Potential distribution of the Orinoco crocodile (*Crocodylus intermedius* Graves 1819) in the Orinoco basin of Colombia and Venezuela

Distribución potencial del caimán del Orinoco (*Crocodylus intermedius* Graves 1819) en la Orinoquia colombiana y venezolana

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Abstract

Crocodylus intermedius (Graves 1819), commonly known at the Orinoco Crocodile, is an endemic species of the Orinoco River Basin that occurs in Colombia and Venezuela. Within the Neotropical Crocodylia, it is considered the most endangered species, listed as Critically Endangered. The use of potential distribution models is an important tool in biogeographical analysis for the conservation of rare and endangered species threatened with extinction. For this reason in this study we determined the potential distribution range for the Orinoco Crocodile using the maximum entropy model Maxent. Initial data to calculate potential range included 654 records of known occurrence for this species, 20 environmental and one limnological variable. The distribution of the Orinoco Crocodile was found to be correlated with precipitation climate variables and the type of water (white, clear or black).

Key words. Orinoco River Basin. *Crocodylus intermedius.* Water type. Endangered species. Conservation.

Resumen

Crocodylus intermedius (Graves 1819) comúnmente denominado caimán llanero o caimán del Orinoco, es una especie endémica de la cuenca del Orinoco, con distribución en Colombia y Venezuela. Dentro de los Crocodylia del Neotrópico, es considerada la especie más amenazada y se encuentra en la categoría de Peligro Crítico. El uso de modelos de distribución potencial en el análisis biogeográfico es una herramienta importante para la conservación de especies raras o en peligro de extinción. Es por ello que en este trabajo se buscó determinar la distribución potencial del caimán llanero mediante el uso del algoritmo de maximización de la entropía, Maxent. Como información de entrada se utilizaron 654 registros de presencia de la especie y 20 variables ambientales incluyendo una limnológica. Se concluye que la distribución del caimán llanero está relacionada con la precipitación y con el tipo de aguas (blancas, claras y negras) presentes en la cuenca.

Palabras clave. Cuenca del río Orinoco. *Crocodylus intermedius.* Tipos de aguas. Especie amenazada. Conservación.

Introduction

Crocodylus intermedius (Graves 1819) is a critically endangered species endemic to the Orinoco River Basin in Colombia and Venezuela (http://www.iucnredlist.org/). Its critical status is due principally to extreme overharvest of their populations during the first half of the twentieth century (Medem 1981).

In the two countries where *C. intermedius* occurs, different conservation actions have been taken. Hunting and egg collection were prohibited in Colombia by Resolution Nº 411 enacted by the Ministry of Agriculture in 1968. In 1997 the species was declared to be critically endangered in Resolution 676 and in 1998 the Ministerio del Medio Ambiente, the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH) and the Universidad Nacional de Colombia-Unal, formulated the National Conservation Plan for the Orinoco Crocodile (Procaimán). Their principal objective was to "prevent the extinction of the species and promote its recovery, to thus contribute to their conservation and integration into regional economic and cultural systems" (MMA *et al.* 1998). Within the framework of that plan various projects and activities have been carried out, mainly by the Tropical Biological Station "Roberto Franco". These initiatives have been focused on *ex situ* conservation, so today development of *in situ* projects are a top priority in Colombia.

Meanwhile in Venezuela, the first legal actions to conserve *C. intermedius* - given the evidence that indicated extremely reduced population numbers - were taken in the 70's of the last century. First, hunting was prohibited (as it was for many other species) by a decree issued on April 4, 1973, a decision later ratified by presidential resolution in 1979 (Seijas 2011). Diverse conservation strategies were then implemented, including a captive breeding program that started in the mid 80's. In addition, the Caño Guaritico Wildlife Refuge, Fishing Reserve and Protection Zone was created by decree Nº 2702 of 1989. This protected area was used as a pilot project for the reintroduction into natural systems of Orinoco crocodiles raised in captivity. Since 1990, the release of captive-raised animals has become routine in several sites of the Venezuelan Llanos (Seijas 2011). Furthermore, in 1993 the Crocodile Specialist Group in Venezuela (GECV) published an Action Plan: Survival of the Orinoco Crocodile in Venezuela 1994 -1999 (FUDENA 1993), and in 1994 the Ministerio del Ambiente published a Strategic Plan: Survival of the Orinoco Crocodile in Venezuela (Profauna 1994). More recently in 2007 the National Strategy for the Conservation of the Orinoco Crocodile in Venezuela and Action Plan was updated and published (GECV 2007).

Breaking a world record for reintroductions of this kind, from 1990 to 2010 more than 7600 Orinoco Crocodiles were released into the wild in Venezuela (Seijas 2011). Studies *in situ* have shown that a new population with at least 400 subadult and adult individuals has been established in the Caño Guaritico Refuge, in the section that is part of Hato El Frío in the state of Apure, which throughout the world is considered to be a remarkable success, especially considering that for the first time a stable crocodile population has become established based exclusively on specimens raised in captivity (Antelo 2008).

These *in situ* conservation projects of the Orinoco Crocodile in Venezuela have generated fruitful local results, and so could serve as examples to be replicated in habitats where crocodiles might be reintroduced, or where extant populations need reinforcement. To be able to do that successfully it is essential to know the potential distribution of the species, which because it continues to be critically endangered, is today absent from much of its original natural range. It should be possible to return the Orinoco Crocodile to regions where it is currently locally extinct, recovering at least part of its previous natural distribution and contributing to the reestablishment of populations that could restore equilibrium in aquatic ecosystems where it has been extirpated.

