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Regional habitat conservation priorities for the American crocodile

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ABSTRACT

The American crocodile is widely distributed in coastal and lowland wetlands in the northern Neotropics. As a result of commercial skin hunting in the 20th century, populations were greatly diminished, but in many areas have initiated a period of recovery since hunting and trade controls were enacted in the 1980s and 1990s. While a great deal of attention has been devoted to regulated commercial use as a management strategy for recovering crocodilian populations, these approaches are limited in their efficacy to deal with issues of habitat loss and fragmentation. Because habitat limitations are expected to be the most critical issue for crocodile conservation in the 21st century, there is an unfulfilled need for alternative strategies that prioritize habitat conservation. Here, we present results of an international effort to identify and prioritize the most critical habitats for this wide ranging species. We quantified information of a group of American crocodile experts and classified 69 areas in eight distinct crocodile bioregions as Crocodile Conservation Units (CCU), the most important areas for the conservation of this species. The relative importance of the CCUs in each bioregion was quantified using an algorithm that weighted factors that the experts considered to be most important for the long term conservation of viable populations of crocodiles. This effort is the initial step in the development of a regional conservation plan for the American crocodile. We identified two bioregions in particular where the creation of protected areas should be given a high priority, the Dry Pacific South America (northern Peru and southern Ecuador) and the Northwest and Central Pacific Mexico.

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1. Introduction

The American crocodile (*Crocodylus acutus*) is broadly distributed from the subtropical tip of Florida to the limits of mangrove habitat in northern Peru. Although frequently found in mangrove-lined coastal lagoons or estuaries, the American crocodile inhabits a variety of environments ranging from landlocked hypersaline lakes to freshwater sections of rivers and reservoirs (Ernst et al., 1999). American crocodiles are also well known from offshore cays and coral atolls (Thorbjarnarson, 1989). American crocodiles were widely hunted for their skins from 1920 to 1970. In virtually all parts of the species range this led to significant population declines. By the 1970s, declines from hunting were exacerbated by habitat loss from development of coastal areas, further endangering populations (Mazzotti, 1999; Garrick, 1986). The American crocodile was listed as Endangered under the US Endangered Species Act in 1973, and it was included in Appendix I of CITES in 1979. National and international trade restrictions, and the availability of legal skins from other crocodilians, have significantly reduced commercial hunting in recent decades. In some areas, this has led to recovery of populations, while in other regions crocodile populations remain small due to negative human-related factors such as deliberate killing or habitat destruction (e.g. Colombia, Ecuador, Jamaica) or ecological limitations of habitat and/or competition with congeners (e.g., Peru, Belize) (Ross, 1998).

Over the last 25 years, the dominant crocodile management paradigm has been controlled commercial use, principally for sale of skins (Thorbjarnarson, 1999). Building on the pioneering efforts of the United States, Papua New Guinea and Zimbabwe, nearly 70 countries have undertaken programs based on crocodile ranching, cropping, or closed-cycle farming. Following this worldwide trend, a few nations have also initiated controlled exploitation of American crocodiles based on closed-cycle breeding (most notably Colombia and Honduras) (Ross, 1998). For many species this strategy has led to significant population recovery. The best known example is the American alligator, which once again is common in wetlands in the southeastern United States (Joanen and McNease, 1987).

While programs based on commercial consumptive use may have some benefits for conservation and management of crocodilians, they do little to promote habitat protection (Thorbjarnarson, 1999; Thorbjarnarson and Velasco, 1999). Currently, habitat loss is the single most important factor influencing the survival of threatened crocodiles (Ross, 1998; Thorbjarnarson, 1999). Because the American crocodile inhabits a wide range of habitats in many countries where its status ranges from highly endangered to recovered, regional conservation needs and priorities for this species are unclear.

Planning for the long-term conservation of a threatened species ideally requires maintenance of viable populations across the full range of ecosystems in which they exist. This goal necessitates planning across the entire range of the species, and identification of regions where species ecology varies significantly. For the American crocodile, this involves consideration of habitat variability, co-existence with conspecifics, and large-scale terrestrial and oceanographic processes.

Here, we present results of a workshop that brought together experts from throughout the region to address range-wide conservation needs of the American crocodile. Our goals were to: (1) summarize current knowledge about its ecology, distribution, and status; (2) prioritize current threats, including a framework for threat mitigation; and (3) identify priority areas for conservation efforts.

2. Methods

Our methods are adapted from the range-wide priority-setting method described by Sanderson et al. (2002) that used expert knowledge to develop a consensus on conservation priorities for the jaguar. This approach used a transparent process that included: (1) systematic consideration of the entire historic range of the species; (2) identification of key regional habitat associations that represent important variations in species ecology; (3) identification of areas where the species status is known (*known areas*) and where the species is presently found (*current range*); and (4) delineation of the areas most important for the species' conservation.

These generic methods were modified to match the ecology and conservation situations of the American crocodile. The American crocodile uses marine, estuarine, freshwater aquatic and terrestrial parts of its environment and we need to include all components of coastal environments in our analysis. However, the American crocodile is an edge species and so we could not use classifications of either terrestrial or marine habitats to delimit bioregions where we would expect differences in the species' ecology. Instead, we defined nine bioregions that represented distinct portions of the species' historic range with reference to general terrestrial and coastal physical and climatic features. The use of strictly marine habitats by crocodiles is largely transitory, usually when moving from one coastal habitat patch to another. To standardize definition of habitat, we calculated areas of historic range, known range, and "Crocodile Conservation Units" (CCU) by excluding marine habitats. To include an explicit consideration of range changes, we included a new data type – "extirpated points", which are populations known to have gone extinct in historical times.

