion in their data (all \hat{c} values > 1.7). In the three models, the variables of percentage riparian vegetative cover and air temperature were not significant and had confidence intervals that included zero (Table 2). For this reason, we present results from the model where channel type had a significant positive effect on abundance, and water depth had a significant negative effect on detectability (model λ -channel, p -depth, Table 2). The density estimate for each SU was $\lambda = 24 \pm 6$ individuals for SJ and $\lambda = 6 \pm 4$ individuals for CN, with a detection probability of $p = 0.17$. The projection of this model over the total length of each channel (13 km for SJ and 3 km for CN) yielded an extrapolated estimate of total population size of 2,493 individuals in SJ and 500 individuals in CN (Table 1).

With the capture-mark-recapture method, we captured 393 individuals (55% of them in SJ), with only six recaptures. This low rate of recapture (1.5%) precluded estimation of survivorships, detection probabilities, or population sizes with these data. Of the individuals we captured, 29.7% were females, 3.6% were males, and 66.7% were juveniles (individuals too small to reliably determine sex based upon secondary

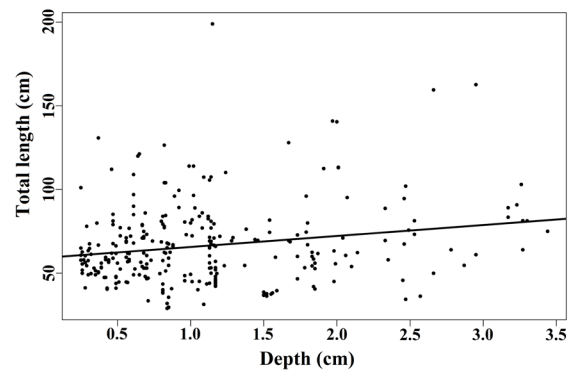


FIGURE 3. Relationship between water depth and total length of the Spectacled Caiman (*Caiman crocodilus*) individuals captured in two channels in the middle Magdalena River drainage, Colombia.

sexual characteristics or cloacal probing). Body sizes of captured individuals varied from 29–199 cm TL, with females significantly larger than males ($F_{1,129} = 6.30$, $P < 0.001$). Females (> 80 cm TL) averaged 106 cm TL, with a mean weight of 3.9 kg, while males (> 80 cm TL) averaged 93 cm TL, with a mean weight of 2.6 kg.

Size class distributions differed significantly among the channels ($X^2 = 45.3$, $df = 2$, $P < 0.001$), with more class I individuals detected in CN and more class III and class IV individuals in SJ (Fig. 2). Sex ratios in both channels were heavily skewed in favor of females (1F:0.16M in CN and 1F:0.14M in SJ), with no significant differences among channels ($X^2 = 0.018$, $df = 1$, $P = 0.890$).

In the evaluation of microhabitat use based on the nocturnal count method, we found significant differences in use among channels ($X^2 = 139.0$, $df = 3$, $P < 0.001$), with more individuals in SJ floating in open water or under woody snags, while in CN we observed more individuals partially submerged in mats of macrophytes. With the capture-mark-recapture data, we found that the only variable significantly associated with TL of the individuals was water depth ($F_{1,277} = 11.09$, $P < 0.001$), with relatively more larger individuals captured in the deeper SJ channel (Fig. 2) and also pooling data from both channels, with larger individuals occurring in deeper sections of these channels (Fig. 3). This regression, however, only explained 4% of the total variation in TL ($r^2 = 0.040$).

DISCUSSION

The nocturnal count and N-mixture model approaches are comparable methods (both being based upon counts of individuals), but in this study, the estimates each method provided for population size and fraction visible/detection probabilities differed. With the nocturnal count method that calculates indices without

TABLE 2. Parameters of the N-mixture models considered for Spectacled Caiman (*Caiman crocodilus*) in two study channels in the middle Magdalena River drainage, Colombia. Symbols are λ = mean density estimated in the sampling units, p = mean detection probability in the sampling units, Parm = number of parameters estimated in the model, AICc = Akaike Information Criteria corrected for small sample sizes, W = model weight, Beta (β) = coefficient estimate, SE = standard error, 2.5% = lower confidence interval limit (CI), 97.5% = upper confidence interval limit, P = probability value.