For this purpose, species distribution modelling tools (MDE) are especially useful. These tools are based, either explicitly or implicitly, on the ecological niche concept of Hutchinson (1957) and take into account climate and geomorphologic parameters that determine the niche of each species (Martínez-Meyer 2005). The delimitation of the niche for each species is created using geographic overlays that plot the records of species occurrence in multidimensional environmental space using climate and geographic layers available in geographic information systems (GIS). Starting there, the different MDE methods use different rules and mathematical algorithms to define niche boundaries for each species. Once an abstract niche definition is obtained, dots from occurrence records are projected into geographic space to produce a predictive map of potential distribution (Tsoar *et al.* 2007).

These models have been widely used to determine places of particular interest for conservation, sites where species can be reintroduced (Martínez-Meyer *et al.* 2006), sites where future exploration is required (Pearson *et al.* 2007) and are currently being used to predict changes in species distributions caused by climate change (Martínez-Meyer 2005, Phillips *et al.* 2006).

In this report our objective is to generate information about the potential distribution of the Orinoco Crocodile that will be useful to the efforts for its conservation, especially with regard to possible areas where reintroduction could be successful, or where reduced populations need reinforcement.

Materials y methods

Study area

The Orinoco River Basin is a binational drainage shared between Venezuela (65 %) and Colombia (35 %), with a total surface area of 991,587 km^2, of which 347,165 km^2 are in Colombian territory (Domínguez 1998) (Figure 1). In water volume the Orinoco is the third largest river in the world. Along its 2,150 km length, tributaries drain the Guyana Shield, the Eastern slopes of the northern Andes Mountains, the Coastal

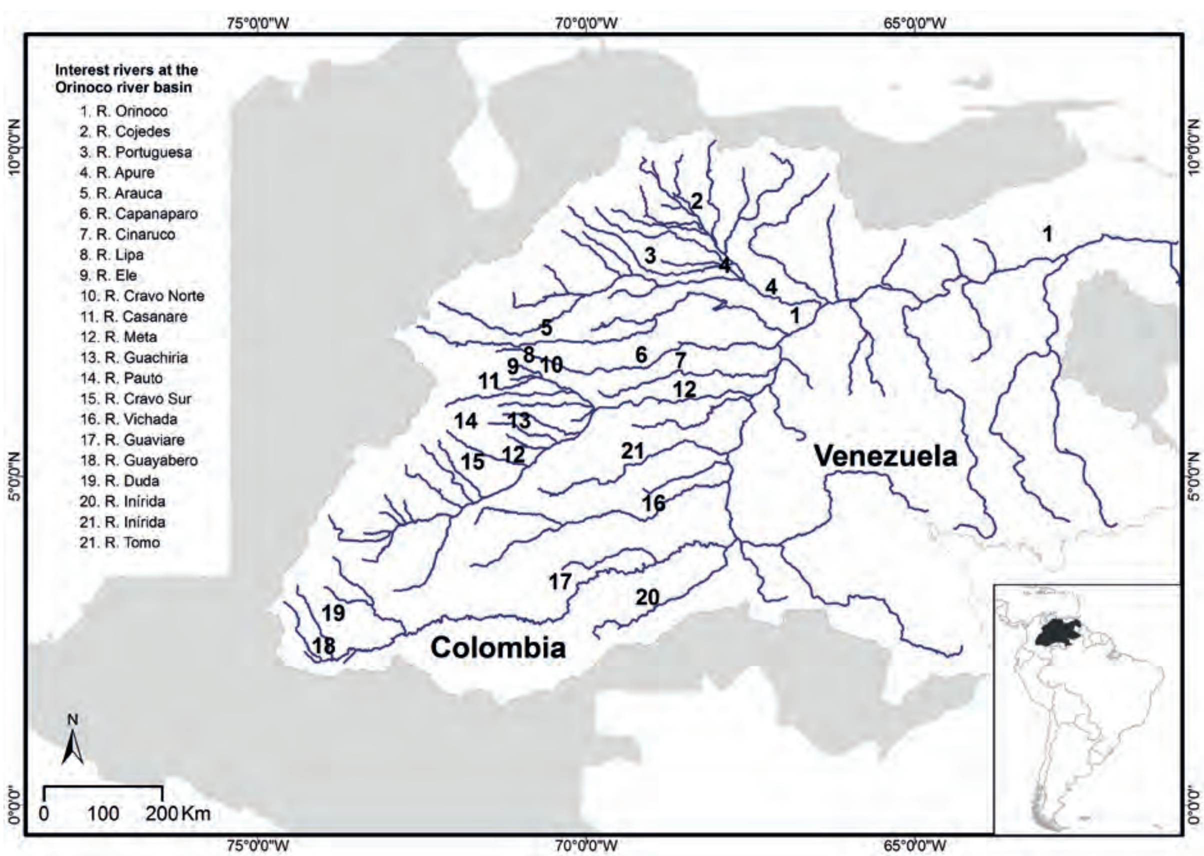

Figure 1. Orinoco River Basin.

Mountain Range of Venezuela, plains of the Amazon Basin transition region, and the seasonally flooding plains and high plains (llanos) of western Colombia and the eastern-central region of Venezuela to finally form a delta at its juncture with the Atlantic Ocean (Rosales *et al.* 2010).

The Orinoco River Basin includes rivers with the three main types of water as defined by Sioli (1975) that mainly differ in their apparent color: white (turbid), clear (more or less transparent) and black (tea-colored). Whitewater rivers are more productive and richer in nutrients and electrolytes, have high conductivity, pH near neutral (6.2-7.2), and owe their color to the turbidity caused by suspended inorganic sediments, such as illite and motmorillonite clays that are transported from the Andes Mountains to the alluvial plains (Lasso 2004).