In 2002, 39 experts were identified with recent field knowledge of the American crocodile from all parts of the species' range and representing all 17 countries where the species currently occurs. Each expert was sent a 1,250,000 scale base map of his/her self-identified geographic area of expertise with national boundaries, rivers, and coastlines from publicly available, standardized 1:1,000,000 datasets (VMAP0, NIMA). Matching transparent overlays, a set of color pens, data forms and instructions were provided. Experts were asked to identify (1) areas for which they could comment on the status of American crocodiles, (2) point observations where the species is known to occur, (3) points where the species was known to occur at sometime in the past, but is now extirpated, and (4) areas where substantive populations (Crocodile Conservation Units = CCUs) currently exist. Each feature marked on the maps was given a unique code and supplemented with information on datasheets. These maps were then digitized and entered into a geographic information system (GIS), relabeled and error-checked.

For each point, experts filled out data sheets that provided additional information. Single point observations represented sightings of crocodiles within a circular area with a 10 km radius. Unlike the previous jaguar analysis, where points represented single observations of an elusive animal, point observations for American crocodiles were sites where ⩾1 crocodile were seen. In some cases a single point observation could represent hundreds of animals seen over a period of years. Because density of point observations on the maps did not necessarily correlate with crocodile population density, experts were asked to estimate size of the crocodile population in each CCU, based on results of their field studies, in one of the following categories (<50, 50–100, 100–500, 500–1000 or more than 1000 non-hatchling crocodiles, or 0, 1–10, 11–50, 51–100, >100 nests/year). CCU data sheets were also used to compile expert information on habitat quality, habitat connectivity, habitat destruction, potential for sustainable use, and killing of crocodiles.

In October 2002, the Wildlife Conservation Society and the University of Florida convened a workshop at the University of Florida (Gainesville, FL) to review and update data assembled prior to the workshop and to establish consensus priorities for American crocodile conservation. Working in groups representing each bioregion the experts reviewed every data point and polygon and associated attribute data, in some cases revising data and/or adding new information, and consolidating information along boundaries of two or more experts' expertise. Differences in opinion were worked out consensually. These changes were made in near real-time and reviewed a second time before the close of the workshop. After the workshop these collected data were analyzed by bioregion.

The experts also developed a weighting scheme for prioritizing crocodile conservation units. A list of factors important for crocodile conservation was created through suggestions and discussion at the workshop. Each expert was allocated 100 points to weight the importance of these factors, and these were summed across all experts and normalized back at 100 point scoring system. The scores were then applied to the CCU assessments to calculate a weighted prioritization score for each area; these areas were then ranked within each bioregion to develop the final list of prioritized CCUs. The experts reviewed the list of ranked CCUs prior to the close of the workshop.

To calculate percentage of each CCU within protected areas (PAs) the spatial dataset for CCUs was intersected in a GIS with the World Database on Protected Areas (UNDP, 2004). However, different types of PAs offer different levels of protection to wildlife, and even more importantly, the level of implementation of management or protection efforts vary widely within PAs. These range from "paper parks" where there is little or no implementation and enforcement of management regulations to model PAs that are adequately staffed and funded and work in harmony with local communities. We estimated effectiveness of the PAs in each of CCU by asking the experts to classify the level of protection as fully effective (F) in implementing management and protection regulations, partially effective (P) or ineffective (I).

3. Results

3.1. *Extent of crocodile knowledge*

The extent of knowledge of American crocodiles covered 50% of the historic range of the species (Table 1), but varied considerably between bioregions, ranging from 89% in the Rio Grijalva system in southern Mexico to only 1% in the Moist Pacific coast of Colombia and Ecuador, where heavy, year-round rainfall may limit American crocodiles to very low natural densities. Several areas stood out for lack of information on the status of American crocodiles. These included the Pacific coastal regions of El Salvador and Guatemala in the South Mexico/Central America Pacific and Ecuador in the Dry Pacific Bioregion. Information from Jamaica was rudimentary, allowing definition of three CCUs but insufficient to score the value of these areas and rank them with other CCUs in the Florida-Greater Antilles bioregion.

3.2. *Known, currently occupied American crocodile range*

From the distribution of extirpated crocodile points we calculated that American crocodiles have disappeared from 8.9% of

Table 1 – Analysis of American crocodile status and conservation information by bioregion

American crocodile bioregion	Area (km^2)	Extent of knowledge (%)	# CCUs	Area CCUs (km^2)	CCU (%)	# Points	# Extirpations	% Area extirpated
Caribbean Central America	161,590	73	13	47,535	29	117	31	14.3
Caribbean South America	140,588	68	9	4253	3	53	6	3.6
Dry Pacific South America	51,936	29	2	1078	2	6	3	18.9
Florida-Greater Antilles	115,463	61	11	18,714	16	149	23	12.5
Moist Pacific	34,073	1	0		0	1	0	0.0
North West and Central Pacific Mexico	66,485	21	6	4574	7	35	4	1.0
Rio Grijalva	8925	89	4	5556	62	27	0	0.0
South Mexico/Central America Pacific	56,120	60	14	15,583	28	110	5	1.5
Yucatan	20,076	68	10	6918	34	53	0	0.0
Total	737,764	50	69	104,210	14	551	72	8.9

their historical range (Table 1), largely reflecting habitat loss and other human impacts in regions where habitat was limited or patchily distributed. In some bioregions (Dry Pacific South America, the Caribbean Central America and Florida-Greater Antilles) crocodiles have disappeared from one eighth to nearly one fifth of their former range. The only country where the species has been completely extirpated is the Cayman Islands (which ironically were named after crocodiles that the first Europeans found there). Other areas include portions of the coast of Hispaniola, and localized areas in Mexico, Central and South America. However, in other bioregions crocodiles are found essentially throughout their entire former distribution.

3.3. Crocodile point observations

The experts reported a total of 551 point observations of American crocodiles, with at least one in each of nine bioregions (Table 1). The largest number of point observations (149) was in the Florida-Greater Antilles bioregion, with significant numbers also in the Caribbean Central America and South Mexico. In the Moist Pacific bioregion only one observation was reported. To some extent, the number of point observations reflected the size of the bioregion. This was partly a result of using each point to represent observations within a circular area of 10 km radius. In areas of contiguous habitat known to harbor populations of crocodiles, such as the mangroves on Cuba's south coast or up major rivers like the Rio Coco-Segovia between Honduras and Nicaragua, this meant spacing point observations every 20 km. The number of crocodile researchers working in the different bioregions may also have had an effect on the number and density of point observations, as certain areas (El Salvador, Guatemala, Ecuador) are underrepresented in terms of field surveys.

