A three-year mark-recapture study in a remnant population of *Crocodylus acutus* Cuvier in Portete Bay (Guajira, Colombia)

Estudio de captura-recaptura en una población remanente de *Crocodylus acutus* Cuvier en Bahía Portete (Guajira, Colombia)

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RESUMEN

El Cocodrilo Americano *Crocodylus acutus*, ha experimentado importantes declines poblacionales a lo amplio de su distribución debido a la persecución humana, la sobreexplotación y la pérdida de hábitat. *C. acutus* permanece en peligro crítico en algunos países tales como Colombia donde la ausencia de estudios detallados sobre su ecología y distribución constituyen una de las barreras principales para el desarrollo de efectivas estrategias de conservación. Durante tres años desarrollamos un estudio de captura-recaptura para investigar el estatus demográfico de *C. acutus* e identificar las variables medioambientales más influyentes en su distribución en Bahía Portete (Colombia). Nosotros estimamos que la población de cocodrilos es relativamente pequeña (< 140 animales), incluye muy pocos adultos y demuestra un fuerte déficit de hembras en la clase juvenil. La humedad relativa y la temperatura promedio del aire estuvieron positivamente correlacionadas con el número de avistamientos de cocodrilos. Por el contrario, la salinidad promedio del agua se encontró relacionada con la baja probabilidad de observación, presumiblemente debido a la preferencia de los juveniles por áreas de baja salinidad. Nuestros resultados sugieren que la población de *C. acutus* en Bahía Portete está en riesgo y puede requerir la intervención humana para asegurar su persistencia.

Palabras claves: Captura-recaptura, cocodrilo, variables medioambientales, manglar

ABSTRACT

The American crocodile, *Crocodylus acutus*, has experienced important population declines worldwide due to human persecution, overexploitation and habitat loss. *C. acutus* remains critically endangered in some countries such as Colombia where the lack of detailed surveys on its ecology and distribution constitutes a major barrier to the development of effective conservation strategies. We conducted a three-year capture-recapture study to investigate the demographic status of *C. acutus* and to identify environmental variables likely to influence its distribution in Portete Bay (Colombia). We estimated the crocodile population to be relatively small (< 140 animals), to include very few adults, and to demonstrate a very strong deficit in females in the juvenile class. Both mean air temperature and relative humidity were positively correlated with the number of sightings. In contrast, mean water salinity was found to decrease the probability of observing a crocodile, presumably due to juvenile preference for low salinity areas. Our findings suggest that the population of *C. acutus* in Portete Bay is at risk and may require human intervention to assure its persistence.

Keywords: Capture-recapture, crocodile, environmental variables, mangrove.

INTRODUCTION

Historically, the American crocodile (*Crocodylus acutus* Cuvier, 1807) has faced serious population declines throughout its range as a result of human persecution, overexploitation and habitat loss (Thorbjarnarson *et al*. 2006). In some countries, such as Colombia, illegal killing of this keystone species and intentional destruction of its habitat continue to threaten local populations (Thorbjarnarson *et al*. 2006), thereby compromising aquatic ecosystems health and equilibrium in these regions.

In the late 1990s, the IUCN Crocodile Specialist Group set as highest priority the determination of the status and distribution of *C. acutus* in Colombia (Ross 1998). While recent estimates stress the pressing need for appropriate management of the American crocodile in Colombia, the lack of detailed surveys on *C. acutus* ecology and distribution in this country still constitutes a major barrier to the development of effective conservation strategies (Thorbjarnarson 2010).

We describe here the results of a three-year capture-recapture survey to investigate the size and structure of the *C. acutus* population in Portete Bay, Alta Guajira (Colombia). While this region was recently identified as the "Crocodile Conservation Unit" of highest priority in Caribbean South America for long-term conservation of the American crocodile (Thorbjarnarson *et al*. 2006), it does not benefit from any form of legal protection (Gutiérrez-Moreno & Segura-Quintero 2008), and current knowledge of *C. acutus* populations in this region remains rudimentary. The goals of our study were thus to clarify the present status of the American crocodile in this region and to provide robust information necessary for the establishment of effective management strategies.