Blackwater rivers originate in the Orinoco Guiana Shield or the peneplains of Precambrian origin, and drain sandy soils of floodplain forests, acquiring their characteristic tea color from the great quantity of decomposing organic material that leach from podsoils or histosoils. Their transparent but darkly stained water is low in conductivity, with acid pH due to the large number of soluble acids (especially fulvic and humic) that leach from organic material (Sioli 1975, Lasso 2004). Because of these characteristics they are less productive (oligotrophic) than white or clearwater rivers.

Most rivers with clear water originate on flat terrain, covered with forests that attenuate the erosive effects of the rains that penetrate the soil without producing runoff (Sioli 1975). These waters are transparent or greenish, depending on the hydrochemistry characteristics of the soil through which they flow. They tend to become turbid in the rainy season, have varying pH (from 4.5-7.8) less acid than blackwaters but more acid than clearwater streams (Lasso 2004). They are typically found on the Guiana Shield and high plains (Rosales *et al.* 2010). In figure 2 rivers of each water type are shown.

In an ecosystemic framework including both terrestrial and aquatic ecoregions (taking into account shoreline corridors), Rosales *et al.* (2010), recognized ten major regions: the Guyanese Orinoco, Orinoco Andes, coastal Orinoco, the Orinoco plains, the Orinoco high plains, the Orinoco-Amazon transition zone and the flooded riparian corridors of the main channel and its tributaries: Upper Orinoco, and lower Orinoco Delta.

Model of potential distribution

To model potential distribution of the Orinoco Crocodile (*Crocodylus intermedius*) the MaxEnt algorithm was considered to be more efficient than other predictive models (Elith *et al*. 2006, 2011). MaxEnt is based on the principle of maximized entropy (version 3.3.3.k) (Phillips *et al.* 2006, Phillips and Dudík 2008), that seeks to generate distributions of probability that involve the greatest level of uncertainty in situations with incomplete data (Raynal 2008), that is to say, it only uses presence data (occurrence sites). The result from MaxEnt is a geographic potential distribution model for the species inferred from climate parameters (Elith *et al*. 2006). The model correlates presence data for the species with environmental parameters. Each site of occurrence is taken to be a source location instead of a sink location, assuming that the conditions where the species is present are optimal to define its fundamental niche (Phillips *et al.* 2006). Based on these correlations MaxEnt determines the ecological niche of each species and assigns a probability of occurrence to each pixel (cell) in the predetermined space (Phillips *et al.* 2006).

The variables that were used to apply the model were: records for the occurence of the species, climate information, limnological or hydrochemical information (water type: white, clear, or black). The algorithm was given occurrence records from both countries based on collection or observation of the species from different sources such as scientific publications (Godshalk 1978, Medem 1981, Thorbjarnarson y Hernández 1992, Castro *et al*. 2012, Clavijo & Anzola 2013), grey literature (Lugo & Ardila-Robayo 1998), databases and personal observations of researchers. If occurrence records are geographically skewed (for example by oversampling in some regions) valid predictive models can be applied, if and when the geographic array of records is representative of the environmental habitat variability present in the study area (García *et al.* 2011).

Figure 2. Types of water in the Colombian Orinoco River Basin: a) Guaviare river (whitewater), b) caño Dagua (clearwater), c) Atabapo river (blackwater), d) confluence of Inírida river (black) with Guaviare river (whitewater).

Nineteen Worldclim bioclimatic variables and one hydrological variable were used (Table 1) for the selected area, with a resolution of 30 seconds (1 km aprox.) (Hijmans *et al.* 2005). The climate layers available in Worldclim were interpolated using a world meteorological network that incorporates averages mainly from the period from 1960-1990 (Hijmans *et al.* 2005).

With respect to the limnological information, a map of water types using the Sioli (1975) system was constructed: white, clear and black. This was done using the Arcgis 10.1 program. Information was compiled from various sources: bibliographic information (Vegas-Villarrubia *et al.* 1988a, b, Lasso 2004, Galvis *et al.* 2007), limnological databases from NGOs, and consultation with experts.

Two models were tested, one with occurrence data and climate (model 1) and the other adding the water type variable (model 2), to see which gave a better fit, taking into consideration that the Orinoco Crocodile is an aquatic species.

In each model the records were divided into 75 % for training and 25 % for evaluation. The models were evaluated using the statistical procedure “area below the curve” (AUC) by cross validation. This procedure assumes values from 0 to 1 and measures the discriminatory capacity of the models. A value of 1 corresponds to perfect discrimination between areas of presence and absence; a value of 0.5 indicates discrimination not significantly different from that expect by chance. Models with scores above 0.7 are considered acceptable (Fielding & Bell 1997).

Table 1. Bioclimatic variables.

Variable	Significance
BIO 1	Mean annual temperature
BIO 2	Mean diurnal temperature range [(T^0 máx-T^0 min) monthly mean)].
BIO 3	Isothermality [(Bio2/Bio7) x 100]
BIO 4	Temperature seasonality (standard deviation x 100)
BIO 5	Maximum temperature in hottest month
BIO 6	Minimum temperature in coolest month
BIO 7	Annual temperature range (Bio5-Bio6)
BIO 8	Mean temperature in trimester with highest rainfall
BIO 9	Mean temperature in driest trimester
BIO 10	Mean temperature of hottest trimester
BIO 11	Mean temperature of coolest trimester
BIO 12	Annual precipitation
BIO 13	Precipitation of wettest month
BIO 14	Precipitation
BIO 15	Precipitation seasonality (coefficient of variance)
BIO 16	Precipitation of wettest trimester
BIO 17	Precipitation of driest trimester
BIO 18	Precipitation of hottest trimester
BIO 19	Precipitation of coolest trimester

Results

To use the models, 654 occurrence records from both countries were used l (Figure 3) and a water type map was constructed for the Orinoco River Basin (Figure 4).