3.4. Crocodile conservation units

A range-wide assessment of the status of American crocodiles was based on identification of CCUs and their characteristics. CCUs did not include all known crocodile populations but only those that based on our criteria are most important for the long-term conservation of the species. A total of 69 CCUs were identified, with at least 1 CCU in each bioregion with the exception of the Moist Pacific (Fig. 1, Table 1). The

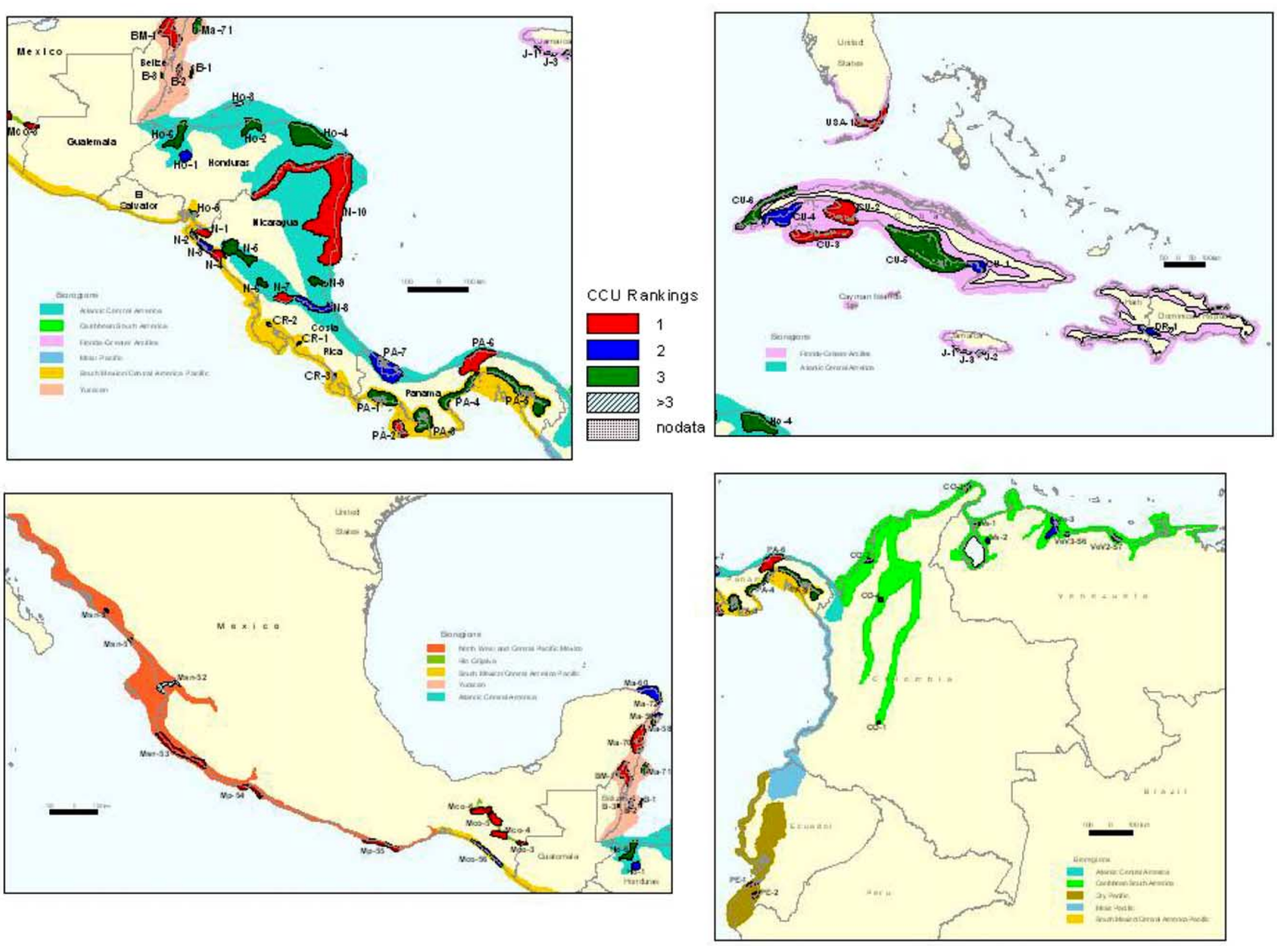

Fig. 1 – American crocodile bioregions and location of the Crocodile Conservation Units (CCU). For each bioregion the CCUs are classified into importance level based on their weighted score. 1, highest priority (top three scoring CCUs in each bioregion); 2, high priority (fourth to sixth highest scoring CCU in each bioregion); 3, important areas (seventh to ninth highest scoring CCUs); and 4, other CCUs. CCUs for which not enough information was available for scoring are marked with crosshatching. CCU codes are listed in Table 2.

largest number of CCUs in one bioregion was 14 in the South Mexico/Central America Pacific bioregion, which to a large degree reflects the patchy distribution of suitable habitat in that region. This was closely followed by 13 in the Caribbean Central America, 11 in Florida-Greater Antilles, and 10 in the Yucatan. By far the largest total area of CCUs in any one bioregion was 47,535 km^2 in the Caribbean Central America, which was dominated by one large CCU, the Costa Miskito-Rio Coco CCU in Nicaragua, by far the largest CCU identified by the experts (Table 2).