Model	Parameters	AICc	Δ AICc	W	BETA	2.5–97.5% CI	P
λ (channel + cover), p (depth)	5	397.8	0	0.44			
	λ (intercept)				1.79 \pm 0.40	1.00–2.58	< 0.001
	λ (channel)				1.42 \pm 0.30	0.83–2.01	< 0.001
	λ (cover)				-0.17 \pm 0.10	-0.37–0.03	< 0.001
	p (intercept)				-1.93 \pm 0.41	-2.73, -1.12	< 0.001
	p (depth)				-0.39 \pm 0.13	-0.64, -0.15	< 0.001
λ (channel), p (depth)	4	398.7	0.96	0.71			
	λ (intercept)				1.82 \pm 0.37	1.08–2.56	< 0.001
	λ (channel)				1.30 \pm 0.30	0.71–1.88	< 0.001
	p (intercept)				-1.85 \pm 0.38	-2.60, -1.09	< 0.001
	p (depth)				-0.41 \pm 0.13	0.13, -0.16	< 0.001
λ (channel + cover), p (temp + depth)	6	399.7	1.97	0.87			
	λ (intercept)				1.78 \pm 0.41	0.98–2.58	< 0.001
	λ (channel)				1.43 \pm 0.31	0.82–2.04	< 0.001
	λ (cover)				0.17 \pm 0.10	-0.38–0.03	< 0.001
	p (intercept)				-1.92 \pm 0.41	0.41, -1.11	< 0.001
	p (depth)				-0.39 \pm 0.12	-0.64, -1.14	< 0.001
	p (temp)				0.02 \pm 0.09	-0.16–0.19	< 0.001

accounting for temporal variation in detectabilities, it is possible to obtain inaccurate estimates of the demographic characteristics of a population (in cases where temporal variation occurs). Our evidence of decreasing detectabilities in both channels over eight successive nights of conducting nocturnal counts suggests this may be a common problem with this method. Even so, in many parts of the world, including Colombia, this is the most used method for monitoring crocodilian populations because it provides information on the population with a minimal investment of time and resources (García-Grajales et al. 2007; Minambiente 2016). Some authors even argue that indices of relative abundance and density produced by nocturnal counts, while inexact, may legitimately be compared because the lack of precision is similar among studies (Sánchez et al. 1998). In our study, both the estimates of the fraction of individuals present that were visible for both channels, as well as the relative abundances, were among the highest ever registered for Colombian populations of *C. crocodilus*, including even estimates of populations inhabiting protected areas (Minambiente 2016). However, the standard deviations around our estimates of relative abundance (37 ± 31 for SJ and 11 ± 12 for CN) were so great that the usefulness of

making comparisons with other studies seems dubious to us. Moreover, the values obtained of the fraction of individuals present that were visible for both channels (76% for SJ and 69% for CN) were comparable to those reported for a protected area in Costa Rica (35.49% and 98%; Cabrera et al. 2003). Among the factors that may affect the fraction visible in monitoring efforts of crocodilian populations are water depth, air and water temperatures, and inaccessibility of the habitat (Hutton and Woolhouse 1989; Sai et al. 2016).

In contrast, thanks to the manner in which population size is calculated with N-mixture models by statistically correcting for detectabilities and other biases associated with the observation of individuals, it is possible to more confidently estimate this parameter and make comparisons with other such studies (McCoy et al. 2011; Keever et al. 2017). It has been shown for a variety of wildlife species (Couturier et al. 2013; Dennis et al. 2015; Keever et al. 2017) that the proper implementation of N-mixture models requires a substantial sample size (multiple sites and/or multiple observations), which provides greater power to the statistical analyses and permits more confident estimation of population sizes and detection probabilities, along with estimation of the spatial and temporal variation associated with them

(Kery and Royle 2015). In our study, small sample sizes may have contributed to the general lack of fit of the different models examined and to the over-dispersion that was apparent in the data. This, coupled with the low detection probabilities in our study, suggests we may have over-estimated abundances in both channels. Mazzoti et al. (2019) also documented low detection probabilities using this method for a population of the American Crocodile (*Crocodylus acutus*) in Florida, arguing that when the number of sampling occasions is low, a high relative density of crocodiles could skew estimates of detection probabilities. Alternatively, low estimates of detection probabilities may be genuine, reflecting the general wariness of crocodilians. Also, N-mixture models do not distinguish whether the environmental variables examined affect detection probabilities or relative densities. Finally, our estimates of fraction visible (obtained with the nocturnal count method) and of detection probabilities (obtained with the N-mixture model approach) were different, perhaps in part because the former method estimates the proportion of all members of the population that were detected (Morales-Betancourt et al. 2013) while the latter is more precisely an individual detection probability (Kery and Royle 2015).