Application of model 1 included the 19 climate parameters and occurrence of *C. intermedius*. The graphic output from the MaXent is shown in figure 5. The model had an AUC value of 0.86. According to the potential distribution model, it can be observed that the north-western region of the basin has a high probability of favorable conditions for the Orinoco Crocodile, and that the probability diminishes to the southeast. In the eastern part of the basin, the probability of favorable conditions is very low.

The result from model 2 had a higher AUC value of 0.93. The graphic output (Figure 6) shows that in the Venezuelan Orinoco Basin only in the northwest section are favorable conditions indicated for this species. In the Apure River drainage (and its subdrainge, the Portuguesa River), specifically in the Cojedes River systems, the area of highest probability of favorable habitat conditions for the species is found, followed by the Arauca River drainage. On the Colombian side, there are high probabilities of favorable habitat in the Meta River drainage, especially in the Lipa-Ele-Cravo Norte systems and its mouth with the Casanare River, as well as the lower portion of the Meta River drainage. To a lesser degree, the upper Vichada and Guaviare River were classified as favorable, especially the Duda-Guayabero system.

In table 2 the percent contribution of the most significant (> 10 %) parameters are shown for both models. Variables Bio14 (precipitation in driest month) and Bio15 (precipitation seasonality), contributed most to model 1, but in model 2 water type (distance to blackwater rivers and distance to whitewater rivers, and temperature seasonality contributed more.

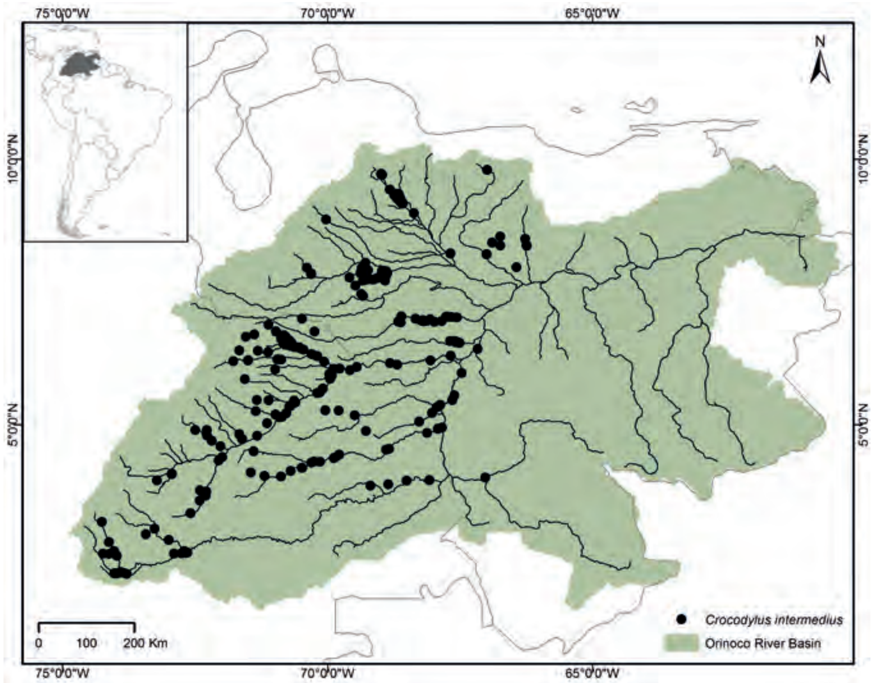

Figure 3. Records of occurrence of C*rocodylus intermedius.*

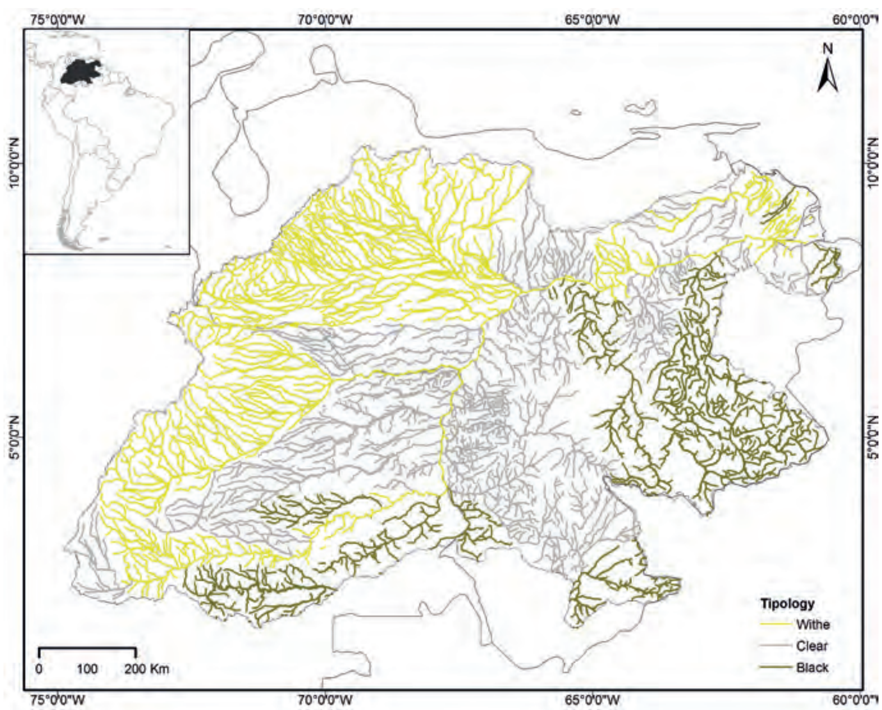

Figure 4. Water type map for the Orinoco River Basin.