While all CCUs identified by the experts are important for long-term conservation of the American crocodile, there was substantial variability in habitat quality, size of CCUs, connectivity, and other, management-related issues. Scores for determining the conservation priority of CCUs were based on the weighting of eight factors: habitat quality = 24, nesting habitat = 18, CCU size = 13, crocodile population size = 13, habitat connectivity = 12, habitat destruction = 10, sustainable use = 7, crocodile killing = 3 (weighted score out of a total of 100). Because of the rigid nesting habitat requirements of the species, and that occurrence of nesting areas is frequently quite distinct from availability of habitat for juvenile and adult crocodiles, nesting habitat was separated as a distinct factor. Habitat destruction was a measure of negative human impacts on crocodile habitat, with higher scores given to areas with fewer negative impacts. Sustainable use reflected a potential for managed commercial use programs in each CCU. Overall, factors describing habitat quality were considered to be most important in defining the relative importance of CCUs, followed by CCU size, and current size of the crocodile population. Factors that represent current management of CCUs, such as sustainable use and current levels of killing of crocodiles, were considered to be least important.

We divided CCUs in each bioregion into four categories, three of which reflected their priority, highest, higher, and high (Table 2) based on their weighted scores. Areas that were delimited as CCUs, but for which we did not have sufficient information to evaluate the seven factors to score CCU priority, were classified in a "no data" category (one in Honduras, Caribbean Central America; three in Jamaica, Florida-Greater Antilles; and two in North West and Central Pacific Mexico).

The nature of the CCUs was widely divergent, reflecting the variety of habitats where American crocodiles are found. The most typical habitat for American crocodiles is coastal mangrove swamp in regions with seasonally dry climates. In the Yucatan, CCUs were represented exclusively by mangrove habitats along the mainland coast and offshore cays. A similar situation was found in the Florida-Greater Antilles bioregion, with two exceptions, the landlocked lakes in the Cul-de-Sac–Lago Enriquillo CCU in Haiti and the Dominican Republic, and the Zapata Swamp freshwater wetland in Cuba. Coastal fringe and patchily distributed mangrove swamps typified the CCUs along the entire Pacific coast distribution of the species, including three bioregions, the North West and Central Pacific Mexico, the South Mexico and Central America Pacific, and the Dry Pacific of South America. In the Caribbean South America bioregion the three highest priority CCUs are coastal lagoon systems. However, this bioregion is notable in that American crocodiles are found far upstream in the Magdalena/Cauca River system in Colombia, remnant populations in these areas were classified as CCUs.

The very wet Moist Pacific bioregion in Colombia and Ecuador appears to have few American crocodiles and no CCUs were identified. The Caribbean Central America bioregion has characteristics intermediate between the dry and wet Pacific regions, with moderate to high levels of rainfall, extensive coastal wetlands and large rivers. In high rainfall coastal sections of this bioregion crocodiles were found in moderate to low densities over a wide area, which resulted in the delineation of the largest CCU for any bioregion (Costa Miskito y Rio Coco). Other important CCUs in this bioregion were in the great lakes of Nicaragua (Lago de Nicaragua) and the enormous Gatun Lake reservoir (Bahia de Panama-Este). The Rio Grijalva in southern Mexico was the most unusual bioregion and contained an isolated population of American crocodiles divided into four CCUs in a series of reservoirs.

3.5. *CCUs and protected areas*

Of the total of 104,210 km^2 of CCUs that was defined in this analysis, 25,625 km^2 (24.6%) were within existing protected areas (Table 3). The Yucatan bioregion had the largest percentage of CCUs in PAs with 52.2%, followed by Florida-Greater Antilles (41.9%). Two bioregions had very low percentages of their CCUs within PAs, Dry Pacific South America (2.8%), and the Northwest and Central Pacific Mexico (4.0%). Based on the surface area of CCUs included in PAs (Table 2), we divided the CCUs into two groups, those that have a significant amount ($\geqslant$50%) of their area protected (Table 4), and those that have very little ($\leqslant$10%) protected (Table 5). The CCUs in Table 4, particularly those whose management is considered to be fully (F) or partially (P) effective can be considered the "jewels" of a range-wide habitat-based conservation plan for the American crocodile. Conversely, the CCUs in Table 5 are those where priority should be given to designating new protected areas.

4. Discussion

This study is the first range-wide assessment of the status of a crocodilian that integrates shared knowledge of a group of experts from throughout the species range. The principal result of the workshop was identification of 69 Crocodile Conservation Units that are considered to be the highest priority sites for long-term conservation of the species. These sites were distributed across 8 bioregions and represented a wide variety of habitat types. The GIS-based approach, with its spatially explicit methodology, allowed us to use quantitative information to rapidly generate consensus for conservation priorities. The workshop provided an opportunity for participants to share information and discuss crocodile conservation using a conservation paradigm which emphasizes cooperation and consensus across the species range. The workshop gave participants a regional and habitat-based perspective and also provided insights for development of national-level conservation planning.

In six of nine bioregions American crocodiles are predominantly found in euryhaline coastal habitats characterized by tidal creeks and protected lagoons fringed by mangrove

Table 2 – Prioritized list of Crocodile Conservation Units (CCUs) for the American crocodile by bioregion