Although the capture-mark-recapture method is considered the most realistic and robust model for the quantification of wildlife populations (García-Grajales et al. 2007), in this study it was not possible to use the data obtained for estimation of population size, detection probabilities, or survivorships due to the low recapture rates. In crocodilians, several explanations for low recapture rates have been proposed, including: (1) one-trial learning or wariness, where captured individuals learn to avoid subsequent recapture (Bustard 1968; Webb and Messel 1979; Ron et al. 1998); (2) differential mortality among the different size classes of individuals, or among male and female neonates (Lance et al. 2000); and (3) dispersal of individuals prior to attaining sexual maturity (Tucker et al. 1998). Whatever the cause, the capture effort made during our attempt to use this method was not entirely wasted, as the data obtained from captured individuals did provide estimates of the size structure of the populations and their sex ratios. We recognize these estimates may have been influenced by differences among size classes or sexes in capture probabilities, but without more recaptures for each group, it is not possible to attempt to correct for these biases.

Despite the absolute differences in the estimates obtained using the different methods in this study, there was concurrence in that they all indicated SJ had the larger population size, with greater estimated relative abundances and densities and with a good representation of all size classes, even of larger individuals. This site

experiences less fishing activity because the closest human settlement is 6 km distance and the site has greater vegetative cover along its shoreline (Páez et al. 2015). In contrast, CN is located < 2 km from the city of Puerto Berrío, whose inhabitants frequently use the channel for fishing (and to hunt crocodiles; Viviana Cartagena-Otálvaro, pers. obs.). Also, the shorelines of CN and the wetlands it drains have been heavily deforested and are dominated by crops and pasture (Páez et al. 2015). In a comparable study examining the demographics of the Magdalena River Turtle (*Podocnemis lewyana*) in these same two channels (Páez et al. 2015), similar differences were encountered, with SJ supporting a larger population containing all size classes of turtles. Because the SJ channel is more isolated and better conserved, it should be considered a priority location for conducting conservation efforts for these and other threatened wildlife species in this region.

In addition to the apparent differences among the channels in *Caiman* harvest rates, the SJ channel also differed from CN in being deeper, wider, and with more riparian vegetation that may provide better food resources, cover, and conditions for nesting to this population (Medem 1981; Ardila-Robayo et al. 2009). This also may help explain not only why abundances were greater in SJ, but also why there were more larger individuals there. Both channels, however, had relatively low numbers of class III and class IV individuals, precisely the most important size classes for insuring the persistence of a crocodilian population (Balaguera-Reina and González-Maya 2009). Populations with a paucity of larger individuals are typical of sites that have been over-harvested (Ayarzagüena 1983; Velasco and Ayarzagüena 1995), which is unfortunately the most commonly documented population condition for crocodilians in Colombia (Balaguera-Reina and González-Maya 2009; Moreno-Arias et al. 2013). Thus, to increase *Caiman* densities in CN, we recommend efforts to reforest its shorelines, although because it is a shallow channel, these actions might primarily benefit juvenile individuals (Platt and Thorbjarnarson 2000). To increase densities in both channels, we also recommend the implementation of existing environmental legislation intended to protect this species from harvest (Instituto Nacional de los Recursos Naturales Renovables y del Ambiente 1990).

Sex ratios were similar in both channels, with a strong female bias. Deeming and Ferguson (1989) noted that sex ratio estimates for crocodilians usually exhibit a female bias, and that this could be caused by: (1) differences in habitat selection by the two sexes (Thorbjarnarson 1997); (2) genuine differences in primary sex ratios arising from their temperature-dependent sex determination mechanism (Piña et al. 2003); (3) hunting pressure directed preferentially

towards males (Crawshaw 1990); or (4) differences among the sexes in dispersal tendencies, as females apparently make more restricted movements (Da Silveira et al. 2010). We have no data to distinguish among these factors but suspect the latter two are more likely for our populations. The differences documented in use of microhabitats in the two channels may have been related to habitat heterogeneity and differences in microhabitat availability (Thorbjarnarson 1989), which also may have contributed to the differences in population structure in the two channels, with a greater proportion of neonates and juveniles in CN. Smaller individuals have been shown to prefer floating vegetation and woody snags due to the abundance there of fish, macroinvertebrates, and molluscs that form the bulk of the diet for these individuals (Moreno-Arias et al. 2013). In contrast, we found larger individuals in deeper microhabitats, consistent with reports from other studies of this species in the Magdalena-Cauca drainage of Colombia (Agudelo-Henríquez and Vergara-Gil 2005). Water depth also was the only covariable that was significantly (negatively) associated with detection probabilities, perhaps because submerging in response to an approaching boat is facilitated in deeper water, especially for larger individuals. Deeper sites may offer better refuge sites for larger individuals, as well as contain larger prey.