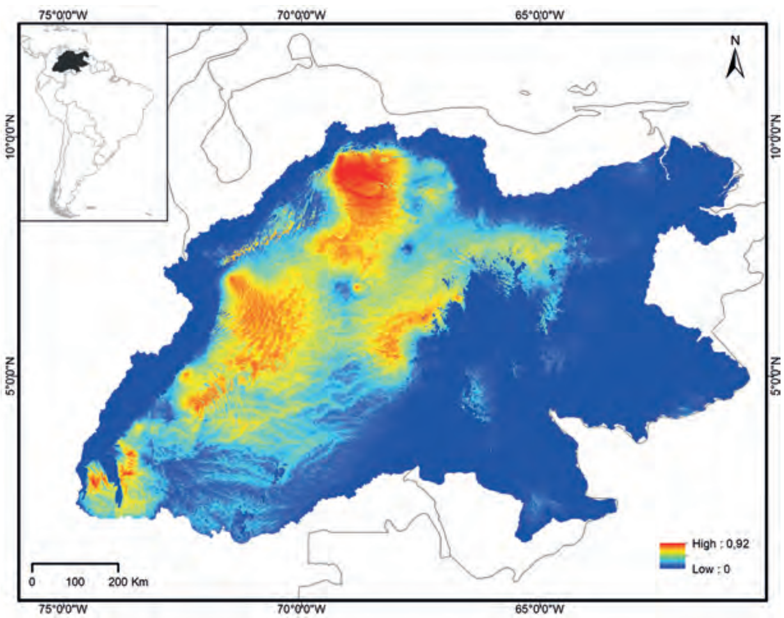

Figure 5. Model 1 of potential distribution of *Crocodylus intermedius*. In the image, colors indicate the probability of favorable conditions. Red indicates high probability of adequate conditions for the Orinoco Crocodile, yellow indicates conditions similar to those where this species is currently found, and shades of blue indicate low and lowest probabilities of adequate habitat conditions for this species.

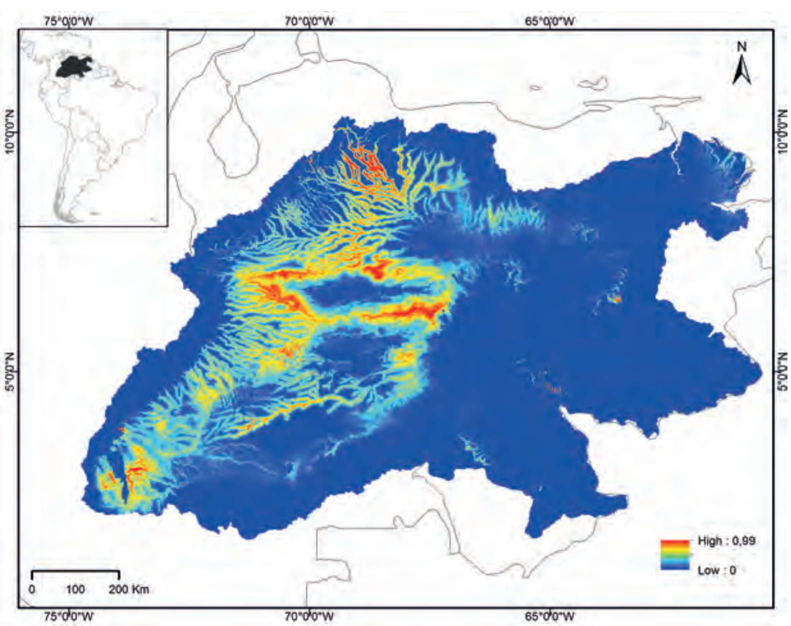

Figure 6. Model of potential distribution for *Crocodylus intermedius*. In the image, colors indicate the probability of favorable conditions. Red indicates high probability of adequate conditions for the Orinoco Crocodile, yellow indicates conditions similar to those where this species is currently found, and shades of blue indicate low and lowest probabilities of adequate habitat conditions for this species.

Table 2. Percent contribution of each variable to model results (model 1: AUC = 0.86; model 2: AUC = 0.93).

Variable	Model 1	Model 2
Black waters	18.5	
White waters	18.4	
Bio 4	16.6	
Bio 14		15.2
Bio 15		14.7
Clear waters	12.2	
Bio 3		11.3

Discussion

Both models indicate a high probability of favorable habitat conditions for the Orinoco Crocodile in the north-western part of the Orinoco River Basin (the Cojedes, Apure, Portuguesa, Arauca and Meta River drainages), with diminishing probability towards the south. In the eastern portion of the Orinoco River Basin there is a very low probability of favorable habitat. The area indicated as having favorable habitat conditions correlates with areas known to have abundant Orinoco Crocodile populations in the past according to accounts of naturalists like Alexander von Humboldt (1875) and Federico Medem (1981, 1983). Those authors mention that the rivers with the highest numbers of crocodiles were the Arauca, Meta, Guayabero and Vichada in Colombia and the Apure, Portuguesa, Arauca and mainstem Orinoco in Venezuela.