MATERIALS AND METHODS

Survey strategy

Distribution of *C. acutus* in Alta Guajira was first evaluated during a preliminary investigation consisting of nocturnal searches performed across the region. American crocodiles were observed only in Portete Bay, with the closest other populations being located more than 100 km away (i.e. at Rioacha and Dibulla, FUNGDAHL 2010). Our capture-recapture study thus focused on Portete Bay where eleven transects, totaling 62 km and covering all possible habitats of *C. acutus*, were established. Monitoring of the population was conducted yearly from 2007 through 2009 during three 3-week field sessions performed in July–August, a favorable period for crocodile observations in this region (Abadía 1996). Diurnal and nocturnal census strategies were established according to Platt *et al*. (2004). Diurnal censuses were performed from 10:00 to 14:00 using motorized skiffs, canoes, and on foot, and nocturnal censuses from 18:00 to 03:00 using a motorized skiff only. Crocodile eye-shines were detected using headlights and 2.000.000 candlepower flashlights. Trained personnel from crocodilian captive breeding centers were in charge of handling the captured crocodiles, which were all released within two hours of capture. No nocturnal censuses were performed during full-moon nights due to difficulties for observing crocodiles under such conditions (Platt *et al*. 2004).

Data collection

For each captured animal, total length (TL) was recorded and sex was determined by cloacal examination of the genitalia (Brazaitis 1969; Whitaker *et al*. 1981). The animals were categorized as juveniles (30-90 cm), sub-adults (90-180 cm) and adults (>180 cm) based on their TL (Platt and Thorbjarnarson 2000). Gravid females always exceeded 180 cm TL. Given that mature males are bigger than females, we are confident that the sub-adult category, as defined here, does not include any reproductive animals (Thorbjarnarson 1988).

All captured animals were marked for future identification, both by subcutaneous insertion of microchip identification tag (AVID Identification System Inc., Bta, Colombia) on the right side of the neck, and by unique pattern clipping of their caudal whorls following the instructions from the Columbian Ministry of Environment (Colombia MAVDT 2004, 2007).

For each animal observation, geographical coordinates, air temperature and relative humidity and were recorded using a GPS device (GARMIN MAP 60CSx) and a digital thermo-hygrometer (Model HI 93640-Hanna Instruments), respectively. When animal observations were made in water, water temperature, salinity and pH were measured as well using a refractometer (HI 98203, Hanna Instruments) and a digital potentiometer (Checker-pH Tester, Hanna Instruments).

Statistical analyses

C. acutus abundance was estimated using the mark-recapture models implemented in Rcapture (Baillargeon & Rivest 2007). We ran both closed and open population models. Closed population models assume no recruitment or loss while open population models consider that immigration and death are possible. Rcapture includes eight different closed models incorporating up to three sources of variation in capture probability: temporal effect, heterogeneity between units, and behavioral effect (for more details see Baillargeon & Rivest 2007). The model with the lowest Akaike's information criterion (AIC) was selected and used for subsequent estimations of the population size. Suitability of the selected model was also checked by comparing the observed number of new captures on each census occasion with those predicted by the model (Baillargeon & Rivest 2007). Differences in abundance between sexes and size classes were investigated by carrying out Chi-square tests. Only first capture data were used for these analyses. Probable abundances of each sex and size class were inferred from the observed frequencies of the captured animals and population size estimate.

In order to identify environmental variables that might affect crocodile distribution, we tested the effect of transect characteristics (area of the mangrove swamp, transect length, average air temperature, humidity, and water temperature, salinity and pH) on the total number of crocodile observations (i.e. including captured and non-captured animals) made for each transect over the three-year period. In order to do so, we performed an automatic selection procedure using the regsubset function of the R leaps package (Lumley & Miller 2004). The maximum number of independent variables was set to seven. The selected model was chosen to have the highest adjusted coefficient of determination with all of the predictors being significant. Residuals were checked to see whether they satisfy the conditions required for linear regression.

RESULTS

In total, 215 observations of American crocodiles were made with an average encounter rate of 1.2 crocodile / km. Overall 109 individuals were marked and used for the capture-recapture analysis. Most recaptures (i.e. 7 out of 11) occurred in a transect that was different from the transect in which the animal was captured the first time. Overall, the recapture probability was of 10.1% and no significant differences between the sexes was found (Chi-square test with simulated p-value: $\chi^2 = 0.56$, $P = 0.51$). The model with the lowest AIC (i.e. AIC = 36.7), was found under the assumption of a closed population. It incorporated unit heterogeneity and behavioral effect as sources of variation on capture probability. This finding indicates that the capture probability differs among animals and before and after the first capture. The selected model showed a good fit (P=0.58) and perfectly predicted the number of new captures (i.e. 22, 59 and 28 for 2007, 2008 and 2009 respectively). It yielded to an abundance of 134.3 ± 17.9 crocodiles. Note that under the assumption of an open population (AIC = 38.6), the population was estimated to be bigger including 399 ± 187.