Bioregions and Crocodile Conservation Units (CCUs)		Area	Score	Rank	Habitat quality	Nesting habitat	Population size	Connectivity	Habitat destruction	Potential for sustainable use	Killing of crocodiles	% Protected area	Effectiveness
Caribbean Central America													
N-10	Costa Miskito – Rio Coco, Nicaragua	22,986	295	1	High	Good	>1000	High	Low	High	Some	19	I
N-7	Lago de Nicaragua (Sud), Nicaragua	1330	295	1	High	Good	100–500	High	Low	High	Some	55	
PA-6	Bahia de Panama (este), Panama	3748	292	1	High	Good	>1000	High	Low	High	Low	31	P
N-8	Rio San Juan, Nicaragua	2263	274	2	High	Good	500–1000	High	Moderate	High	Some	55	I
Ho-1	Embalse El Cajon, Honduras	982	247	2	High	Good	>1000	High	Moderate	High	Some	0	
PA-7	Laguna de Chiriqui, Panama	2704	240	2	High	Good	10–50	High	Moderate	High	None	18	P
N-5	Lago de Managua y Lago de Nicaragua (Norte), Nicaragua	3093	237	3	High	Adequate	100–500	High	Moderate	High	Some	5	
N-9	Rio Punta Gorda, Nicaragua	904	235	3	High	Good	10–50	High	Moderate	High	Some	100	I
Ho-4	Mosquitia, Honduras	5382	173	3	Adequate	Adequate	>1000	Moderate	Low	Moderate	Some	0	
Ho-6	Rios Chamelecon y Ulua, Honduras	2189	163	3	Adequate	Adequate	100–500	High	High	Moderate	Low	0	
N-6	Isla de Omotepe, Nicaragua	537	76	3	Adequate	Adequate	<10	Low	Moderate	High	Some	16	
Ho-2	Cabo de Honduras, Honduras	1506	87	3	Adequate	Adequate	No data	Moderate	Moderate	Moderate	Some	13	
Ho-3	P.N. Marino Barbareta, Honduras	33	No data	No data	No data	No data	<10	No data	No data	No data	No data	0	
Caribbean South America													
CO-3	Alta Guaijira	198	210	1	High	Adequate	10–50	High	Low	Moderate	None	0	
VeV2-S7	Tacarigua Lagoon, Venezuela	477	193	1	High	Adequate	100–500	Moderate	Moderate	Low	Some	50	F
CO-2	Bahia Cistapa, Colombia	319	157	1	Adequate	Adequate	10–50	High	Moderate	High	None	0	
CO-1	Rio Bache, Colombia	180	157	2	Adequate	Adequate	10–50	High	Moderate	High	None	0	
Ve-3	Rios Yaracuy y Aroa	2012	119	2	Adequate	Adequate	50–100	Low	High	High	Some	31	P
Vs-2	Embalse Pueblo Viejo, Venezuela	288	118	2	Adequate	Poor	50–100	Low	Low	Moderate	Some	0	I
Vs-1	Los Olivitos, Venezuela	231	102	3	Adequate	Poor	10–50	Low	Low	Moderate	No data	94	P
CO-4	Rio Man, Colombia	370	95	3	Poor	Good	10–50	Low	High	Low	Some	0	
VeV3-S6	Turiamo, Venezuela	179	91	3	Poor	Adequate	<10	Low	Low	Low	Some	99	P
Dry Pacific													
PE-2	Amotape, Ecuador/Peru	611	217	1	High	Good	10–50	Moderate	Low	Moderate	Some	2	P
PE-1	Estero Corrales, Peru	472	140	1	Adequate	Adequate	50–100	Moderate	Moderate	High	Some	4	P

Florida-Greater Antilles													
USA-1	Southern Florida, USA	1393	286	1	High	Good	500–1000	High	Low	Moderate	None	86	F
CU-3	Archipielago de los Canareos, Cuba	1227	280	1	High	Good	500–1000	High	Low	Moderate	Some	79	P
CU-2	Peninsula de Zapata, Cuba	4049	277	1	High	Good	>1000	High	Low	Moderate	Low	90	P
CU-4	Pinar del Rio, Cuba	2534	259	2	High	Adequate	>1000	High	Low	High	Some	3	P
CU-1	Golfo de Guanacayabo, Cuba	372	259	2	High	Adequate	>1000	High	Low	High	Some	62	P
DR-1	Cul de Sac, Dominican Republic / Haiti	1102	247	2	Adequate	Good	100–500	High	Low	High	Some	26	I
CU-5	Golfo de Ana Maria, Cuba	4579	217	3	High	Poor	500–1000	High	Low	Low	Low	7	P
CU-6	Archipielago de los Colorados, Cuba	2575	186	3	High	Poor	50–100	High	Moderate	Moderate	None	20	F
J-2	Portland Bight, Jamaica	230	No data	No data	No data	No data	No data	No data	No data	No data	No data	100	
J-3	Manatee River, Jamaica	36	No data	No data	No data	No data	No data	No data	No data	No data	No data	12	
J-1	Black River, Jamaica	19	No data	No data	No data	No data	No data	No data	No data	No data	No data	0	
Moist Pacific													
None													
North West and Central Pacific Mexico													
Msn-53	Jalisco-Colima Coast, Mexico	2279	113	1	Adequate	Adequate	500–1000	Moderate	Moderate	Moderate	Some	3	F
Mp-54	Bahia de Petucalco, Mexico	273	100	1	Poor	Adequate	100–500	Moderate	Moderate	Moderate	Some	0	
Mp-55	Costa de Oaxaca, Mexico	468	90	2	Adequate	Adequate	50–100	Moderate	High	Moderate	Some	22	I
Msn-3	Presa A.L. Mateos, Mexico	154	78	1	Adequate	Adequate	10–50	Moderate	High	High	Some	0	
Msn-52	Rio Santiago, Mexico	1328	No data	No data	No data	No data	No data	No data	No data	No data	No data	0	
Msn-51	Estero El Verde, Mexico	73	No data	No data	No data	No data	10–50	No data	No data	No data	No data	0	
Rio Grijalva													
Mco-5	Presa Chicoasen, Mexico	1669	143	1	Adequate	Poor	100–500	Moderate	Low	High	Some	14	P
Mco-6	Presa Nezahualcoyotl, Mexico	1798	121	1	Adequate	Adequate	50–100	Moderate	Low	Moderate	Some	34	P
Mco-3	Presa de la Angostura, Mexico	1522	100	1	Adequate	Adequate	50–100	Moderate	Moderate	Moderate	Some	0	
Mco-4	Boca Del Rio Grijalva, Guatemala/Mexico	566	100	2	Adequate	Adequate	50–100	Moderate	Moderate	Moderate	Some	0	

(continued on next page)