Model 1 is a conventional model since it employs commonly selected variables (records of occurrence and climate data) for this type of analysis. The inclusion of water type (white, clear, or black) in model 2 gave a better fit of potential habitat with areas known to have abundant crocodile populations in the past. The distribution of aquatic organisms is highly correlated to the productivity of the waters, and so perhaps reflects the availability of potential prey to a carnivorous species like *C. intermedius*.

In general terms, the highest probability of favorable habitat conditions corresponds to the Orinoco llanos, or seasonably flooding savannahs (Rosales *et al.* 2010). This region is drained by rivers flowing from the Andean piedmont (around 200 m a.s.l.), through high and low llanos to join with the mainstem of the Orinoco River at elevations less than 100masl (Rosales *et al.* op. cit.), the Orinoco Crocodyle is found up to 300 m a.s.l. (Godshalk 1978). These rivers begin in the Andes as clear water streams that gather ever more sediments from lateral terrestrial erosion as they descend eventually becoming turbid whitewater rivers carrying heavy loads of sediment and nutrients (Rosales *et al.* 2010). In the map in figure 6 for example, the intensity of color increases towards the lower parts of the rivers tributary to the Meta River (Guapanapalo, Pauto, and Guachiría rivers). Thus, in the lowest portion of the Meta River Basin we observe a high probability of favorable crocodile habitat. This pattern of increasing turbidity due to sediments is associated with both suspended and dissolved solids, and is directly related to the productivity of these waters (Lasso 2004).

The Cojedes River (Venezuela) where the highest probability of favorable habitat conditions was observed is home to the most robust *C. intermedius* population known to still exist at this time (Medem 1983, Espinosa-Blanco & Seijas 2012). It is a whitewater river, with a pH near neutral (pH 7 - 8) (Seijas 1998), characteristic of rivers of its type, such as the Arauca (pH 6.7 Yánez & Ramírez 1988) and the Meta (pH 7-8).

In the Orinoco llanos some rivers originate in the plains, such as the eolic plains of the Capanaparo and Cinaruco rivers (Iriondo 1997). These rivers have clear water that darkens during the dry season to a dark tea color as observed in rivers classified as blackwater. For this area we can see how water type influences model predictions. Model 1 predicts medium habitat suitability for the upper stretches of these two rivers but with model 2, where water type is included, the predicted suitability drops considerably. In any case, there is a viable population of Orinoco Crocodiles living today in the lower stretch of the Capanaparo River (Medem 1983, Llobet & Seijas 2003, Espinosa-Blanco & Seijas 2012).

The hydrochemistry (water type) and hence the productivity of the system is determinant for the distribution, abundance and biomass of the aquatic biota, especially fishes which are the principal food source for Orinoco Crocodiles. It is for this reason that water type affects the distribution of *C. intermedius* and other crocodilians in the Orinoco River Basin. However, other parameters are also related such as soil type and climate, among others. For example, in the whitewater Guaviare River (Colombia) one might reasonably expect high probability of favorable habitat conditions, but the model predicts the opposite. This is possible due to the presence of relictual formations of the Guyana Shield in this region similar to those found in the eastern part of the Venezuelan llanos where low probabilities of suitable habitat are also predicted by the model. Although the Guaviare River is whitewater, it has lower conductivity (30 µS) (Ideam 1995), and is not as productive as other whitewater rivers such as the Arauca (120 µS, Yánez & Ramírez 1988). Along the length of the Guaviare River's flow towards the Orinoco, the left-bank tributaries are clearwater rivers that originate in the poor soils of the high plains, and the right-bank tributaries are blackwater streams that come from the Guiana Shield (Galvis *et al.* 2007). The Guyana region of the Orinoco River Basin has scarcely evolved soils, poor in nutrients and quite acid (Rosales *et al.* 2010), that in turn affects the productivity of the rivers there.

In addition, in the north-western part of the basin of the Cojedes River drainage where the models predict the highest habitat favorability, rainfall is low (Rosales *et al.* 2010). In model 1 the variables that most contribute to predictions are precipitation in the driest month (Bio14) and seasonality of precipitation (Bio15). According to Gorzula *et al.* (1988), this species' populations are associated with low precipitation (644 ± 1.797 mm). The distribution of rainfall throughout the year also influences the distribution of this species. In the south-eastern portion of the basin, where northeast trade wins bring the highest amount of annual rainfall (2.500 to 3.500 mm) (Rosales *et al.* 2010) we find the least probability of favorable crocodile habitat.

Conclusions

According to the model of potential distribution, the geographic distribution area of *C. intermedius* is to a large degree influenced by physical factors such as water type, soils and precipitation. Its distribution is associated principally with high productivity rivers (whitewater) that provide abundant prey in regions marked by highly seasonal rainfall.

The model permitted a more precise calculation of potential favorable habitat for the Orinoco crocodile in the Orinoco River Basin. It also identified zones where environmental conditions (climate, water type)

Figua 7. C*rocodylus intermedius.*

are most suitable for crocodile populations. This permits concentration of conservation efforts in areas where crocodile populations are most likely to thrive.

The Orinoco Crocodile is endemic to the Orinoco River Basin, but is only found in a small part of that basin. The very restricted distribution pattern is of great relevance because it indicates that the areas where current populations remain and those thought to be most favorable to Orinoco crocodiles are crucial to the successful conservation of this species. For this reason, it is imperative that the environmental authorities of both countries seriously take into account the areas indicated as most favorable habitat when making decisions about territorial planning and development, and avoid ongoing and future negative impacts of agro-industrial, mining, hydropower, and other projects.

The high degree of endemism and small number of existing populations indicate the urgency of implementing *in situ* conservation strategies already proposed in the conservation plans and strategies of both countries, again, and especially in those drainages where favorable habitat conditions exist for this species.