Significant differences in abundance were detected between sexes and size classes (Chi-square test for two-way contingency tables: $\chi^2 = 21.42$, $df = 2$, $P < 0.001$). Overall, the adult class included few individuals (Figure 2). The sex-ratio was significantly male-biased ($\chi^2 = 6.69$, $df = 1$, $P < 0.01$) due to the strong under-representation of females in the juvenile class (14.9%, $\chi^2 = 23.17$, $df = 1$, $P < 0.001$ after Bonferroni corrections, Figure 2). Based on the observed frequencies and population size estimate, we predict the adult class to comprise 13 individuals only and to include more females than males (Fig. 3).

The total number of observations significantly differed between transects (Chi-square test: $\chi^2 = 125.6$, $df = 10$, $P < 0.001$). Based on our model selection procedure, three environmental variables explained a relatively large part of the spatial variation in crocodile distribution ($R^2 = 0.88$, $F_{3,4} = 10.48$, $P = 0.02$): air temperature, relative humidity and water salinity (Table 1). Both mean air temperature and relative humidity were positively correlated with the number of observations (Table 1). In contrast, the probability of observing a crocodile was negatively correlated with higher mean water salinity (Table 1). Note that neither transect length nor area of the mangrove swamp were found to influence the number of crocodile observations made in each transect.

Table 1. Multiple regression parameters for selected environmental variables on the number of crocodile observations for each transect. The selected model was chosen to have the highest adjusted coefficient of determination with all of the predictors in the model being significant after performing an automatic selection procedure of the environmental variables (see text).

Tabla 1. Parámetros de la Regresión múltiple obtenidos a partir de las variables ambientales seleccionadas sobre el número de observaciones de cocodrilos para cada uno de los transectos. El modelo seleccionado fue elegido por mostrar el más alto coeficiente ajustado de determinación, con todos los predictores en el modelo, siendo significativo después de ejecutar un procedimiento de selección automático de las variables ambientales (ver texto).

	Estimate ± Std.Error	t	P
Relative humidity	1.56 ± 0.52	2.98	0.041
Air temperature	14.52 ± 4.06	3.58	0.023
Water salinity	-1.76 ± 0.63	-2.78	0.049