Table 2 – *continued*

Bioregions and Crocodile Conservation Units (CCUs)		Area	Score	Rank	Habitat quality	Nesting habitat	Population size	Connectivity	Habitat destruction	Potential for sustainable use	Killing of crocodiles	% Protected area	Effectiveness
South Mexico/Central America Pacific													
N-4	Puerto Sandino, Nicaragua	747	295	1	High	Good	100–500	High	Low	High	Some	0	
PA-2	Isla de Coiba, Panama	504	280	1	High	Good	500–1000	High	Low	Moderate	Some	100	F
N-1	Estero Real, Nicaragua	882	274	1	High	Good	100–500	High	Moderate	High	Some	65	I
N-3	Corinto, Nicaragua	694	269	2	High	Good	50–100	High	Low	High	Some	8	I
Mco-56	Puerto Arista to Rio Huixtla, Mexico	1230	253	2	High	Good	100–500	High	Low	Moderate	Some	78	P
CR-3	Rio Terraba, Costa Rica	31	245	2	High	Good	100–500	High	Low	Moderate	None	0	
CR-2	Tempisque, Costa Rica	100	234	3	High	Good	>1000	High	Moderate	High	Some	46	P
PA-5	Punta Manzanillo, Panama	4421	224	3	Adequate	Good	>1000	High	Moderate	High	Low	2	P
PA-1	Bahia Charco de Azul, Panama	1997	212	3	High	Adequate	50–100	High	Moderate	High	Some	0	
N-2	Padre Ramos, Nicaragua	243	208	3	High	Good	10–50	High	Moderate	High	Some	28	I
PA-3	Bahia Montijo, Panama	1787	191	3	Adequate	Adequate	100–500	High	Moderate	High	Some	0	
CR-1	Tarcoles River, Costa Rica	87	151	3	Adequate	Good	500–1000	Low	High	High	Low	37	P
PA-4	Bahia de Panama (oeste), Panama	2351	74	3	Poor	Poor	10–50	Moderate	High	High	Low	3	P
Ho-5	Golfo de Fonseca, Honduras	387	59	3	Poor	Adequate	50–100	Moderate	High	Low	Some	0	
Yucatan													
Ma-70	Sian Ka'an Biosphere Reserve, Mexico	2691	280	1	High	Good	100–500	High	Low	Moderate	Some	95	F
BM-1	Bahia de Chetumal, Belize/Mexico	1643	238	1	High	Adequate	100–500	High	Moderate	High	Some	9	P
B-2	Turneffe Atoll, Belize	150	236	1	High	Good	100–500	Moderate	Moderate	Moderate	Some	0	
Ma-60	Northern Yucatan, Mexico	1967	226	2	High	Adequate	100–500	Moderate	Low	Moderate	None	40	P
Ma-59	Isla de Cozumel (Norte), Mexico	68	199	2	High	Good	10–50	High	Moderate	Moderate	None	0	
Ma-72	Cancun, Mexico	143	190	3	Adequate	Good	50–100	High	No data	High	Some	4	P
Ma-58	Isla del Cozumel (Sud), Mexico	91	183	2	High	Good	10–50	Moderate	Low	Moderate	None	5	P
Ma-71	Banco Cinchorro, Mexico	50	184	3	High	Good	10–50	Low	Low	Moderate	None	100	P
B-3	Gales Point, Belize	109	179	3	High	Adequate	10–50	High	Low	Moderate	Some	49	P
B-1	Lighthouse Atoll, Belize	6	114	3	High	Adequate	10–50	Low	Moderate	Moderate	None	0	

The locations of CCUs are indicated in Fig. 1 by each CCU's alpha-numeric code.

Table 3 – Area (km^2) of CCUs in protected areas by bioregion

Bioregion	IUCN Protected Area Category[a]						CCU		
	I	II	III	IV	V	VI	Total	Area	% in PA
Caribbean Central America	1616	1016	215	2567	203	3868	9483	47,535	19.9
Caribbean South America		498		286	480		1265	4253	29.7
Dry Pacific South America		10	20				30	1078	2.8
Florida-Greater Antilles		4735		842	237	2028	7842	18,714	41.9
North West and Central Pacific Mexico	50	102				30	182	4574	4.0
Rio Grijalva	354	229				256	838	5556	15.1
South Mexico/Central America Pacific	551	684		708		432	2375	15,583	15.2
Yucatan	1657	35	56	93	27	1742	3611	6918	52.2
Total	4213	7308	291	4497	948	8355	25,625	104,210	24.6

a IUCN Categories, I, strict nature reserves/wilderness areas; II, national parks; III, natural monuments; IV, habitat/species management areas; V, protected landscapes; VI, managed resource protected area.

Table 4 – CCUs with significant percentage of area protected (⩾30%)