The model applied predicted which areas are the most appropriate as suitable habitat for the Orinoco Crocodile, confirming and reinforcing the hypothesis that water type and climate variables are strong determinant factors influencing the geographic distribution of this species. The model is a useful tool for decision makers when planning conservation of endangered species. However, it should be remembered that this type of analysis only takes into account the physical (and in part biological) habitat parameters that should be complemented with an analysis of the human impacts on the habitat of this species (threats and opportunities). A study evaluating the availability and quality of nesting beaches is also needed.

Acknowledgements

We thank Andrés Seijas (UNELLEZ-Venezuela) and Omar Hernández (FUDECI-Venezuela) for sharing their Orinoco Crocodile sighting databases. Rafael Antelo provided limnological data from the Palmarito Foundation. Thanks to German Gálvis for his help to build the water type map. We also thank María Cecilia Londoño, Liliana Corso, Marcela Portocarrero and Lina Mesa (IAvH), Antonio Castro (Asociación Chelonia Colombia) and Myriam Lugo for their assistance in data acquisition. To Donald Taphorn for the translation of this manuscript. We thank the IAvH and the Ministerio de Ambiente y Desarrollo Sostenible de Colombia for technical assistance and funding.

Bibliography

Antelo, R. 2008. Biología del cocodrilo o caimán del Orinoco (*Crocodylus intermedius*), en la Estación Biológica El Frio, en el Estado de Apure (Venezuela). Tesis Doctoral. Departamento de Ecología, Universidad Autónoma de Madrid. 336 pp.

Antelo, R. 2012. Conservación. Pp. 133-147. *In:* Fundación Chelonia (Ed.). Historia natural y conservación del caimán llanero (*Crocodylus intermedius* Graves, 1819) en Colombia. Asociación Chelonia.

Castro, A., M. Merchán, M. Garcés, M. Cárdenas & F. Gómez. 2012. New data on the conservation status of the Orinoco crocodile (*Crocodylus intermedius*) in Colombia. Pp. 65-73. *In:* Crocodiles. Proceedings of the 21st Working Meeting of the IUCN-SSC Crocodile Specialist Group. IUCN: Gland, Switzerland.

Clavijo, J. M. & L. F. Anzola. 2013. Elementos claves para la conservación *in situ* de *Crocodylus intermedius* derivados del seguimiento de metapoblaciones y hábitats en Arauca, Colombia. *Revista Colombiana de Ciencia Animal* 5 (2): 560-573.

Domínguez, C. 1998. La gran cuenca del río Orinoco. Pp. 39-67. *In:* Domínguez, C. (Ed.). Colombia Orinoco. Fondo FEN, Instituto de Estudios Orinoquenses, Bogotá, Colombia.

Elith, J., C. Graham, R. Anderson, M. Dudı´k, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L.G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz & N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129-151.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. Chee & C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and distributions* 17: 43–57.

Espinosa-Blanco, A. & A. E. Seijas. 2012. Declinación poblacional del caimán del Orinoco (*Crocodylus intermedius*) en dos sectores del sistema del río Cojedes, Venezuela. *Ecotrópicos* 25 (1): 22-35.

Fielding, A. H. & J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation precense/absence models. *Environmental Conservation* 24: 38-49.

FUDENA. 1993. Plan de acción: Supervivencia del caimán del Orinoco en Venezuela 1994 -1999. FUDENA-GECV. 24 pp.

Galvis, G., J. Mojica, F. Provenzano, C. Lasso, D. Taphorn, R. Royero, C. Castellanos, A. Gutiérrez, M. Gutiérrez, Y. López, L. M. Mesa, P. Sánchez & C. Cipamocha. 2007. Peces de la Orinoquia colombiana con énfasis en especies de interés ornamental. Incoder. Universidad Nacional. Instituto Sinchi. Bogotá, Colombia. 425 pp.

García, J, C., F. Dormann, J. H Sommer, M. Schmidt, A. Thiombiano, S. Da, C.Chatelain, S. Dressler & W. Barthlott. 2012. A methodological framework to quantify the spatial quality of biological databases. *Biodiversity and Ecology* 4: 25-36.

GECV-Grupo de Especialistas en Crocodilos de Venezuela. 2007. Estrategia nacional para la conservación del caimán del Orinoco en Venezuela y su plan de acción. Pp. 59-63. *In*: Seijas, A. E. (Ed.). Memorias del III Taller para la conservación del caimán del Orinoco, San Carlos, Venezuela. 17-19 de enero de 2007. *Biollania* Edición Especial 8.

Godshalk, R. 1978. El caimán del Orinoco, *Crocodylus intermedius*, en los llanos occidentales de Venezuela con observaciones sobre su distribución en Venezuela y recomendaciones para su conservación. FUDENA, Caracas. 58 pp.

Gorzula, S. J., J. Paolini & J. B. Thorbjarnarson. 1988. Some hydrochemical and hydrological characteristics of crocodilian habitats. *Tropical Freshwater Biology* 1 (1): 50-61.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones & A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.

Humoldt, A. 1975 (1859-1869). Del Orinoco al Amazonas. Viaje a las regiones equinocciales del nuevo continente. Ed. Labor, Barcelona. 429 pp.

Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415-427.

Ideam. 1995. Estadísticas hidrológicas de Colombia 1990-1993. Tomo 2. Diego Samper Ediciones.

Iriondo, M. H. 1997. Models of deposition of loess and loessoids in the upper Quaternary of South American. *Journal of South American Earth Sciences* 10 (1): 71-79.