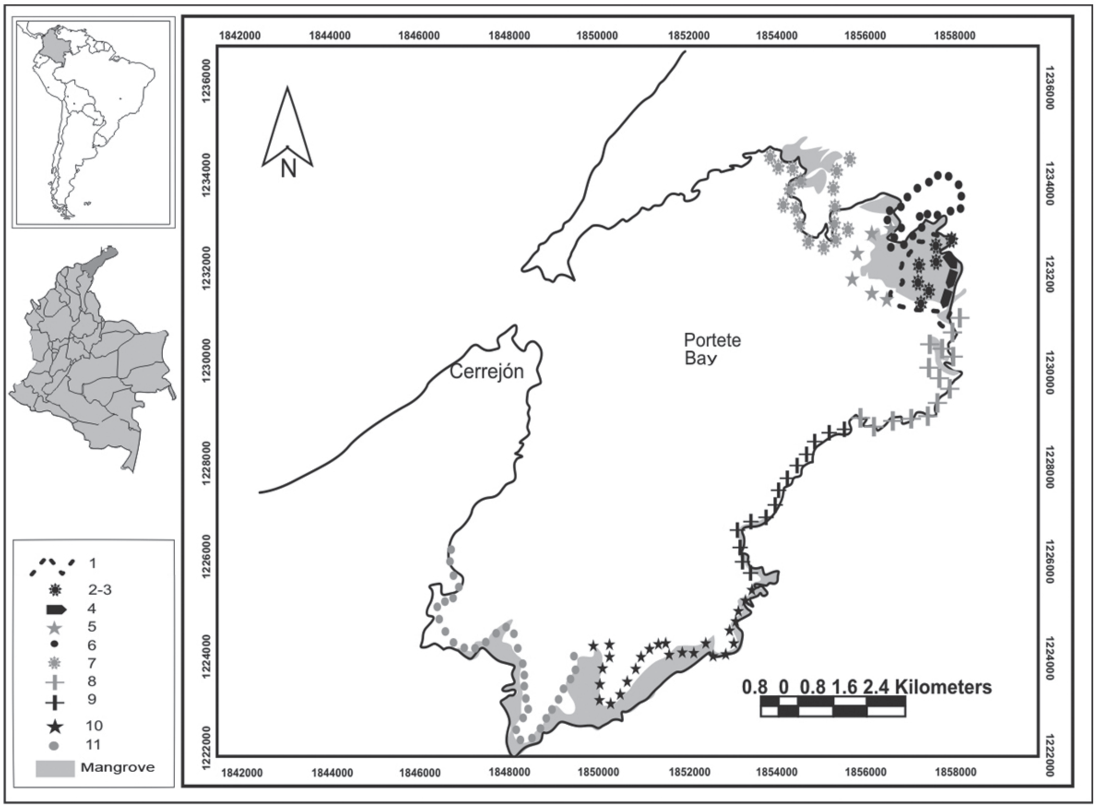

FIGURE 1. Study area and pre-established transects-route

FIGURA 1. Área de estudio y rutas de los transectos preestablecidos

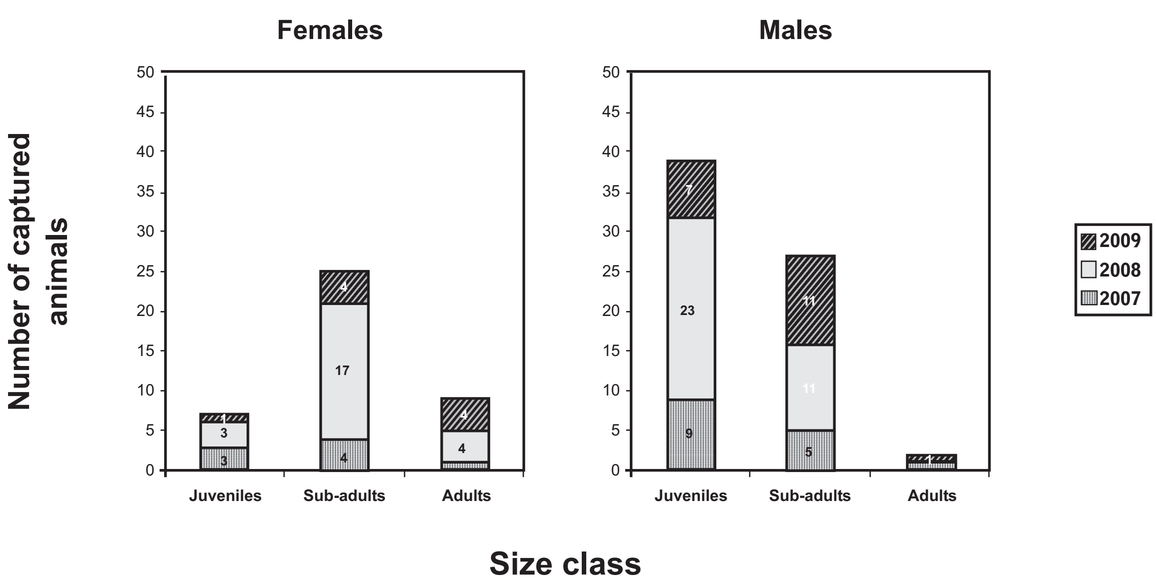

Figure 2. Numbers females and males captured in relation to their size class and for each census period.

Figura 2. Número de hembras y machos capturados en relación a su clase de tamaño y según cada periodo de censo.