Bioregion	CCU	Management	Protected areas
Caribbean Central America	Bahia de Panama (este), Panama	P	Portobelo NP, Chagres NP, Lago Gatun RA, Metropolitano NP, Soberania NP, Camino de Cruces NP.
	Rio Punta Gorda, Nicaragua	I	Cerro Silva FR, Río Indio Maíz BGR
	Lago de Nicaragua (Sud), Nicaragua	I	Corredor Fronterizo WR; Los Guatuzos WR
	Rio San Juan, Nicaragua	I	Río Indio Maíz BGR, Corredor Fronterizo WR, Barra del Colorado WR, Cerro El Jardin FR, La Cureña FR
Caribbean South America	Tacarigua Lagoon, Venezuela	F	Laguna de Tacarigua NP.
	Rios Yaracuy y Aroa, Venezuela	P	Cuare NP, Morrocoy NP, Sierra de Bobare PZ, Cuenca Alta de Rio Cojedes PZ, Yuribí NP, Sierra de Aroa PZ, Sierra de Nirgua PZ
	Los Olivitos, Venezuela	I	Ciénaga Los Olivitos WR.
	Turiamo, Venezuela	P	Henri Pittier NP, San Esteban NP
Dry Pacific	None		
Florida-Greater Antilles	Southern Florida, USA	F	Everglades NP, Cape Florida SP, Florida Keys NMS, Biscayne NP, John Pennekamp Coral Reef SP, Crocodile Lake NWR.
	Archipielago de los Canareos, Cuba	P	Sur de la Isla de la Juventud PAMR, Los Indios ER, Cayo Largo ER, Punta del Este ER, Punta Francos NP.
	Peninsula de Zapata, Cuba	P	Cienaga de Zapata PAMR, Cienaga de Zapata NP
	Golfo de Guanacayabo, Cuba	P	Ojo de Agua - Guairajal WR, Delta del Cauto WR.
North West and Central Pacific Mexico	None		
Rio Grijalva	Presa Nezahualcoyotl, Mexico	P	Selva El Ocote BR
South Mexico/ Central America Pacific	Isla de Coiba, Panama	F	Coiba NP
	Estero Real, Nicaragua	I	Estero Real NR
	Puerto Arista to Rio Huixtla, Mexico	P	Playa de Puerto Arista S, La Encrucijada BR
	Bahia Montijo, Panama	P	Cerro Hoya NP
	Tempisque, Costa Rica	P	Palo Verde NP, Mata Redonda WR
	Tarcoles River	P	Carara NP, Fernando Castro Cervantes WR, Cerros de Turrubares PZ, Finca Hacienda La Avellana WR
Yucatan	Sian Ka'an Biosphere Reserve, Mexico	P	Tulum NP, Arrecifes de Sian Ka'An BR
	Northern Yucatán, Mexico	P	Yum Balam FFPA, Ria Lagartos BR, Playa Ria Lagartos S, Isla Contoy NP, Costa Occidental de Isla Mujeres, Punta Cancun y Punta Nizuc NP
	Banco Cinchorro, Mexico**	P	Banco Chinchorro BR
	Gales Point, Belize	P	Manatee FR, Gales Point WS

Abbreviations: F, Fully effective management; P, partially effective; I, ineffective; FR, Forest Reserve; NM, Natural Monument; WS, Wildlife Sanctuary; NP, National Park; SR, Scenic Reserve; PR, Private Reserve; MR, Marine Reserve; NWR, National Wildlife Refuge; PZ, Protective Zone; WR, Wildlife Refuge; PAMR, Protected Area of Managed Resources (excluding NP); ER, Ecological Reserve; MFR, Managed Flora Reserve; PA, Protected Area; FFPA, Flora and Fauna Protection Area; BR, Biosphere Reserve; NR, Nature Reserve; NRR, National Resources Reserve; NTM, National Monument; HM, Historic Monument; BGR, Biological Reserve; HPZ, Hydrological Protection Zone; RA, Recreation Area; PF, Protected Forest; NMP, National Marine Park; NS, National Sanctuary; SP, State Park; NMS, National Marine Sanctuary.

Table 5 – CCUs with few or no protected areas (<10%)

Bioregion	CCU
Caribbean Central America	Embalse El Cajon Lago de Managua y Lago de Nicaragua (Norte), Nicaragua Mosquitia, Honduras Rios Chamelecon y Ulua, Honduras
Caribbean South America	Alta Guajira, Colombia Bahia Cistapa, Colombia Rio Bache, Colombia Rio Man, Colombia
Dry Pacific	Amotape, Peru/Ecuador Estero Corrales, Peru
Florida-Greater Antilles	Black River, Jamaica Piñar del Rio, Cuba Golfo de Ana Maria, Cuba
North West and Central Pacific Mexico	Jalisco-Colima Coast, Mexico Presa A.L. Mateos, Mexico Bahia de Petucalco, Mexico Rio Santiago, Mexico Estero El Verde, Mexico
Rio Grijalva	Presa de la Angostura, Mexico Boca Del Rio Grijalva, Guatemala/Mexico
South Mexico/Central America Pacific	Puerto Sandino, Nicaragua Golfo de Fonseca, Honduras Corinto, Nicaragua Punta Manzanillo, Panama Bahia Charco de Azul Bahia de Panama (oeste), Panama
Yucatan	Turneffe Atoll, Belize Bahia de Chetumal Isla de Cozumel (Norte), Mexico Cancun, Mexico Isla de Cozumel (Sud), Mexico Lighthouse Atoll, Belize

swamps. In these areas it can be described as an "edge" species, occupying the biologically productive ecotone where freshwater meets the sea. These habitats are patchily (Pacific bioregions) or continuously (south Florida, eastern Yucatan, Caribbean Central America) distributed along the coast, with the greatest amount of habitat associated with the mouths of rivers or streams, coastal lagoons or protected bays. Conservation of these coastal areas is complicated by a juxtaposition of terrestrial and marine ecological processes in highly productive environments. Coastal wetlands are among the richest ecosystems on earth and usually support economically important sport and commercial fishing industries. Mangroves, in particular, are extremely productive ecosystems that in the Caribbean are critical nurseries for penaeid shrimp, spiny lobsters, and >200 species of fish (Ellison and Farnsworth, 1996). Nearby upland areas are used by humans for a variety of purposes such as sites for fishing camps, villages, tourist areas, or expensive residential properties. The combination of resource extraction and development pressure imperils coastal ecosystems as well as species.

While coastal wetlands are the most characteristic habitat of the American crocodile, the species is extremely adaptable. Offshore cays and even coral atolls are important habitats for American crocodiles in the Yucatan and Florida-Greater Antilles bioregions. In the Caribbean South America bioregion American crocodiles are found more than 1200 km up the Rio Magdalena (Rio Bache CCU). Crocodiles are also known from the freshwater sections of rivers in all Pacific bioregions (with the exception of the Moist Pacific), and currently or historically from river systems in the Greater Antilles. A bioregion where American crocodiles are perhaps best characterized as a riverine species is in the Caribbean Central America.