Lasso, C. A. 2004. Los peces de la Estación Biológica El Frio y Caño Guaritico (estado Apure), Llanos del Orinoco, Venezuela. Publicaciones del Comité Español del Programa MaB y de la red IberoMaB de la UNESCO. Sevilla. 458 pp.

Lugo, L. M. & M. C. Ardila. 1998. Programa para la conservación del caimán del Orinoco (*Crocodylus intermedius*) en Colombia. Proyecto 290. Programa Research Fellowship NYZS. The Wildlife Conservation Society. Proyecto 1101-13-205-92 Colciencias. Universidad Nacional de Colombia. Facultad de Ciencias. Estación de Biología Tropical Roberto Franco. Villavicencio. Informe no publicado. 58 pp.

Llobet, A. & A. E. Seijas 2003. Estado poblacional y lineamientos de manejo del caimán del Orinoco (*Crocodylus intermedius*) en el río Capanaparo, Venezuela. Pp. 117-129. *In:* Polanco-Ochoa, R. (ed.). Manejo de Fauna Silvestre en Amazonía y Latinoamérica. Selección de Trabajos V Congreso Internacional. Bogotá, CITES, Fundación Natura.

Martínez-Meyer, E. 2005. Climate change and biodiversity: some considerations in forecasting shifts in species potential distributions. *Biodiversity Informatics* 42-55.

Martínez-Meyer, E., A. Townsend, J. I. Servín & L. F. Kiff. 2006. Ecological niche modelling and prioritizing areas for species reintroductions. *Oryx* 40 (4): 411.

Medem, F. J. 1981. Los Crocodylia de Colombia. Volumen 1. Los Crocodylia de Suramerica. Colciencias. Bogotá. 354 pp.

Medem, F. 1983. Los Crocodylia de Sur América. Volumen II. Los Crocodylia de Suramerica. Colciencias. Bogotá. 406 pp.

Ministerio de Medio Ambiente, Instituto von Humboldt & Universidad Nacional de Colombia. 1998. Programa Nacional para la Conservación del Caimán Llanero. Ministerio del Ambiente Dirección General de Ecosistemas Subdirección de Fauna. Santafé de Bogotá. 22 pp.

Pearson, R. G., C. J. Raxworthy, M. Nakamura & T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34: 102–117.

Phillips, S. J. & M. Dukí. 2008. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography* 31: 161-175.

Phillips, S. J., R. P. Anderson & R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190 (2006): 231–259.

Profauna. 1994. Plan estratégico: supervivencia del caimán del Orinoco en Venezuela. Ministerio del Ambiente y de los Recursos Naturales Renovables, Servicio Autónomo de Fauna Profauna. 15 pp.

Raynal J. 2008 Comparación del método del principio de la máxima entropía en la estimación de parámetros de la distribución de valores extremos tipo I. *Información Tecnológica* 19 (2): 103-112.

Rosales, J., C. Suárez & C. A. Lasso. 2010. Descripción del medio natural de la cuenca del Orinoco. Capítulo 3. Pp. 51-73. *In:* Lasso, C. A., J. S. Usma, F. Trujillo & A. Rial (Eds.). 2010. Biodiversidad de la cuenca del Orinoco: bases científicas para la identificación de áreas prioritarias para la conservación y uso sostenible de la biodiversidad. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, WWF Colombia, Fundación Omacha, Fundación La Salle e Instituto de Estudios de la Orinoquia-Universidad Nacional de Colombia. Bogotá, D. C., Colombia.

Seijas, A. E. 1998. The Orinoco crocodile (*Crocodylus intermedius*) in the Cojedes river system, Venezuela: Population status and Ecological characteristics. Tesis Doctoral, Universidad de Florida. 192 pp.

Sioli, H. 1975. Tropical rivers as expressions of their terrestrial environments. Pp. 275-288. *In:* Goley, F. & E. Medina (Eds.). Tropical ecological system. Trend in terrestrial and aquatic research. Springer-Verlag. New York Inc.

Thorbjarnarson, J. & G. Hernández. 1992. Recent investigations on the status and distribution of Orinoco crocodile *Crocodylus intermedius* in Venezuela. *Biological Conservation* 62: 179-188.

Tsoar, A., O. Allouche, O. Steinitz, D. Rotem & R. Kadmon. 2007. A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions* 13: 397-405.

Vegas-Villarrubia, T., J. Paolini & R. Herrera. 1988a. A physic-chemical surrey of blackwater rivers from the Orinoco and the Amazon basin in Venezuela. *Archiv fuer Hidrobiologie* 111 (4): 491-506.

Vegas-Villarrubia, T., J. Paolini & J. García. 1988b. Differenciation of some Venezuelan blackwater rivers based upon physico-chemical properties of their humic substances. *Biogeochemistry* 6: 59-77.

Yánez, C. & A. Ramírez. 1988. Estudio geoquímico de grandes ríos venezolanos. *Memoria de la Sociedad de Ciencias Naturales La Salle* 48: 41-58.

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Potential distribution of the Orinoco crocodile (*Crocodylus intermedius* Graves 1819) in the Orinoco basin of Colombia and Venezuela

Cítese como: Morales-Betancourt, M. A., C. A. Lasso, L. C. Bello y F. de P. Gutiérrez. 2014. Potential distribution of the Orinoco crocodile (*Crocodylus intermedius* Graves 1819) in the Orinoco basin of Colombia and Venezuela. *Biota Colombiana* 15 (Supl. 1): 124-136.

Recibido: 4 de julio de 2014
Aprobado: 1 de octubre de 2014