Fujisaki et al. (2011) also used N-mixture models with a population of American Alligator (*Alligator mississippiensis*) in Florida and found detection probabilities decreased with increasing water levels, speculating that higher water levels may lead to more movement of individuals. Also, crocodilians can sink out of sight in response to approaching boats more readily in deeper water (SJ) than in shallow water (CN). Finally, other studies of crocodilian species have found the detectability of individuals varies with water temperature, but not always in the same direction (Mazzoti et al 2019). Hutton and Woolhouse (1989) documented a positive relationship between these variables (individuals were easier to detect in shallower, hence warmer waters). Individuals in warmer waters also may be more active, and hence are more likely to be detected. In contrast, Waddle et al. (2015) concluded that because crocodiles are more active and so spend more time submerged in warmer water temperatures, the probability of detection decreases as water temperature increases.

Our study is one of several recent efforts to compare methods for studying crocodilians in terms of their effectiveness and suitability for estimating population parameters (Escobedo Galván 2003; García-Grajales et al. 2007; Balaguera-Reina et al. 2018). It also is one of the first studies to explore new methods (N-mixture models) for providing rigorous, standardized, repeatable

measures of the spatial and temporal dynamics of their populations (Balaguera-Reina et al. 2018). This is the first study to use N-mixture models (Royle 2004) for estimating population size and detection probabilities in the genus *Caiman*. Like previous studies, we showed that the nocturnal count method, while easy to implement, provides population estimates with large standard errors that also likely suffer from biases that are difficult to quantify. Capture-mark-recapture provided us with another method of estimating population parameters (size structure, sex ratios), but the low recapture rates prevented our estimating the direction and magnitude of biases in these estimates due to differing detectabilities of different classes/sexes, as well as precluded our estimation of population sizes. This is unfortunate, because precise unbiased estimates of population size would permit the evaluation of carrying capacities, energy fluxes, and the function of crocodilians in their communities and ecosystems (Balaguera-Reina et al. 2018). We therefore feel that HMs, specifically N-mixture models, may represent an attractive alternative for implementation in crocodilian monitoring projects seeking to precisely estimate demographic parameters, assuming the assumptions of the model are not violated, and sample sizes are adequate.

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VIVIANA M. CARTAGENA-OTÁLVARO obtained her undergraduate degree from the Universidad de Antioquia in Medellín, Colombia, and is currently a Master's degree student at the same university. She is interested in population ecology and conservation of amphibians and reptiles. (Photographed by Laura Cristina Osorno-Giraldo).



VIVIAN P. PÁEZ obtained her Ph.D. degree in Ecology, Ethology, and Evolution from Ohio University, Athens, Ohio, USA, in 1995 and is currently a Professor in the Instituto de Biología of the Universidad de Antioquia in Medellín, Colombia, where she teaches courses in Population Ecology and Herpetology. She has edited two books and published over 60 scientific articles and book chapters. Her research interests have focused on the influence of nest microclimatic conditions and paternal effects on different fitness components of turtles with temperature-dependent sex determination. She also is conducting demographic projects using population matrix models to permit the elaboration of management plans for several species of freshwater turtles. Since arriving in Antioquia, Colombia, she has been involved in several projects on the natural history and diversity of the herpetofauna in this region, including the founding of the Museo de Herpetología of the Universidad de Antioquia (MHUA). (Photographed by Mónica Nieto).



DIEGO ALZATE-ESTRADA is a Biologist with a degree from the Universidad de Antioquia in Medellín, Colombia, and currently is a Master's degree student at the same university. He is interested in population ecology and conservation of freshwater turtles and crocodylians. (Photograph by Lucas Burgos Alvarez).



BRIAN C. BOCK obtained his Ph.D. degree in Ethology from the University of Tennessee, Knoxville, USA, in 1984 and held Smithsonian, Fulbright, and AAAS fellowships before moving to Colombia, first as a Professor at the Universidad Nacional de Colombia, Medellín, Colombia, and now as a Professor in the Instituto de Biología of the Universidad de Antioquia in Medellín, Colombia, where he teaches courses in Conservation Biology and Behavioral Ecology. He has edited two books and published over 60 scientific articles and book chapters. His initial research focused on how reptile movement patterns influence population structure, but he also has conducted studies on reptile nesting ecology and demography, as well as on the population genetics of other species of Colombian flora and fauna. (Photographed by Jessica Bock Páez).