American crocodiles also adapt well to lacustrine habitats and several CCUs are found in the great lakes of Nicaragua in the Caribbean Central America (Lago de Nicaragua (south), Lago de Managua and Lago de Nicaragua (north), Isla de Omotepe). Other lacustrine CCUs are brackish lakes in the Cul de Sac valley in Haiti and the hypersaline Lago Enriquillo in the Dominican Republic (Thorbjarnarson, 1986). Man-made lakes comprise an important habitat for American crocodiles in the Caribbean Central America (Embalse El Cajon, Honduras; Bahia de Panama (este) [Gatun Lake]), the Caribbean South America (Rios Yaracuy and Aroa, Embalse Pueblo Viejo), and NW and Central Pacific Mexico (Presa A.L. Mateos, Rio Santiago). The Rio Grijalva is the most unusual American crocodile bioregion with crocodiles found in three reservoirs in a river system isolated from any other known populations (Sigler, 2002). Presumably, at some point in the past American crocodiles were distributed along the western Yucatan, or the population in the Grijalva (and neighboring Usamacinta River) was established by individuals dispersing from the northern Yucatan (Sigler and Ramírez, 2000).

Interplay between habitat type and the population ecology of the American crocodile result in important considerations for the management and conservation of this species. In coastal habitats used by American crocodiles, suitable nesting beaches are usually the product of wave-exposed shores or periodic storms such as hurricanes. Juxtaposition of suitable nesting areas and habitat for adult and juvenile crocodiles is one of the most critical measures of habitat quality for American crocodiles (Thorbjarnarson, 1989; Mazzotti, 1999). One consequence of population and nesting biology is that the best sites for American crocodiles in coastal areas have a variety of aquatic and terrestrial habitats. Areas with large amounts of mangrove habitat, but limited nesting sites may have comparatively small crocodile populations (e.g., Turneffe Atoll, Belize), or extremely dense nesting aggregations that result in high levels of egg mortality (Golfo de Guacanayabo, Cuba; Soberón et al., 2002). Coastal populations of American crocodiles appear to have a complex metapopulation dynamic involving movement between habitat patches suitable for adult crocodiles, which include elevated ground for nesting, and sites that function as dispersal areas for large juvenile and subadult crocodiles to avoid agonistic encounters with adults (Delany and Abercrombie, 1986; Hunt, 1990; Magnusson, 1986; Mazzotti and Brandt, 1994; Mazzotti and Cherkiss, 2003). In a certain sense these dispersal sites serve as "rearing stockyards" for intermediate sized crocodiles before they return to breeding areas (Messel et al., 1981).

One of the strengths of this range-wide approach was that by conducting parallel analyses in each bioregion we were able to identify important crocodile habitats that ran the spectrum from freshwater rivers and landlocked, hypersaline lakes to coastal mangroves and offshore coral atolls. Because of the extreme variability of habitats they occupy, American crocodiles are variable in terms of their ecology and behavior. In essence these are distinct ecotypes of a hyper-adaptable species. Our range-wide analysis by bioregion was predicated on the belief that it is important to conserve viable populations of these American crocodile ecotypes in as wide a variety of their ecological settings as possible. In some sense this parallels the concept of preservation of genetic diversity. Expressions of genetic variability may not manifest themselves unless the full range of a species ecotypes is conserved.

We also identified CCUs where there currently is little or no protected habitat (<10% of the CCU in PAs). This represents 33 of the 69 CCUs, including some of the highest ranking CCUs in several bioregions. Two bioregions stood out in terms of lack of protected areas in CCUs, the Dry Pacific, and Northwest and Central Mexico. One of the most important recommendations to come out of this analysis is the need to establish effective PAs in the highest priority CCUs in each of these bioregions. Specifically, these are the Amotape region in Peru, the Jalisco-Colima coast in Mexico, and the Presa Chicoasen, also in Mexico. Other priorities for establishing protected areas are, for each bioregion, CCUs with the highest category score and little or no PAs. These are Alta Guajira and Bahia Cistapa regions of Colombia, Puerto Sandino in Nicaragua, and Turneffe Atoll in Belize.

The establishment of protected areas is only part of a comprehensive conservation strategy. However, it is one aspect of global crocodile conservation efforts that has been given short shrift amidst a rush of management plans based on controlled commercial use (Thorbjarnarson, 1999). While across its range the American crocodile is not as threatened by habitat loss as are some other crocodilians, on a regional scale it is an issue. This is particularly true of the Dry Pacific bioregion in Peru and Ecuador, the Rio Grijalva, and parts of the Florida-Greater Antilles (Jamaica) and Yucatan (Belize) bioregions. As development of coastal habitat continues, other areas may be equally threatened in the future. Protection of vast swaths of coastal areas will not likely be an option in many of these areas in the future, so an unbiased method of identifying the most significant sites is important. We feel that this analysis has been an important first step in this direction.

In addition to identifying the most important areas for American crocodiles throughout the species' range, and highest priorities for establishment of new protected areas, we also made an attempt to characterize each CCU in terms of effectiveness of protection. This resulted in the identification of the CCUs where American crocodiles and their habitat have been adequately protected, including such areas as Tacarigua Lagoon, Venezuela; Isla de Coiba, Panama, and South Florida, USA. Conversely, we identified CCUs that are largely within protected areas, but where current levels of management implementation are poor (e.g., Rio Punta Gorda, Nicaragua; Rio San Juan, Nicaragua, Estero Real, Nicaragua, Los Olivitos, Venezuela).

The American crocodile is a large charismatic species and top predator with diverse aquatic and terrestrial habitat requirements. These characteristics make it an excellent candidate as a flagship species for the conservation of coastal ecosystems. American crocodiles thrive in healthy estuarine environments and in particular are dependent on natural freshwater flows and a diverse array of habitats including uplands for nesting and an array of aquatic and wetland habitats to meet all of the species' life history requirements. Calling attention to conservation or restoration of crocodiles can focus attention on conservation of critical coastal ecosystems and habitats that they contain. Our analyses resulted in a geographically referenced, range wide assessment of the conservation status of the American crocodile with explicit recommendations for site conservation and the long-term survival of the species. The database that was produced from this project was distributed to all workshop participants and will be available to all those responsible for research, conservation and management of the American crocodile.

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