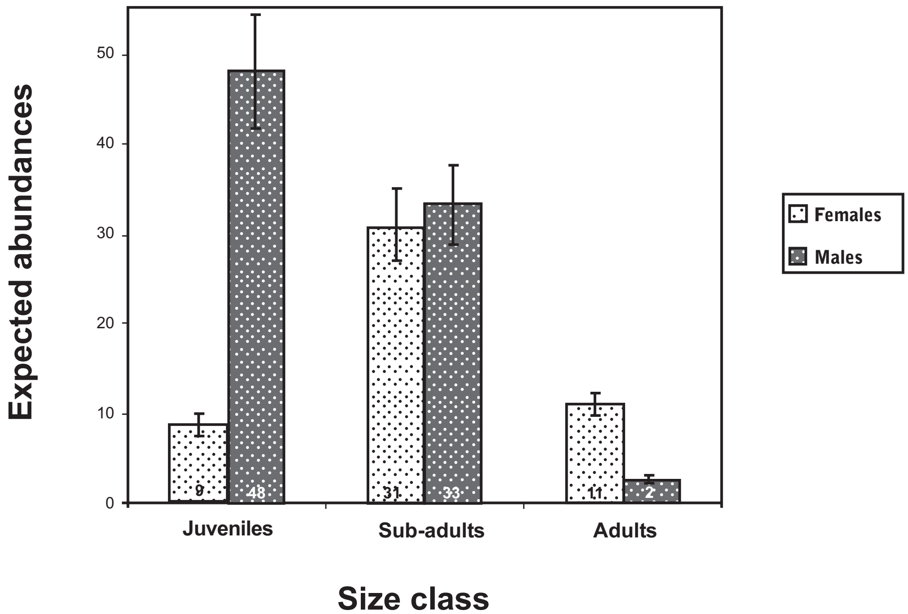

FIGURE 3. Population structure estimated for *C. acutus* in Portete Bay.

FIGURA 3. Estructura estimada de la población de *C. acutus* en Bahía Portete.

DISCUSSION

By estimating the crocodile population of Portete Bay to be < 140 individuals, our study suggests that it is one of the largest populations of *C. acutus* currently known in Colombia (Thorbjarnarson *et al*. 2006). However, our results suggest that only a very few animals are contributing to reproduction (i.e. 13 animals). A similar deficit in adults was also revealed by a previous distance-sampling study performed in the same region in 1992-1993 by Abadía (1996), who argued that such population structure, typical of heavily exploited populations, resulted from intense hunting that occurred in the region between 1979 and 1981. Given that *C. acutus* is expected to reach its reproductive size in 8-12 years, it seems unlikely that the unbalanced demographic structure detected here results solely from the overexploitation that happened 30 years ago. Unfortunately, illegal hunting may still occur. During our field work, we found nine skins of *C. acutus*, freshly and carefully cut which suggests that hunting for crocodile skins is still occurring, at least on a small scale, and reduces the already small reproductive population.

Small reproductive populations are particularly vulnerable to environmental and demographic stochasticity, both of which seriously increase extinction risks (Frankham *et al*. 2002; Engen *et al*. 2003). Genetic stochasticity may also jeopardize the short-term persistence of such small populations by accelerating the loss of genetic diversity and consequent inbreeding depression (Frankham *et al*. 2005; O'Grady *et al*. 2006). Another issue of concern is the apparent lack of genetic input (gene flow) from other populations. Indeed, the Portete Bay population is relatively distant from other known *C. acutus* populations and the model best fitting our data was a closed population model which suggests little immigration. If correct, such a situation could hinder numeric population recovery and the maintenance of substantial genetic diversity.

In addition to the immediate pressures posed by the low number of adults, our results suggest that the *C. acutus* population of Portete Bay may be facing a significant decrease in population growth in the near future. Indeed, only 16% of the juvenile class was represented by females. Unless juvenile females were restricted to non-sampled areas, this result suggest a strong skewed sex-ratio. Skewed sex-ratios are commonly reported in crocodilians (Hall 1990; Campos 1993; Thorbjarnarson 1997), which can sometimes be extreme with 100% of hatchlings of one sex as found in *Crocodylus moreletii* (López-Luna *et al*. 2011). They are generally considered to reflect variations in environmental conditions (Lutz & Dunbar 1984; Lance *et al*. 2000; Leslie & Spotila 2001) and/or differential mortality of females *vs* males during the first years of life (Lance *et al*. 2000). Demographic stochasticity could also be contributing to the unbalanced sex ratio (Lande, 1998; Courchamp *et al*. 1999). Whatever the mechanisms involved, the strongly skewed sex-ratio of the juvenile class suggests that the number of reproductive females will decrease even further in the near future, a situation that could negatively impact population growth by reducing offspring production.

Our results suggest a heterogeneous distribution of *C. acutus* in Portete Bay that may mirror preferences of this species for specific habitat characteristics. Given that our analyses used average data over a three-year period, environmental variables very likely depict real differences in habitat characteristics among the transects. We found that *C. acutus* were preferentially located in areas of high temperature, relative humidity and low water salinity. We hypothesize that such a distribution might be a result of the predominance of juveniles in this population. Indeed, evidence indicates a low tolerance of *C. acutus* to water salinity (Mazzoti & Dunson 1989), particularly in juveniles (Dunson 1970; Evans & Ellis 1977). Similarly, habitat selection by crocodilians may reflect thermal preferences for physiological needs (Downs *et al*. 2008; Stuebing *et al*. 1994), with still-growing crocodiles likely to prefer hot environments due to increased growth rates at higher temperatures (Mazzoti & Brandt 1994; Pérez & Escobedo-Galván 2009). Finally, relative humidity is known to limit evaporative water loss in reptiles (Winne *et al*. 2001; Brown & Shine 2002; Nicholson *et al*. 2005), which may explain the higher abundance of *C. acutus* in areas of higher relative humidity.

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LITERATURE CITED

Abadía, G. 1995. *Crocodylus acutus* (Cuvier 1807) in Bahía Portete. Crocodile Specialist Group Newsletter 14:12.

Abadía, G. 1996. Population dynamics and conservation strategies for *Crocodylus acutus* in Bahía Portete, Colombia. In Crocodiles. Proceedings of the 13th Working Meeting of the Crocodile Specialist Group. The World Conservation Union, Gland, Switzerland.

Baillargeon, S. & L. P. Rivest. 2007. Rcapture: loglinear models for capture-recapture in R. Journal of Statistical Software 19:1-31.

Brazaitis, P. J. 1969. The determination of sex in living crocodilians. British Journal of Herpetology 4:54-58.

Brown, G. P. & R. Shine. 2002. Influence of weather conditions on activity of tropical snakes. Austral Ecology 27:596-605.

Campos, Z. 1993. Effect of habitat on survival of eggs and sex ratio of hatchlings of *Caiman crocodilus yacare* in the Pantanal, Brazil. Journal of Herpetology 27:127-132.

Colombia. Ministerio del Medio Ambiente y Desarrollo Territorial – MAVDT. (2004). Resolución 1172. Sistema Nacional de Identificación de Fauna Silvestre.

Colombia. Ministerio del Medio Ambiente y Desarrollo Territorial –MAVDT. 2007. Resolución 923. Modificación del Sistema Nacional de Identificación de Fauna Silvestre.

Courchamp, F., T. Clutton-Brock & B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 14:405-410.

Downs, C. T., C. Greaver & R. Taylor. 2008. Body temperature and basking behaviour of Nile crocodiles (*Crocodylus niloticus*) during winter. Journal of Thermal Biology 33:185-192.

Dunson, W. A. 1970. Some aspects of electrolyte and water balance in three estuarine reptiles, the diamondback terrapin, American and "salt water" Crocodiles. Comparative Biochemistry and Physiology 32:161-174.

Engen, S., R. Lande & B. E. Sæther. 2003. Demographic stochasticity and Allee effects in populations with two sexes. Ecology 84:2378-2386.

Evans, D. H. & T. M. Ellis. 1977. Sodium balance in the hatchling American crocodile, *Crocodylus acutus*. Comparative Biochemistry and Physiology Part A: Physiology 58:159-162.

Frankham, R., J. D. Ballou & D. A. Briscoe, 2002. Introduction to conservation genetics. Cambridge University Press: New York. pp. 175-195

Frankham, R. 2005. Genetics and extinction. Biological Conservation 126:131-140.

Fundación Hidrobiológica George Dahl (FUNGDAHL). 2010. Diagnóstico Poblacional del Caiman aguja (*Crocodylus acutus*) y la Babilla (*Caiman crocodylus fuscus*) en el municipio de Dibulla, La Guajira. Informe Final. Pp. 134. La Guajira, Colombia.

Gutiérrez-Moreno, C. & C. Segura-Quintero. 2008. Diseño de un área marina protegida para Bahía Portete-La Guajira, Caribe colombiano. Boletín de Investigaciones Marinas y Costeras 37:189-212.

Hall, P. M. 1990. Harvest patterns of New Guinea (*Crocodylus novaeguinea*) and saltwater (*C. porosus*) crocodiles in Papua New Guinea, 1969-1980. Australian wildlife research 17:261-284.

Lance, V. A., R. M. Elsey & J. W. Lang. 2000. Sex ratios of American alligators (Crocodylidae): male or female biased? Journal of Zoology 252:71-78.

Lande, R. 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. Oikos 83:353-358.

Leslie, A. J. & J. R. Spotila, 2001. Alien plant threatens Nile crocodile (*Crocodylus niloticus*) breeding in Lake St. Lucia, South Africa. Biological Conservation 98:347-355.

López-Luna, M., Hidalgo-Mihart, M. & Aguirre-León, G. 2011. Descripción de los nidos del cocodrilo de pantano *Crocodylus moreletii* en un paisaje urbanizado en el sureste de méxico. Acta Zoológica Mexicana 27:1-16.

Lumley, T. & A. Miller, 2004. leaps: Regression Subset Selection. R package version, 2.7.

Lutz, P. L. & A. Dunbar-Cooper 1984. The nest environment of the American crocodile (*Crocodylus acutus*). Copeia 1984:153-161.

Mazzotti, F. J. & W. A. Dunson. 1989. Osmoregulation in crocodilians. American Zoologist 29:903-920.

Mazzotti, F. J. & L. A. Brandt. 1994. Ecology of the American alligator in a seasonally fluctuating environment. In: Everglades: The Ecosystem and its Restoration. (Eds. Davis, S.M. & Ogden, J.C.). pp. 485-505. St. Lucie Press. Delray Beach, Florida.

Nicholson, K. L., S. M. Torrence, D. M. Ghioca, J. Bhattacharjee, A. E. Andrei, J. Owen, N. A. Radke & G. Perry. 2005. The influence of temperature and humidity on activity patterns of the lizards *Anolis stratulus* and *Ameiva exsul* in the British Virgin Islands. Caribbean Journal of Science 41:870-873.

O'Grady, J. J., B. W. Brook, D. H. Reed, J. D. Ballou, D. W. Tonkyn & R. Frankham. 2006. Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. Biological Conservation 133:42-51.

Pérez, O. & A. H. Escobedo-Galván. 2009. Potential effects of El Niño-South Oscillation (ENSO) on growth of the American crocodile, *Crocodylus acutus* (Crocodylia: Crocodilydae) in captivity. Journal of Thermal Biology 34:14-16.

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

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

Ross, J. P. 1998. Crocodiles: Status Survey and Conservation Action Plan. Crocodile Specialist Group, IUCN, Gland, Switzerland: pp. 33-35.

Stuebing, R. B., G. Ismail & L. H. Ching. 1994. The distribution and abundance of the Indo-Pacific crocodile *Crocodylus porosus* Schneider in the Klias River, Sabah, east Malaysia. Biological Conservation 69:1-7.

Thorbjarnarson, J. 1997. Are crocodilian sex ratios female biased? The data are equivocal. Copeia 1997:451-455.

Thorbjarnarson, J. 1988. The status and ecology of the American crocodile in Haiti. Bulletin of the Florida State Museum 33:1-86.

Thorbjarnarson, J., F. Mazzotti, E. Sanderson, F. Buitrago, M. Lazcano, K. Minkowski, M. Muñiz, P. Ponce, L. Sigler, R. Soberon, A. M. Trelancia & A. Velasco. 2006. Regional habitat conservation priorities for the American crocodile. Biological Conservation 128:25-36.

Thorbjarnarson, J. B. 2010. American Crocodile *Crocodylus acutus*. In: Crocodlies. Status Survey and Conservation Action Plan. (Eds. Manolis, C. & C. Stevenson), pp. 46-53. Crocodile Specialist Group, Darwin; Australia

Whitaker, R., Z. Whitaker & A. Vaughan. 1981. Notes on sexing crocodilians. Journal of the Bombay Natural History Society 77:341-343.

Winne, C. T., T. J. Ryan, Y. Leiden & M. E. Dorcas. 2001. Evaporative water loss in two natricine snakes, *Nerodia fasciata and Seminatrix pygaea*. Journal of Herpetology 35:129-133.

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